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Identification of Rice Genotypes Carrying the *Pup1* Locus as Potential Donors for Phosphorus Deficiency Tolerance Breeding in Southern India

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Authors' contributions

This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

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Abstract

Phosphorus deficiency is a major constraint for rice production. The *Pup1* locus confers tolerance to low-P conditions. We screened 40 rice genotypes adapted to southern India using 10 *Pup1* specific markers. Five genotypes (including Kasalath and IR64-*Pup1* checks) showed the complete Kasalath-type haplotype. Three local genotypes (APO, Vandhana, Kalakeri) representing ~7.5% of the positive genotypes (excluding checks) carried the full *Pup1* locus and are proposed as promising donors for marker-assisted breeding programs targeting phosphorus use efficiency in southern India.

Keywords: Phosphorus; Pup1; haplotype; markers; rice.

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1. Introduction

Rice (*Oryza sativa* L.) serves as a vital food staple across many countries in Asia and Africa, contributing significantly to the daily caloric intake, particularly in Asian populations where it is a primary energy source. However, numerous popular rice varieties, hybrids, and their parental lines are susceptible to various biotic and abiotic stresses. The growth and productivity of rice depend on 16 essential nutrients, among which the macronutrients nitrogen (N), phosphorus (P), and potassium (K) play a fundamental role. Phosphorus, often regarded as the "king-pin" of Indian agriculture (Dey et al., 2017), is especially crucial during the early stages of plant growth and overall development, with no effective alternative currently available (Cordell and White, 2011). Plants take up phosphorus primarily as orthophosphate ions, which stimulate tillering, root growth, early flowering, and ripening. However, only about 10–20% of applied fertilizer is actually taken up by plants, as most phosphorus exists in forms that are inorganic and not readily available (Ibrahim et al., 2022). Low phosphorus (P) availability in soils is a major limiting factor for plant growth and crop yields globally, including in rice, making it a significant challenge for rice cultivation. Increasing P fertilizer application to overcome this deficiency not only raises production costs and dependency on imports but also contributes to environmental issues like water pollution from fertilizer runoff (Dobermann and White, 1998; Zhang et al., 2014). Therefore, improving the phosphorus deficiency tolerance of rice varieties presents a more sustainable and cost-effective solution compared to heavy reliance on fertilizers. A Rapid approach like marker-assisted breeding (MAB) offers a promising alternative (Aluwihare et al., 2018). As a widely accepted and minimally controversial biotechnological tool, MAB enables targeted genetic improvement in crops. However, to implement an effective MAB strategy for enhancing P-deficiency tolerance, a thorough understanding of the genetic basis of this trait is essential. A few studies have successfully developed and identified pyramided and improved rice lines combining deeper rooting, BB and BLB resistance, and low-phosphorus tolerance through marker-assisted backcross breeding (MABB), without compromising yield (Singh et al., 2020; Subburaj et al., 2024; Duppala et al., 2025 and Mishra et al., 2025).

The discovery of *Phosphorus Uptake 1* (Pup1) has been a key advancement in improving phosphorus uptake and enhancing yield performance under phosphorus-deficient conditions (Wissuwa et al., 1998; Chin et al., 2010). *Pup1* was identified in the traditional rice variety *Kasalath* as a major quantitative trait locus (QTL) located on chromosome 12 of *Oryza sativa*, accounting for approximately 70% of the phenotypic variation related to phosphorus deficiency tolerance (Wissuwa et al., 1998, 2002). The *Pup1* region in *Kasalath* includes a 278 Kb insertion/deletion (INDEL), and near-isogenic lines (NILs) carrying this QTL have demonstrated improved phosphorus uptake. A high proportion of transposable elements (45–54%) within the *Pup1* locus contributes to variations in locus size and complicates gene model predictions (Heuer et al., 2009). Molecular markers targeting candidate genes within the *Pup1* region have been developed and successfully applied to detect *Pup1* haplotypes in a wide range of rice genotypes (Chin et al., 2010,2011). Studies have shown that the OsPSTOL1 gene, encoding a protein kinase, plays a key role in enhancing root growth and improving phosphorus uptake from the soil (Gamuyao et al., 2012; Yumnam et al., 2017). The identification of novel donor genotypes with strong abiotic stress tolerance and favorable agronomic backgrounds remains crucial for breeding programs, especially in rainfed rice-growing regions. This study was conducted to assess the haplotypes of the *Pup1* locus among rice varieties adapted to the Tamil Nadu region. In India, crop productivity is severely hindered due to poor utilization of phosphorus availability. Understanding the distribution of the *Pup1* locus among local rice genotypes will support the development of effective breeding strategies tailored to the agro-climatic conditions of this region.

2. Materials and Methods

2.1 Plant Material

In this study, a collection of rice genotypes including 26 landraces, 11 released varieties, and one improved variety (collectively referred to as cultivars) along with two check lines, Kasalath and IR64 *Pup1*, commonly used in rice breeding and cultivation, were evaluated in 2020 at Centre of Excellence in Molecular Breeding (CEMB), Coimbatore (Table 1). The seeds were sourced from verified stocks provided by the Department of Rice, Coimbatore; the International Rice Research Institute (IRRI), Philippines; and Tamil Nadu Rice Research Institute (TRRI), Aduthurai.

2.2 Genomic DNA Extraction and Molecular Markers

Leaf samples were collected from 20-day old rice seedlings for genomic DNA extraction used in molecular screening. DNA was isolated by grinding the tissue in liquid nitrogen and using the CTAB method (100 mM Tris-HCl pH 8, 20 mM EDTA pH 8, 1.3 M NaCl, 2% CTAB) as described by Murray and Thompson (1980), followed by chloroform isoamyl alcohol extraction, RNase treatment, and ethanol precipitation. DNA concentration was measured using a Nanodrop Spectrophotometer (ND 1000), adjusted to 50 ng/µl, and stored at –20°C for further use. PCR was performed using an Eppendorf Master cycler with the following conditions: initial denaturation at 94°C for 4 minutes, followed by 35 cycles of denaturation at 94°C for 1 minute, annealing at 58°C for 1 minute, and extension at 72°C for 1 minute, with a final extension at 72°C for 10 minutes. Genotyping was conducted using ten gene-specific markers, including three co-dominant markers (K29-1, K29-2, K29-3) and seven dominant markers (K42, K43, K46-1, K46-2, K48, K52, and K59) to detect the presence or absence of the *Pup1* QTL (Chin et al., 2010) (Table 2).

PCR products were separated on 3% agarose gels stained with 0.8 mg/ml ethidium bromide and run in 1X TBE buffer (pH 8.0). A 50 bp DNA ladder was used as a molecular size marker. Electrophoresis was conducted at 2.5 V/cm for 2 hours, and gels were visualized using a Bio-Rad Gel Documentation System. The presence or absence of amplification products for each genotype primer combination was recorded, and the data were compiled and analyzed using Microsoft Excel.

3. Results and Discussion

A total of ten *Pup1*-linked markers K29-1, K29-2, K29-3, K42, K43, K46-1, K46-2, K48, K52, and K59 (Chin et al., 2011) were used to genotype all 40 rice genotypes. The results are summarized in Table 3 and illustrated in Fig. 1. Amplification was scored on a scale from 0 to 10, where 0 indicated absence of the target allele across all markers, and 10 indicated its presence at all loci. Based on the marker data, approximately 30% of the genotypes exhibited the likely presence of the *Pup1* QTL. Among the ten *Pup1*-linked markers, K46-1 showed the highest frequency across genotypes (42.5%), followed by K29-3 (40%), K43 (30%), and K29-2, K46-2, and K52 (each at 27.5%). Markers K29-1, K42, and K59 were detected in 25% of genotypes, while K48 had the lowest presence at 22.5%. Five genotypes Kasalath, APO, Vandhana, Kalakeri, and IR64 *Pup1* exhibited amplification (~12.5% of positive genotypes) for all ten markers, indicating the full presence of the *Pup1* allele. In contrast, 14 genotypes including Norungan, Kaatuyanam, Tetep, Mysore Malli, Sigappu Kavuni, Karudan Samba, Anjali, Thulasi Vasanai Samba, ADT47, CO52, TKM13, Nootripathu, Kothamalli Samba, and Mattaikar devoid of any *Pup1*-specific marker amplification, indicating the absence of the *Pup1* locus in these genotypes. Among the remaining genotypes, UPLRI5 exhibited amplification for seven markers, while sornamugi showed six, and Improved Samba Mashuri had five amplified markers. Eight genotypes Singinikar, Ottadam, Kuruvai Kalanjiyam, Bhavani, Kattanur, Kullakar, Thuyamalli, and ASD16 displayed four marker amplifications. ADT43 showed three, whereas five genotypes Navara, Kullarkar, Kallurandaikar, MDU5, and Basmathi had two amplified markers. Additionally, four genotypes Kuruvai Kalanjiyam, Kuzhiyadicham, Salem Samba, and Kavuni exhibited amplification for only a single *Pup1*-specific marker. The amplicons of codominant markers amplified in the expected sizes.

In our study most rice genotypes (21 genotypes) displayed mosaic patterns at the *Pup1* locus, carrying a mix of Kasalath-type and non-Kasalath alleles. Such variation likely arises from recombination, partial introgression, or natural polymorphism, suggesting that the locus has undergone complex evolutionary and breeding processes that may influence phosphorus uptake efficiency.

Molecular characterization indicated that the *Pup1* region was absent in the majority of the lines analyzed. Based on the presence of Kasalath-type alleles across the ten markers, the genotypes were classified into two groups: the K-group (Kasalath allele), containing all ten Kasalath alleles; and the N-group (Non Kasalath allele), lacking at least one core Kasalath allele. Including the check varieties, five genotypes were assigned to the K-group, while the remaining 35 were categorized into the N-group. The findings from our study using *Pup1*-specific markers align with those reported by Tyagi et al. (2012), who described Kasalath-like alleles at the *Pup1* locus in 13 out of 60 diverse rice genotypes (approximately 21%) using a set of six markers.

Table 1. Details of Rice cultivars characterised for *Pup1* linked DNA marker haplotypes

S. No.	Genotypes	Source / Parentage			
1	Norungan	Landrace	**21**	Anjali	Sneha / RR 149-1129
2	Kasalath	Landrace	**22**	Kalakeri	Landrace
3	Singinikar	Landrace	**23**	Thulasi vasanai sambha	Landrace
4	Navara	Landrace	**24**	Salem sambha	Landrace
5	Ottadam	Landrace	**25**	Thuyamalli	Landrace
6	Kuruvai kalanjiyam	Landrace	**26**	Kavuni	Landrace
7	Bhavani	Peta / BPI 76	**27**	Kallurandaikar	Landrace
8	Apo	IR5523-01	**28**	Sornamugi	Landrace
9	Karunkuruvai	Landrace	**29**	ADT43	IR 50 / White ponni
10	Vandana	C-22 / Kalakeri	**30**	ADT47	ADT 43 / Jeeragasamba
11	Kaatuyaanam	Landrace	**31**	ASD16	ADT 31 / CO 39
12	Kattanur	Landrace	**32**	TKM13	WGL 32100 / Swarna
13	Tetep	Landrace	**33**	CO52	CO 50 / BPT 5204
14	Mysore Malli	Landrace	**34**	MDU5	*O.glaberrima / Pokkali*
15	Kuzhiyadicham	Landrace	**35**	Nootripathu	Landrace
16	Sigappukavuni	Landrace	**36**	UPLRI5	ADT 39 / Co 45
17	Karudan sambha	Landrace	**37**	Kothamalli sambha	Landrace
18	Kullakar	Landrace	**38**	Basmathi	Landrace
19	Improved samba mashuri	Samba Mahsuri / SS1113	**39**	Mattaikar	Landrace
20	Kullarkar	Landrace	**40**	IR64 Pup1	IR64 harbouring Pup1 from kasalath

Table 2. The details of the *Pup1* linked DNA markers used to detect haplotypes

S.No	QTL/Gene	Chromosome	Markers	Primer sequence	AT ˚c	Amplicon size (bp) K/N	Reference
1	*OsPupK29-1*	12	K29-3 (co-dominant)	F: TTCGTCCAGATGCTGCTATG R: TCTTCGGTGTAATTGGCACA	58	236/248	Chin et al., 2011
2	*OsPupK29-1*	12	K29-1 (co-dominant)	F: ATGGCCAACGGGGTAGAG R: GTCCAGGTAACCACGAGGAA		212/206	
3	*OsPupK29-1*	12	K29-2 (co-dominant)	F: CCCGTCTGCGTTCTACCTTA R: CTCCCGTCAAGCACAAATCT		291/212	
4	*OsPupK42-1*	12	K42 (dominant)	F: CCCGAGAGTTCATCAGAAGGA		918/null	

S.No	QTL/Gene	Chromosome	Markers	Primer sequence	AT ˚c	Amplicon size (bp) K/N	Reference
				R:AGTGAGTGGCGTTTGCGAT			
5	*OsPupK43-1*	12	K43 (dominant)	F: AGGAGGATGAGCCTGAAGAGA R:TCGCACTAACAGCAGCAGATT		912/null	
6	*OsPupK46-2*	12	K 46-1(dominant)	F: TGAGATAGCCGTCAAGATGCT R: AAGGACCACCATTCCATAGC		523/null	
7	*OsPupK46-2*	12	K46-2(dominant)	F: AGGAAGATGGTTGTCGTTGG R: TTCACACCAAACAGTGTTGTC		227/null	
8	*OsPupK48-1*	12	K48(dominant)	F: CAGCATTCAGCAAGACAACAG R:ATCCGTGTGGAGCAACTCATC		847/null	
9	*OsPupK52-1*	12	K52(dominant)	F: ACCGTTCCCAACAGATTCCAT R:CCCGTAATAGCAACAACCCAA		505/null	
10	*OsPupK59-1*	12	K59(dominant)	F: GGACACGGATTCAAGGAGGA R:TGCTTTCCATTTGCGGCTC		550/null	

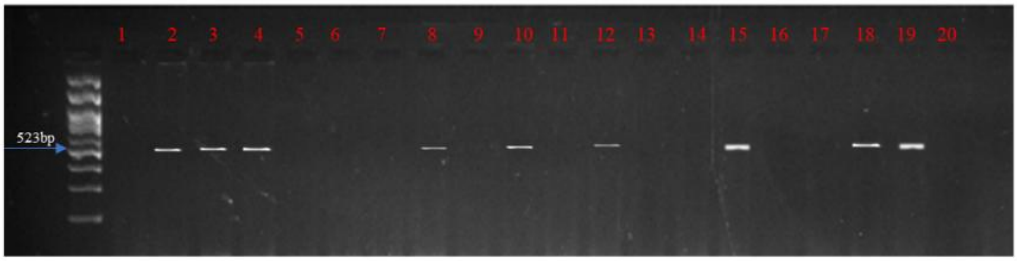
Table 3. Allelic profile of *Pup1* specific markers among the 40 rice genotypes evaluated in the study

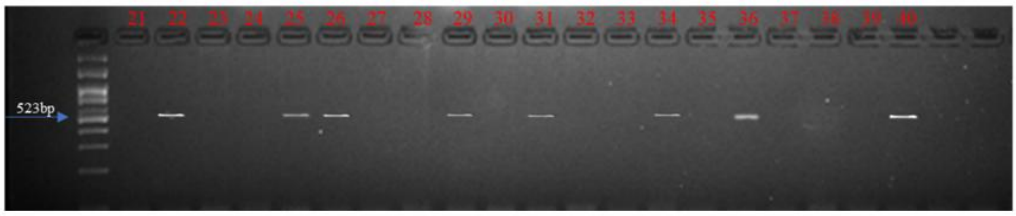
S.No	Genotypes	K29-3	K29-1	K29-2	K42	K43	K 46-1	K46-2	K48	K52	K59	Allele type	Assessment of *Pup1*-Linked Marker Alleles (Score/10)
1	Norungan	0	0	0	0	0	0	0	0	0	0	N	0/10
2	Kasalath	1	1	1	1	1	1	1	1	1	1	K	10/10
3	Singinikar	1	0	0	1	1	1	0	0	0	0	N	4/10
4	Navara	0	1	0	0	0	1	0	0	0	0	N	2/10
5	Ottadam	1	0	0	0	0	0	1	1	1	0	N	4/10
6	Kuruvai kalanjiyam	1	0	0	0	1	0	1	0	1	0	N	4/10
7	Bhavani	1	0	1	1	1	0	0		0	0	N	4/10
8	Apo	1	1	1	1	1	1	1	1	1	1	K	10/10
9	Karunkuruvai	0	0	0	0	0	0	0	0	1	0	N	1/10
10	Vandana	1	1	1	1	1	1	1	1	1	1	K	10/10
11	Kaatuyaanam	0	0	0	0	0	0	0	0	0	0	N	0/10
12	Kattanur	1	1	1	0	0	1	0	0	0	0	N	4/10
13	Tetep	0	0	0	0	0	0	0	0	0	0	N	0/10
14	Mysore Malli	0	0	0	0	0	0	0	0	0	0	N	0/10
15	Kuzhiyadicham	0	0	0	0	0	1	0	0	0	0	N	1/10

S.No	Genotypes	K29-3	K29-1	K29-2	K42	K43	K 46-1	K46-2	K48	K52	K59	Allele type	Assessment of *Pup1*-Linked Marker Alleles (Score/10)
16	Sigappukavuni	0	0	0	0	0	0	0	0	0	0	N	0/10
17	Karudan sambha	0	0	0	0	0	0	0	0	0	0	N	0/10
18	Kullakar	1	0	1	0	0	1	1	0	0	0	N	4/10
19	Improved samba mashuri	1	0	0	0	0	1	0	1	1	1	N	5/10
20	Kullarkar	0	0	0	1	1	0	0	0	0	0	N	2/10
21	Anjali	0	0	0	0	0	0	0	0	0	0	N	0/10
22	Kalakeri	1	1	1	1	1	1	1	1	1	1	K	10/10
23	Thulasi vasanai sambha	0	0	0	0	0	0	0	0	0	0	N	0/10
24	Salem sambha	0	1	0	0	0	0	0	0	0	0	N	1/10
25	Thuyamalli	1	0	0	1	1	1	0	0	0	0	N	4/10
26	Kavuni	0	0	0	0	0	1	0	0	0	0	N	1/10
27	Kallurandaikar	1	0	0	0	1	0	0	0	0	0	N	2/10
28	Sornamugi	1	0	1	0	0	0	1	1	1	1	N	6/10
29	ADT43	0	1	1	0	0	1	0	0	0	0	N	3/10
30	ADT47	0	0	0	0	0	0	0	0	0	0	N	0/10
31	ASD16	0	0	0	0	0	1	1	0	1	1	N	4/10
32	TKM13	0	0	0	0	0	0	0	0	0	0	N	0/10
33	CO52	0	0	0	0	0	0	0	0	0	0	N	0/10
34	MDU5	0	0	0	0	0	1	0	0	0	1	N	2/10
35	Nootripathu	0	0	0	0	0	0	0	0	0	0	N	0/10
36	UPLRI5	1	1	1	1	0	1	1	1	0	0	N	7/10
37	Kothamalli sambha	0	0	0	0	0	0	0	0	0	0	N	0/10
38	Basmathi	0	0	0	0	1	0	0	0	0	1	N	2/10
39	Mattaikar	0	0	0	0	0	0	0	0	0	0	N	0/10
40	IR64 *Pup1*	1	1	1	1	1	1	1	1	1	1	K	10/10

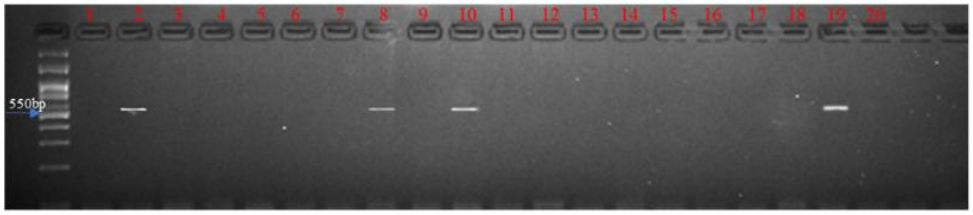
(1) present and (0) absent; "N" and "K" denote Non Kasalath and Kasalath allele group

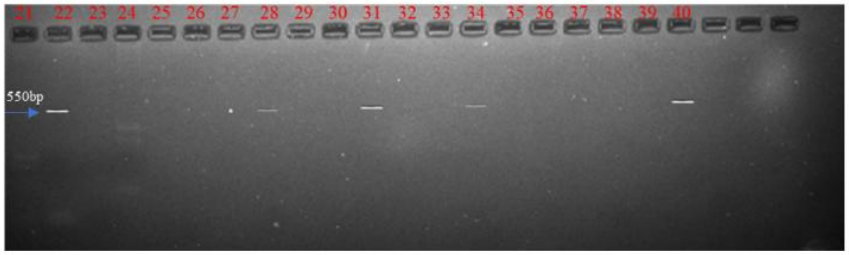
K46-1



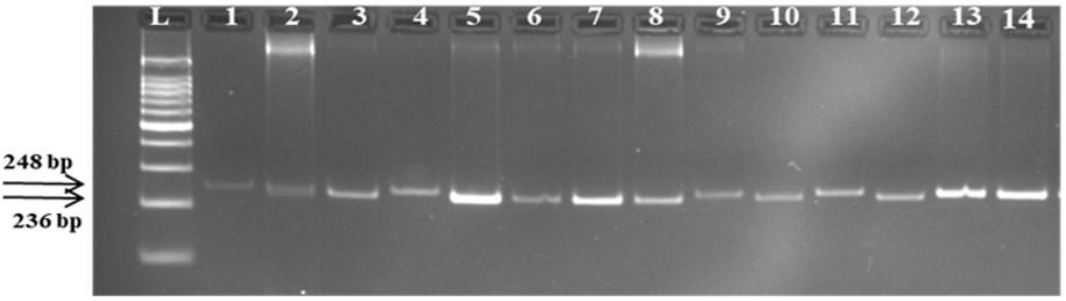


K59





K29-3



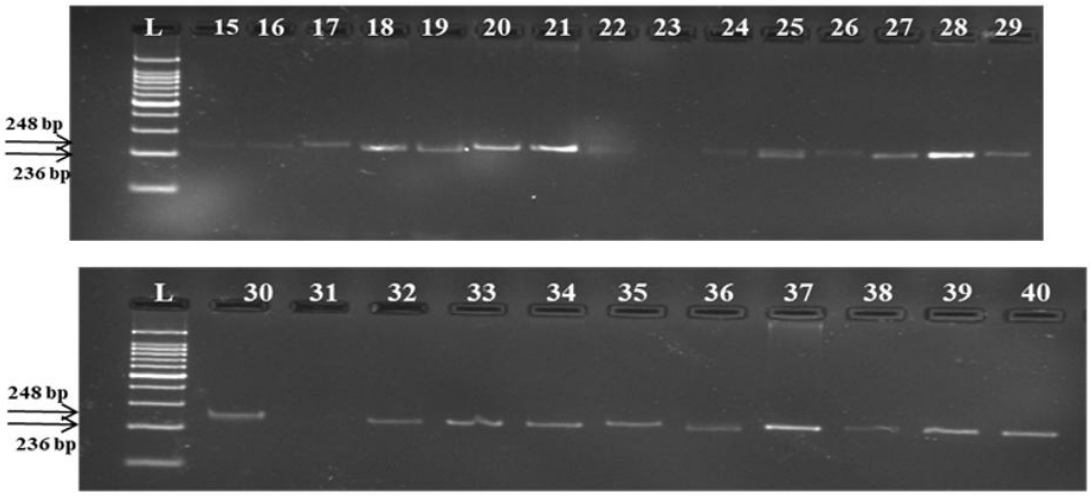


Fig. 1. Genotypic profile using *Pup1* QTL linked markers in 40 rice genotypes

Our results also closely matched previous reports by Roy et al. (2021), particularly for genotypes such as Apo and Vandhana, which were found to carry Dular/Kasalath alleles, as well as Nirubana et al. (2020), which confirmed the presence of Pup1 in ASD16 and Samba Mahsuri *pup1*. In line with this, Pariasca et al. (2014) developed several allele-specific markers for molecular breeding to facilitate the transfer of the PSTOL1 gene from Kasalath into African mega-varieties, including NERICAs, highlighting the potential of marker-assisted approaches to improve phosphorus uptake. Similar genotypic surveys targeting the *Pup1* QTL have also been conducted by Heuer et al. (2009), Pandit et al. (2018) and Chankaew et al. (2019), further supporting our observations.

The identification and introgression of phosphorus deficiency tolerance alleles represent a promising breeding strategy for developing rice cultivars capable of thriving under low-phosphorus conditions, thereby enhancing yield and contributing to food and nutritional security. This study successfully identified genotypes exhibiting Kasalath-like alleles, with APO, Vandhana, and Kalakeri emerging as potential donor parents for the *Pup1* locus. The remaining genotypes, lacking the full complement of *Pup1* markers, can serve as recurrent parents in future breeding programs aimed at improving phosphorus use efficiency.

4. Conclusion

This work is relevant for rice breeding programs in areas with low phosphorus availability, particularly in southern India where many soils are P-deficient. Identifying local (or regional) donors for the *Pup1* locus is useful because traditional Indian varieties adapted to local conditions are often agronomically more acceptable than Kasalath, which has many drawbacks. The three genotypes proposed (APO, Vandhana, Kalakeri) could genuinely serve as donor parents in marker-assisted selection (MAS) programs in southern India.

Disclaimer (Artificial Intelligence)

Author(s) hereby declares that No generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

Competing Interests

Authors have declared that no competing interests exist.

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