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REVIEW

Genetic study and molecular breeding for high phosphorus use efficiency in maize

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Abstract Phosphorus is the second most important macronutrient after nitrogen and it has many vital functions in the life of plants. Most soils have a low available P content, which has become a key limiting factor for increasing crop production. Also, low P use efficiency (PUE) of crops in conjunction with excessive application of P fertilizers has resulted in serious environmental problems. Thus, dissecting the genetic architecture of crop PUE, mining related quantitative trait loci (QTL) and using molecular breeding methods to improve high PUE germplasm are of great significance and serve as an efficient approach for the development of sustainable agriculture. In this review, molecular and phenotypic characteristics of maize inbred lines with high PUE, related QTL and genes as well as low-P responses are summarized. Based on this, a breeding strategy applying genomic selection as the core, and integrating the existing genetic information and molecular breeding techniques is proposed for breeding high PUE maize inbred lines and hybrids.

Keywords maize, phosphorus use efficiency, quantitative trait loci, genetic study, molecular breeding, genomic selection

1 Introduction

Phosphorus is a macro element required for biological growth and development, in particular it is essential for the synthesis of important biochemical substances such as DNA, RNA and ATP in all living organisms[1,2]. In its natural state in soil, P exists in the form of organic phosphorus (P_o) and inorganic phosphorus (P_i), with the former accounting for 50% to 80% of soil P[3,4]. As for the latter, phosphate (PO_4^{3-}) is the main form. Conversion of P_o and P_i can be achieved via orthophosphate[5–7]. P_i has three states in the soil: water-soluble, adsorbed and mineralized. However, most of the phosphates are chelated or precipitated with Fe^{2+}, Al^{3+} and Ca^{2+} ions, which results in the fixation of phosphate ions in the soil. Only a very small number of the water-soluble ions $H_2PO_4^-$ and HPO_4^{2-} can be directly used by plants, accounting for less than 0.01% of available P in the soil and even less than 0.001% in the low-P fields. As a result, P use efficiency (PUE) in the soil ranges from 20% to 30%, limiting crop yields by 30%–40%[1,7–12]. Meanwhile, temperature, moisture, pH and other soil factors also affect the P concentration and form. The dynamic balance of P in the soil is important for regulating the circulation of nutrients in nature[3,5]. Moreover, the worldwide status of P resource utilization has been of great concern in that 5.7 billion hectares of soil is deficient in P. Meanwhile, the demand for P fertilizers will reach its peak in 2033[13,14]. In addition, the excessive application of P fertilizers has caused serious environmental pollution problems. Hence, it is extremely urgent to improve the PUE of crops.

Facing the increasing contradiction between the global population growth and the shortage of P resources, it is paramount to understand the molecular mechanisms of crop P utilization in order to further improve crop PUE. By using genetics and molecular biology methods to select P-efficient crops, significant economic and ecological benefits can be derived. In this review, the characteristics of P-efficient inbred lines are summarized by comparing the phenotypic and omics changes of different genotypes under low-P stress. Furthermore, PUE-related quantitative trait loci (QTL) or genes in maize, which have previously been mined, are assessed for their suitability to conduct molecular breeding. Differences in the tolerance to low-P conditions between different heterotic groups and the changes of heterotic patterns under low-P stress are reanalysed and summarized. Finally, we propose an integrated molecular breeding strategy taking genomic

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selection (GS) as core to select P-efficient inbred lines and hybrids, which will provide a theoretical basis for breeders to select high PUE materials.

2 Phosphorus use efficiency in plants

Plants absorb P mainly through roots, which is a complex process affected by the chemical and physical state of soil, the interaction between roots and soil, and the interaction between roots and microorganisms[15]. PUE, as used here, is the ratio of grain yield or biomass per unit P supply in a low-P environment[16–19]. PUE can be split into two parts, P uptake efficiency (PupE) and P utilization efficiency (PutE). The relationship among these is PUE = PupE × PutE[18,20,21]. PupE can be calculated using the formula, PupE = P_t / P_{soil}, where P_t is the total P content including grain and shoot tissues and P_{soil} is the total amount of P available in soil. PutE can be calculated using the formula PutE = grain yield / P_t[18,22]. PupE refers to the ability of plants to absorb P from the soil, which is affected by the root morphological architecture, soil state and microorganism[23,24]. Furthermore, PutE is related to the ability of plants to transfer absorbed P into yield[25]. In plants, the P_i transporters, for instance, promote the transport of P between roots and soil surface as well as between different tissues and organs[9,24]. Under low-P stress, in a maize recombinant inbred lines (RIL) population, the correlation between PupE and PUE is different from that between PutE and PUE. The former ranges from 0.48 to 0.53, and the latter from 0.32 to 0.38[26]. Also, the respective contribution of PupE and PutE to PUE is different, with PupE explaining 71% to 100% of maize hybrid yield variation[27,28]. Therefore, PupE is the focus of genetic improvement.

3 Genotypic differences in response to low-P starvation in maize

Under low-P stress, P-efficient lines show dominance in biomass in that they have greater root: shoot ratio, nodal rooting, nodal root laterals, adventitious roots, root hair density and basal root whorl number but less root cortex than P-inefficient lines[25,29–31]. The regulation of hormones, such as auxin, ethylene, gibberellic acid and abscisic acid, changes the root morphology of plants, namely, the number of primary roots, the length of lateral root and root hair, and increases the secretion of organic acid ions, protons, neutrons and phosphatases, which increase the crop P uptake[19,24,30,32–34]. Physiological responses to P deficiency involve the release of organic acids, protons and enzymes and modifications of root architecture[10,26]. Analyzing the physiological indicators of Qi319 and its mutant Qi319-96, showed P-efficient line Qi319-96 had a better ability to reconstruct lipid composition of membranes and had higher V-ATPase activity under P deficiency condition[35]. Taking the P-efficient maize inbred line W23 and the P-inefficient inbred line W22 as research objects, under a hydroponic low-P environment, H^+ and Ca^{2+} ions in W23 were increased by 89% and 225%, respectively, the shoot biomass of W23 was 38% higher than W22, but there was no difference in root biomass between the two lines. Nevertheless, the W23 root elongation zone was significantly longer than that of W22[36]. Under the low-P stress, carboxylate efflux from roots can also be used as an important reference factor for screening P-efficient lines[37]. Under low-P stress, plant leaves accumulate more anthocyanin pigments to protect chloroplasts and nucleic acids in tissues; additionally, plant height and ear height are reduced, but the plant height: ear height ratio is increased[38,39]. Under two different low-P conditions, for an inbred population, the number of kernels per ear decreased respectively by 24% and 28%, and the yield decreased by 36% and 31%, respectively[40]. When the phenotypes of different traits of a maize population were assessed, it was found that the low-P tolerance in different genotypes was significantly correlated with the phenotype of plants under low P. Both can be used for screening and genetic analysis of low-P tolerant germplasm[41]. According to the definition of PUE, biomass and yield are still the main selection criteria when screening for P-efficient germplasm, but both traits are very complex quantitative traits controlled by many minor QTL[42–44].

4 Plant molecular responses to low-P starvation in maize

Plants have developed a complete system to adjust P absorption, utilization and recycling in order to ensure normal growth and development under low-P stress. This process is known as the phosphate starvation response (PSR)[19,45] and involves changes to transcriptional, genomic, and metabolic regulatory networks. By analyzing the maize root transcriptome of P-efficient lines on different days after P deficiency, 820 upregulated and 363 downregulated response genes involved in metabolic, signal transduction, and developmental gene networks were identified[46]. In maize, five *Pht1* genes which contribute to phosphate uptake and allocation across soil and shoot have been identified[47]. Through comparison of sequencing RNA reads of Qi319 and 99038 under normal and low-P environments, the researchers identified seven novel and known miRNA families[48]. Additionally, a study by Du et al.[49] showed that the *miRNA399-ZmPHO2* pathway is key in the regulation of P uptake, and *LncRNA1* interacts with *miRNA399* to make plants adapted to low P. By comparing and the root proteome of Qi379 and its mutant 99038, 73 upregulated and 95 downregulated differentially expressed proteins were identified. These proteins were involved in cellular and metabolic processes,

especially in carbon metabolism and cell proliferation[50]. By analyzing the phosphoproteome and proteome of Qi319 roots in four stages, it was revealed that 6% phosphoprotein involved in metabolic and cellular pathways changed under low-P treatment, and low P induced the modifications of carbon flux in metabolic processes[51]. P-sensitive line HM-4 and P-tolerant line PEHM-2 were used to investigate the P starvation effect at the metabolite level. Analysis of the results showed that accumulation of di- and trisaccharides and metabolites of ammonium metabolism, particularly in leaves, and decrease of phosphate-containing metabolites and organic acids as well as increase of glutamine, asparagine, serine in shoot and root occurred[52].

5 Genetic study of PUE-related traits

The PSR of plants leads to changes in plant phenotype, which are the basis for selecting high PUE genotypes. However, genetic analyses are the foundation for understanding the metabolic pathways and molecular breeding. The genetic structure of the target trait includes the number of QTL controlling the traits, the QTL effect, the mode of action of QTL (additive, dominant and epistatic effects) and the genotype-by-environment interactions[53]. Based on the research purpose, the traits related to P efficiency are divided into four categories: (1) traits related to P_i availability in the soil; (2) traits related to P uptake by plant roots; (3) traits related to P utilization; and (4) yield-related traits[25]. In maize research, information on many effective QTL has been mined using different genetic populations (Table 1).

The genetic architecture of PUE, PutE and PupE traits of a population of 140 RILs backcrossed with both parental lines, P-efficient inbred line L3 and the P-sensitive inbred line L22, showed that the dominant effects contributed more to PUE and its components than the additive effects. Importantly, the QTL detected for PUE correspond to 80% of those found for PupE traits, indicating that PupE and PUE have a similar genetic basis[22]. Using a BC_1F_5 established by crossing rice varieties Nipponbare and Kasalath, traits such as P uptake, PUE, dry weight and tiller number were identified in a low-P environment. QTL were found on chromosomes 2, 4, 6, 10 and 12, and of those QTL, a QTL at the interval of G227–C365 on chromosome 2 was found for both P uptake and PUE. Likewise, a QTL at the marker interval G2110–C443 on chromosome 12 was found consistently for the traits of P uptake, PUE, dry weight, and tiller number. Subsequently, by constructing a chromosome segment substitution line population, the important QTL Phosphorus uptake 1 (*Pup1*) was identified[69,70]. Phosphatase activity is also very important for plant roots to absorb P. Qiu et al[68]. used the inbred lines, 082 and Ye107, as parents to construct a $F_{2:3}$ population of 180 individuals. A stable QTL in the bnlg1350–bnlg1449 region of chromosome 10 was found for the acid phosphatase activity in roots. Two stable QTL, one at umc2083–umc1972 on chromosome 1 and the other at umc2111–dupssr10 on chromosome 5, were found for acid phosphatase activity in rhizosphere soil. Subsequently, phosphatase activity in leaf tissue in two low-P environments was assessed for QTL mapping, and six QTL were identified. Only QTL *AP9*, located within the 546 kb interval of chromosome 9 ac219–ac2096 marker interval, was found in different environments[67]. Cai et al.[39] used plant and ear height combined with yield-related traits in a low-P environment for QTL mapping, which resulted in a total of 25 QTL. QTL mapping was performed for leaf area, leaf chlorophyll content, flowering and yield traits under low-P in bin 2.03/2.04, bin 2.06/2.08, bin 4.01/4.02, bin 5.03/5.04, bin 6.07, bin 9.03, bin 10.03/10.04 intervals, when mining QTL for the different traits[65]. By taking the root traits of the RIL population (including the lateral root length, the lateral root number and the plasticity of lateral root number) under low-P as target traits, five QTL were mined on chromosomes 1, 2, 3 and 6 for lateral root length, with the largest phenotypic variance explained (PVE) of 9.98% and the smallest PVE of 4.04%. A QTL with a PVE of 10.4% was found on chromosome 2 for lateral root number, and a QTL with a PVE of 10.2% was found on chromosome 4 with regard to the plasticity of lateral root number[56].

In addition to QTL mapping using a biparental population, genome-wide association analysis (GWAS) based on linkage disequilibrium using the historical recombination of inbred lines results in a higher resolution of mapping and has achieved great success in resolving complex traits of plants[71–74]. However, there are only a few reports on using GWAS to analyze PUE or low-P tolerance-related traits. Xu et al[40]. used two association populations to perform GWAS analysis using phenotypes under low-P stress and low-P tolerance index (LPTI). The target traits comprised biomass, development-related traits and yield-related traits. Using the differentially expressed genes in the transcriptome data of the P-tolerant line CCM454 and the P-sensitive line 31778 as a validation, a total of 259 significantly associated genes were mined, which were mainly involved in four biochemical pathways, viz., transcriptional regulation, reactive oxygen scavenging, hormone regulation and remodeling of cell wall. Luo et al[75]. used 338 inbred lines to perform GWAS analysis and found five significant peaks for morphological traits. Metabolites with significant differences in the extreme pools of six P-sensitive inbred lines and six P-tolerant inbred lines were detected. Furthermore, by combining significantly associated SNPs with genes involved in different metabolite pathways, five genes, *GRMZM2G050570*, *GRMZM2G039588*, *GRMZM2G051806*, *GRMZM2G039588*, *GRMZM5G841893* were identified. These two studies combined GWAS with transcriptome or metabolome data to mine genes involved in the P

Table 1 QTL mapping information for PUE-related traits in maize

Environment	Parents[a]	Population type	Molecular marker	Population number	Target traits	Main finding	Reference
Hydroponic	NY821/H99	$F_{2:3}$	77 RFLP	90	SDW, RDW, TDW	Six RFLP marker loci related to biomass under P deficiency were identified	[54]
Hydroponic	Mo17/B73	RIL	167 RFLP, SSR and isozyme markers	197	RDW, RV	Substantial variation between maize lines for growth with low P and response to mycorrhizal fungi	[55]
Hydroponic	Mo17/B73	RIL	196 RFLP, SSR and isozyme markers	160	LRL, LRN	Eight QTL were identified for root-related traits	[56]
Cigar roll culture system	Mo17/B73	RIL	196 RFLP, SSR and isozyme markers	160	RHL, TT, SDW, SPC	QTL located at npi409/nc007 on Chr5 related to root hair length plasticity were found with low and normal P	[57]
Cigar roll culture system	Mo17/B73	RIL	196 RFLP, SSR and isozyme markers	160	SRL, SRN	Two coincident QTL flanked by umc34/bn112.09 on chromosome 2 and by bn112.09/umc131 on chromosome 2	[58]
Field	082/Ye107	$F_{2:3}$	275 SSR + 146 AFLP	241	PH, SDW, RDW, TPC, APA, H^+, et al.	Five common regions for same QTL were found in the interval bnlg1556–bnlg1564, mmc0341–umc1101, mmc0282–phi333597, bnlg1346–bnlg1695 and bnlg118a–umc2136	[59]
Hydroponic	082/Ye107	$F_{2:3}$	275 SSR + 146 AFLP	241	SPUE, WPUE, RSR	SPUE and WPUE under LP were controlled by one QTL at interval of bnlg1518–bnlg1526 (bins 10.04)	[60]
Field	178/5003	$F_{2:3}$	207 SSR	210	GY, HGW, EL, RN, KNPR, ED	Consistent QTL at umc2215–bnlg1429, umc1464–umc1829 and umc1645–bnlg1839 on chromosome 1, 5 and 10	[61]
Field	082/Ye107	$F_{2:3}$	275 SSR + 146 AFLP	241	Biomass, the leaf age, PH	Two important QTL located at bnlg1832–P2M8/j in chromosome 1 and umc1102–P1M7/d in chromosome 3	[62]
Field	082/Ye107	$F_{2:3}$	275 SSR + 146 AFLP	241	H^+ secretion	Large effect QTL related to H^+ secretion was mined at bnlg2228–bnlg100 (bin 1.08) interval	[63]
Field	082/Ye107	$F_{2:3}$	275 SSR + 146 AFLP	241	FRN, TL, SDR, RDW and TPC	QTL affecting root weight were detected at the dupssr15 locus region (bin 6.06)	[64]
Field	Ye478/Wu312	RIL	184 SSR	218	PH, EH, KNPE, HGW, GY	Seven QTL related grain yield under LP were identified	[39]
Field	Ye478/Wu312	RIL	184 SSR	218	LL, LW, LA, GY, chlorophyll, FT, ASI	Overlapping QTL were located at chromosome bin 2.03/2.04, bin 2.06/2.08, bin 4.01/4.02, bin 5.03/5.04, bin 6.07 and bin 9.03	[65]

(*Continued*)

Environment	Parents[a]	Population type	Molecular marker	Population number	Target traits	Main finding	Reference
Field	178/5003	NIL	9 SSR	/	KNPR	A QTL increasing kernel number under LP called *qKN* was finally localized to a region of ~480 kb on chromosome 10	[66]
Field	082/Ye107	BC_3F_2	12 SRR	1441	APA	A QTL denoted as *AP9* showed a stable expression under different environments on chromosome 9	[67]
Field	L3/L22	RIL backcrossed with parents	60 SSR + 332 KASP	140	GY, PutE, PupE	Approximately 80% of the QTLs mapped for PupE co-localized with those for PUE	[22]
Field	082/Ye107	$F_{2:3}$	295 SSR	180	APR, APS	One stable QTL for APR located in bnlg1350–bnlg1449 on chromosome 3 and two stable QTL located at umc2083–umc1972 on chromosome 1 and umc2111–dupssr on chromosome 5 for APS.	[68]
Hydroponic	L3/L22	RIL	60 SSR + 332 SNP	145	TRL, RD, RAS, TSDW, TPC	Four *ZmPSTOL* candidate genes co-localized with QTLs for root morphology, biomass accumulation and-or P content	[57]
Hydroponic	Ye478/Wu312	RIL and BC_4F_3	184 SSR, 143 SSR, respectively	218 and 187, respectively	PUE and RSA-related traits	Two QTL clusters, Cl^-bin3.04a and Cl^-bin3.04b for PUE and RSA-related traits were found	[26]
Paper roll, hydroponics, vermiculite culture	Ye478/Wu312	RIL	184 SSR	218	RSA and PUE-related traits	Six chromosome regions of bin 1.04/1.05, 1.06, 2.04/2.05, 3.04, 4.05 and 5.04/5.05 were identified for RSA traits	[18]

Note: [a] The former is the P-efficient parent; the latter is the P-inefficient parent. NIL, near isogenic line; PH, plant height; EH, ear height; LL, leaf length; LW, leaf width; LA, leaf area; FT, flower time; ASI, anthesis-silking interval; SDW; shoot dry weight; RDW, root dry weight; TSDW, total seedling dry weight; TRL, total root length; RD, root diameter; RAS, root area surface; RSA, root system architecture; FRN, fibrous root number; TL, taproot length; TT, taproot thickness; SRL, seminal root length; SRN, seminal root number; RHL, root hair number; RV, root volume; PRN, primary root number; LRL, lateral root length; LRN, lateral root number; RSR, root/shoot ratio; TPC, total P content; APA, acid phosphatase activity; APR, acid phosphatase activity in root; APS, acid phosphatase activity in rhizosphere soil; SPC, seed P content; SPUE, shoot P utilization efficiency; WPUE, the whole P utilization efficiency; KNPE, kernel number per ear; HGW, 100 kernel weight; RN, row number; KNPR, kernel number per row; ED, ear diameter; EL, ear length; GY, grain yield; SSR, simple sequence repeat; KASP, kompetitive allele specific PCR; AFLP, amplified fragment length polymorphisms; RFLP, restriction fragment length polymorphism.

metabolic pathway. The approach of combining multiomics data results in a better understanding of the inheritance and regulatory pathways of PUE-related traits.

Some synthetic multiparent populations such as nested association mapping, multiparent advanced generation intercrosses, multiparent population consisting of serval doubled haploid (DH) or RIL populations combine the advantages of linkage analysis and association mapping. At the same time, rich genomic and phenotypic variation and a clear genetic structure of maize make it possible to resolve many complex traits with greater flexibility and efficacy[76–82]. Although such multiparent populations have unparalleled advantages in QTL mapping and genetic analyses, genetic studies of low-P tolerance are currently limited to biparental QTL mapping and association mapping. Hence, there is still considerable scope for improvement of genetic population studies for PUE.

6 Phenotypic difference between heterotic subgroups

Heterosis refers to the phenomenon where the phenotype of the F_1-generation performs better than those of parents, and maize is the most successful crop for the utilization of heterosis. A study using 456 inbred lines and their phenotypic data of shoot and root at the seedling stage in a normal and low-P environment led to the classification of lines into low, medium and high tolerance to low-P conditions, and specifically, the identification of 23 P-efficient and 109 P-sensitive lines. P-efficient lines in the temperate subpopulations were 1323, 81162, 04K5672 and Dan599, P-efficient lines in the tropical/subtropical subpopulations were CIMBL120, CIMBL131, CIMBL14 and CML431, P-inefficient lines in the temperate subpopulations were Dan340, Zheng22, ZZ01, XZ698, and P-inefficient lines in the tropical/subtropical subpopulations were CIMBL10, CIMBL106, CIMBL110 and CIMBL114[83]. Based on the agronomic traits and yield traits of 826 lines (including 580 tropical/subtropical and 246 temperate maize inbred lines), the synthetic LPTI was calculated to screen for high PUE lines. The temperate low-P-tolerant inbred lines in the temperate subpopulations were CXS100, Fu746 and LH51, the low-P-inefficient inbred lines in the tropical/subtropical subpopulations were CML426, CML432 and CML470, the P-inefficient lines in the temperate subpopulation were CXS132, CXS135, CXS18 and CXS21, and the low-P-inefficient lines in the tropical/subtropical subpopulations were CML486, CML454, CML40 and CML29860[41]. By rearranging the data of Zhang et al.[41], it can be found that the temperate lines have higher tolerance to low P ($P < 0.001$) (Fig. 1).

Xu et al.[40] used the same index as Zhang et al.[41] to perform genetic analysis of low-P-tolerant lines to screen germplasm resources. P-efficient inbred lines were CP619F, JI35, 89-1 and 374, whereas P-inefficient lines were 200B, LH193, LH220HT and 4676. It is clear that the genetic materials selected in different studies differed greatly, which was mainly due to (1) differences in genetic materials per se; and (2) the differing target traits and indicators. Therefore, the question of which indicator should be used to screen for low-P-resistant lines is still open to discussion. Most studies use phenotypes under

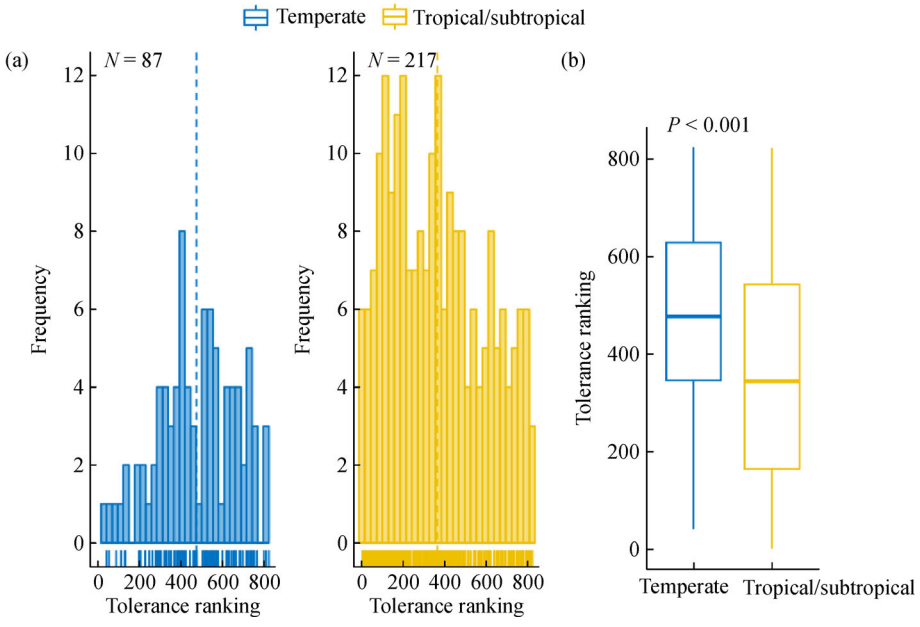

Fig. 1 Distribution of low-P tolerance ranking of temperate and tropical/subtropical subpopulations. (a) Histogram of tolerance ranking of temperate (left) and tropical/subtropical (right); (b) boxplot of tolerance ranking of the two subpopulations. Significance test was based on Student's *t*-test. Data sources from Zhang et al.[41].

low-P stress or LPTI as screening indicators.

Liu et al.[84] used three P-efficient inbred lines (Zao27, 428 and YuanYin1) and three P-inefficient inbred lines (7922, Chen9411 and 8703-2) as parents to produce 15 F_1 hybrids by crossing as a complete diallel. It was found that for most traits, under the stress of low P, the relative midparent heterosis changed from 20.3% to 446%, while it varied between −7.73% and 2308% under high-P conditions, and that the midparent heterosis of most root system architecture-related traits under low P was higher than that under normal P. Ige et al.[85] used 10 open pollinated cultivars to construct hybrids by a complete diallel cross. Their work revealed that the midparent heterosis and the better-parent-heterosis are reduced under low-N stress. Moreover, AMATZBR-WC2B (white flint) with flint endosperm and white grain color showed the highest general combining ability (GCA). DMR-LSR-Y (yellow dent) with dent endosperm type and with yellow grain color and BR9943DMRSRG (white flint) with flint endosperm and white grain color had the lowest GCA. Under low-N conditions, the hybrids DMR-LSR-W (yellow dent) x BR9928DMRSR (yellow flint) and BR9922DMRSR (yellow flint) x TZBRELD-4C0W (white flint) have the highest specific combining ability (SCA). Narang & Altmann[86] used two *Arabidopsis* accessions, C24 and Col-0, which differed in the absorption capacity of hydroxyl phosphate, and found that the heterosis of F_1 hybrids was derived from the accumulation of a large number of excellent dominant genes. The hybrids inherited the long root hair length of C24, the long root length of Col-0, and the enhanced phosphate transporter expression of C24. Physiological genetic changes result in hybrids with a higher PUE. Under low-P stress, phenotypic analysis of lines and hybrids from different heterotic groups is used to identify high GCA inbred lines and high SCA hybrids, which in turn are promising candidates for evaluating, predicting, and selecting high PUE maize hybrids.

7 Molecular breeding methods in plants

Standard breeding mainly chooses individuals according to their phenotypes, which has great utility. Molecular markers can be used to select the background and foreground of genetic material, and to achieve gene pyramiding, which improves the accuracy and predictability of maize breeding[87]. In *Arabidopsis*, *MYB62*, *ARF7* and *ARF19* have been reported to increase the absorption of P by root[88,89]. *Pup1* is a very important QTL located on chromosome 12 of rice, with the rice variety Kasalath serving as the donor of this favorable allele. It was found that in low-P soils, the P uptake and yield of lines carrying *Pup1* were higher, which holds true for different genetic backgrounds and environments[90]. Furthermore, overexpressing the *PSTOL1* gene, which encodes a protein kinase, confers a phenotype of increased root dry weight, P uptake, and yield in the rice varieties IR64 and Nipponbare[13]. By homologous alignment with published PUE-related genes in rice and *Arabidopsis*, many genes with potential applications in maize had been discovered, for example *GRMZM2G017164*[13], *GRMZM2G111354*[32], *GRMZM2G135978*[91,92]. However, there has been no report of the application of genes in maize breeding until now. In recent years, a series of gene editing technologies have become increasingly common in human and plant research, among which the most widely and successfully used technology is CRISPR[93]. The CRISPR system has been used to improve quality and quantity traits of maize[94,95]. CRISPR technology only transforms endogenous genes and has broad prospects for application in the creation of new genetic breeding lines. For maize, there is no report on the use of CRISPR technology to obtain high PUE maize germplasm. This underlines the fact that knowledge of a gene or QTL is necessary for its application via MAS, transgenic approaches, or CRISPR.

In 2001, Meuwissen et al[96]. proposed the concept of GS, in which molecular markers covering a whole genome and phenotypic information of a training population are used to establish linear models (such as rrBLUP, BayesA and GBLUP) to predict the genomic estimated breeding value[97]. Bernardo and Yu[98] performed a simulation analysis in maize DH breeding and demonstrated that genome-wide selection has greater genetic advances than MAS. Subsequently, GS has been widely carried out in the study of maize inbred line selection, hybrid phenotypic and heterosis prediction, and has achieved great efficiencies in important agronomic traits, quality and yield of maize[99–106]. The prediction accuracy of GS is affected by multiple factors, such as the genetic structure of a trait, the number of markers, the size of the training population, and the kinship among individuals[107–110]. Lyra et al.[111] used phenotypes under low-N to calculate different selection indices and used GBLUP and RKHS/GK to evaluate the accuracy of single-trait and multi-trait models. For the two investigated models, the highest accuracy of harmonic mean index was 0.4 and 0.41, respectively. The multi-trait model can also improve the GS accuracy of yield. By using an association population of 11 phenotypes, it was observed that haplotype-GS comprising the information of linkage disequilibrium and wBayes with the information of significant QTL have a higher prediction accuracy for some simple traits[40]. Therefore, the method of GS has a high accuracy and genetic progress for prediction and screening of high PUE lines is enhanced.

8 Molecular breeding for high PUE in maize

Based the research discussed above, we propose a strategy for screening P-efficient maize lines and cultivars by

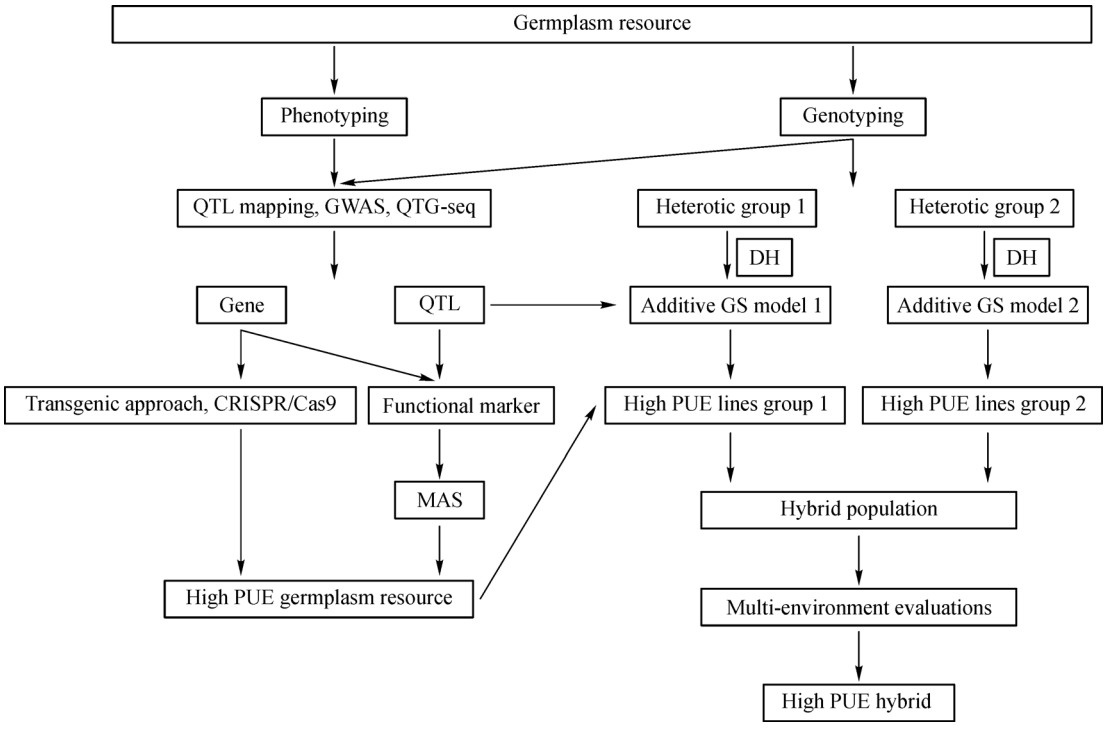

Fig. 2 A strategy for breeding high PUE inbred lines and hybrids.

combining various molecular breeding methods (Fig. 2).

Rich genetic resources are the basis for crop genetic improvement and breeding[112–114]. Organizations such as the Chinese Academy of Agricultural Sciences, the International Maize and Wheat Improvement Center and Leibniz Institute of Plant Genetics and Crop Plant Research have established gene banks, and researchers can order seed resources online. Since the sequencing of maize variety B73 in 2009[115], large-scale whole-genome sequencing of maize has been undertaken, and 1.25 million markers of 540 inbred lines have been constructed by integrating RNA-Seq data, 50K chips and genotyping by sequencing data[116]. By means of the whole genome sequencing data of 1218 inbred lines, researchers constructed the third generation HapMap of maize[117] and the genome sequencing data has been shared on the web page of 'maizego' and 'panzea'. At present, in most studies, the collection of phenotypic data still relies on labor, but large-scale high-throughput automated phenotypic identification platforms have been established to overcome this limitation[118]. For example, candidate gene mining by combining high-throughput agronomic phenotypic data and correlation analysis has been performed in rice[119]. Imaging systems have also been applied to study plant roots[75], and this automated phenotypic identification platform is likely to have broad application in crop phenotypes and genetic research. Also, statistical methods for the association of phenotypic and genotypic data are used for linkage mapping and GWAS. Other methods that only use extreme plant materials for gene mapping (such as MutMap[120], BAR-Seq[121], QTL-Seq[122], QTG-Seq[123] and XP-GWAS[124]) have proved beneficial in genetic research on quality and quantitative traits. Moreover, bulked segregant analysis of genomes, metabolomes, and proteomes has great potential for genetic mapping, plant breeding, and molecular marker development[125]. Overall, with the above resources and technologies that allow increased knowledge for a candidate gene or QTL we then can use MAS, transgenic approaches and CRISPR to verify the candidate gene function(s) and select targeted chromosome fragments for genetic improvement, thereby achieving superior gene selection and broadening the genetic basis for low-P tolerance in maize.

Since maize is a crop with strong heterosis, it is not enough to only select or improve elite inbred lines; rather, it is necessary to select excellent inbred lines in different heterotic groups to form hybrids. Within each heterotic group, DH technology can be used to obtain pure inbred lines in early generations. Based on the genotypic information of these lines, the subgroup structure of the lines can be determined by using the methods of principal component analysis and genetic distance[72,126–128]. There are two main advantages to grouping genetic materials: (1) the farther the genetic distance between subgroups, the greater the heterosis[129,130]; (2) the kinship of the lines within one subgroup is close, and the relationship between the training group and the testing group is close, which can lead to a high accuracy of GS[101,109,131–133]. According to a clustering structure, a GS model can be established in each subgroup. The difficulty in phenotyping a large

number of DHs can be solved by using GS methods to predict the PUE-related traits. At the same time, QTL or genetic information related to PUE traits can also be integrated into a GS model to improve prediction accuracy[134]. Hybrid breeding entails selecting elite inbred lines with a high GCA, followed by crosses of pairs of lines with a high SCA. Therefore, some core germplasm resources should be selected from each subgroup to make test crosses. Then, a hybrid prediction model can be established based on the multienvironment evaluation for hybrids and their parental lines[135,136]. In addition, the genotype by environment interaction can be integrated into a linear model to improve accuracy[137–139], thereby achieving the selection of high PUE hybrids.

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Compliance with ethics guidelines Dongdong Li, Meng Wang, Xianyan Kuang, and Wenxin Liu declare that they have no conflicts of interest or financial conflicts to disclose.

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