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Low straw phosphorus concentration is beneficial for high phosphorus use efficiency for grain production in rice recombinant inbred lines

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ABSTRACT

The objective of this study was to comprehensively investigate the relationship of phosphorus (P) concentration and accumulation with yield formation and P use efficiency for grain production (PUEg) using 127 rice recombinant inbred lines grown in a working field under low (LP) and high P (HP) conditions. Phosphorus concentration and accumulation, P translocation (PT) and translocation efficiency (PTE), PUEg, P harvest index (PHI), grain yield, and grain yield components were investigated. Wide ranges in grain yield, straw P concentration, total P accumulation, and PUEg were observed under LP and HP conditions. Coefficients of variance showed that the grain P concentration was considerably conserved, whereas the straw P concentration was relatively variable among inbred lines. In comparison with grain P, straw P made a larger contribution to total P accumulation (PUP) at maturity. Growth duration had no substantial effect on PUEg and positively affected P accumulation under both P conditions; however, it negatively affected the grain P concentration under the HP condition. The straw P concentration was negatively correlated with the grain filling percentage and harvest index. PUEg was negatively correlated with the grain and straw P concentrations, suggesting that low P concentrations, especially in straw, favored a high PUEg. There was no correlation between the P concentrations in grain and straw. The correlation analysis indicated that low straw P concentrations might be partly attributed to high PTE and PHI values. These results show that low straw P concentrations may simultaneously improve PUEg and grain yield by enhancing P translocation into grain, thus reducing the need for P fertilizer application.

1. Introduction

Phosphorus (P) is a critical element required for crop growth, development, and grain production. Rice is an extraordinarily important staple crop and a focus of significant effort aimed at improving its agricultural traits. A major focus of rice producers is increasing grain yield, which is often limited by the low availability of P in soil. P fertilizers are applied to alleviate P deficiency and have significantly contributed to increases in global food production since the green revolution (Fageria et al., 2011; Richardson et al., 2011). However, less than 20% of applied P is recovered by crops in the first year of growth, because most P applied to soil is converted into unavailable forms that cannot be easily absorbed and used by plants; therefore, farmers often apply additional P fertilizer to support high grain yield (Vance, 2001; Wang et al., 2010). However, excessive P application may exacerbate environmental degradation, so reducing P application by rice producers is desirable from an environmental point of view. Therefore, developing rice cultivars with high P uptake and use efficiency, and thus reduced P demand, is a significant research focus because of the potential for such a cultivar to offer increased grain yield and reduce the amount of P that must be applied during rice production.

Mechanisms for enhancing P efficiency include improvement of 1) P acquisition from the rooting environment; 2) P movement and redistribution within the plant; and 3) P utilization via metabolism and growth (Ahmad et al., 2001). Approaches for increasing P acquisition in a low P environment include alteration of root morphology and architecture (Ramaekers et al., 2010; Richardson et al., 2011), activation of high affinity transporters (Rausch and Bucher, 2002), secretion of phosphate scavenging and recycling enzymes into the

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rhizosphere (Hu et al., 2001), exudation of organic anions by roots .0002194.7542746.407Tm()4TjjEg83jETBT/F11Tf7.9701007.9701186.384777.789 (Hammond et al., 2004), and root symbiosis with mycorrhizae (Bucher, 2007). Further, P remobilization from senescing vegetative parts to young developing parts has been interpreted as a strategy to cope with P deficiency in some plants (Ahmad et al., 2001). P translocation from vegetative parts to grain also plays a key role in the development of wheat grain (Dordas, 2009; Horst et al., 1993). Additionally, low grain P concentration has been considered as a key

Table 1
Mean ± SD, range and coefficient of variance (CV) for the investigated traits of the recombinant inbred lines (RILs) and their parents under low P (LP) and high P (HP) conditions.

Trait	LP						HP					
	Parents		RILs				Parents		RILs			
	Minghui63	Zhenshan97	Mean	Min.	Max.	CV (%)	Minghui63	Zhenshan97	Mean	Min	Max	CV (%)
PUEg (kg kg^{-1})	208 ± 41	225 ± 11	195	128	258	14.2	161 ± 13	188 ± 21	172^{**}	92	227	15.5
Grain yield (g m^{-2})	700 ± 75	435 ± 38	570	316	890	16.5	655 ± 26	444 ± 47	578^{**}	226	832	16.1
Dry weight of straw (g m^{-2})	886 ± 118	432 ± 41	728	434	1055	14.6	939 ± 25	418 ± 24	751^{**}	436	1032	14.6
Grain P concentration (mg g^{-1})	3.43 ± 0.26	3.65 ± 0.35	3.51	2.79	4.08	7.0	3.69 ± 0.33	3.93 ± 0.52	3.58^{**}	2.89	4.44	6.9
Straw P concentration (mg g^{-1})	1.51 ± 0.25	1.45 ± 0.08	1.71	1.14	2.53	16.2	2.09 ± 0.09	2.14 ± 0.16	2.15^{**}	1.45	3.16	15.6
Plant P concentration (mg g^{-1})	2.29 ± 0.20	2.47 ± 0.12	2.44	1.96	2.88	7.0	2.70 ± 0.17	2.99 ± 0.23	2.73^{**}	2.17	3.51	7.7
Grain P accumulation (g m^{-2})	2.06 ± 0.28	1.35 ± 0.08	1.72	0.97	2.56	16.7	2.08 ± 0.15	1.50 ± 0.12	1.77^{**}	0.86	2.46	15.2
Straw P accumulation (g m^{-2})	1.36 ± 0.39	0.63 ± 0.09	1.26	0.60	2.13	23.4	1.96 ± 0.04	0.90 ± 0.12	1.62^{**}	0.84	2.61	22.5
Total P accumulation (g m^{-2})	3.42 ± 0.56	1.98 ± 0.12	2.97	1.98	4.02	12.3	4.04 ± 0.17	2.39 ± 0.23	3.39^{**}	2.32	4.22	11.1
PHI (%)	60.4 ± 7.5	67.8 ± 3.7	58.0	35.4	71.1	12.9	50.9 ± 1.1	62.3 ± 1.4	52.5^{**}	31.6	67.7	14.5
PTE (%)	59.7 ± 10.8	76.3 ± 2.5	59.2	27.7	75.7	16.5	45.6 ± 6.2	71.3 ± 3.8	53.8^{**}	24.4	73.3	20.1
PT (g m^{-2})	1.79 ± 0.28	1.07 ± 0.03	1.38	0.72	2.12	18.4	1.54 ± 0.33	1.41 ± 0.08	1.49^{**}	0.68	2.12	19.5

PHI, P harvest index; PTE, P translocation efficiency; PT, P translocation; PUEg, P use efficiency for grain yield. *and ** represent significant differences for a trait at $p < 0.05$ and $p < 0.01$ between the low P and high P conditions among the RILs, respectively, as shown by two-way analysis of variance.

2.2. Sampling and measurement of traits

Heading date was defined as the time at which 50% of the hills in a plot had at least one panicle completely emerged and was quantified as the number of days from seeding to heading. The duration from heading to maturity showed very small variation across the lines (29–31 days), so the number of days from seeding to heading was considered as the growth duration in this study. Rice plants from each plot were diagonally sampled at ground level in the inner rows at the heading and maturity stages (8 and 12 hills, respectively). At heading, the samples were separated into leaves (including senesced and green leaves) and stems (including the young panicles and sheath). At maturity, the samples were separated into leaves, stems (including sheath) and panicles. The panicles were threshed by hand, after which filled and unfilled spikelets were divided by submerging them in tap water. Leaves, stems, rachis, and filled and unfilled spikelets were oven dried at 80 °C to a constant weight for determination of dry weight. Grain yield (g m^{2}) and its components (panicle number per m^{2}, spikelets per panicle, grain filling percentage (%), 1000 grain weight (g), and harvest index (%)) were calculated.

Subsequently, oven dried leaves, stems (including sheath and rachis) and grains were separately ground into powder using a grinder, mixed thoroughly, and passed through a 1 mm sieve. Approximately 0.2 g of sample powder was digested with 5 mL of concentrated sulfuric acid and hydrogen peroxide, after which the P concentration of the sample was determined via the molybdenum blue colorimetric method described by Murphy and Riley (1962) using a continuous flow analyzer (Futura, Alliance, France). The P concentration (mg g^{-1}) was defined as the amount of P per g dry matter of each plant part. The straw P concentration (mg g^{-1}) was calculated as the amount of P per g dry weight of stems and leaves.

At maturity the whole rice plant was divided into full filled grains and straw. The P accumulation (g m^{-2}) in each plant part was calculated by multiplying the P concentration by the dry weight. The P harvest index (PHI, %) was calculated as the ratio of the grain P accumulation to the total P accumulation of the aboveground parts at maturity (PUP). The P use efficiency for grain yield (PUEg, kg kg^{-1}) was calculated as the grain yield divided by the total aboveground P accumulation.

Phosphorus translocation (PT, g m^{-2}) and P translocation efficiency (PTE, %) were estimated according to the methods of Dordas (2009). PT (g m^{-2}) was defined as the plant P accumulation at heading minus the P accumulation in the leaves and stems at maturity. PTE (%) was calculated as the ratio of PT to the P accumulation at heading.

2.3. Data analysis

Mean values over the two years of the experiment were used for statistical analyses. The coefficient of variance (CV, %) was used to assess the degree of variation of a certain trait among RILs. The CV was calculated as the ratio of the standard deviation to the mean across 127 RILs. Two-way analysis of variance (ANOVA) was performed to determine significant trait differences among the RILs exposed to the low P and high P conditions. Pearson correlation analysis and Student's *t* test (two tailed) were performed using SAS 9.1 software (SAS Institute Inc., Cary, NC, USA). Direct (path coefficient) and indirect effects were calculated using a specific program performed with SAS software. Direct and indirect path coefficients (effects) were calculated as described by Dewey and Lu (1959) and Li (1975).

3. Results

3.1. Phenotypic variation

Under both P conditions, Minghui 63 showed higher performance in grain yield, dry weight of straw, grain and straw P accumulation, total P accumulation, and PT; however, Zhenshan 97 had higher PUEg, grain P concentration, plant P concentration, PHI, and PTE (Table 1). For the RILs, the mean values of PUEg, PHI and PTE were higher under LP conditions in comparison with those measured under HP conditions, while the mean grain yield, straw dry weight, and PT were lower under LP conditions. In general, the RILs showed wide variation in all investigated traits (Table 1).

Noticeably, under both P conditions, grain and whole plant P concentrations showed relatively little variation, with less than 8% coefficient of variance (CV), while the other ten traits showed more variation, with CVs from 11% to 23% (Table 1). However, the grain P concentrations and accumulations of the parent lines and the average values of these parameters across the RILs showed relatively small differences between the two P treatment groups. The straw P concentration and accumulation were higher under the HP condition in comparison with those measured under the LP condition. These findings indicate that the grain P concentration was relatively stable in comparison with the straw P concentration.

3.2. Relationships between P concentrations and grain yield-related traits

The whole plant P concentration at maturity was significantly negatively correlated with grain yield, especially under the HP con

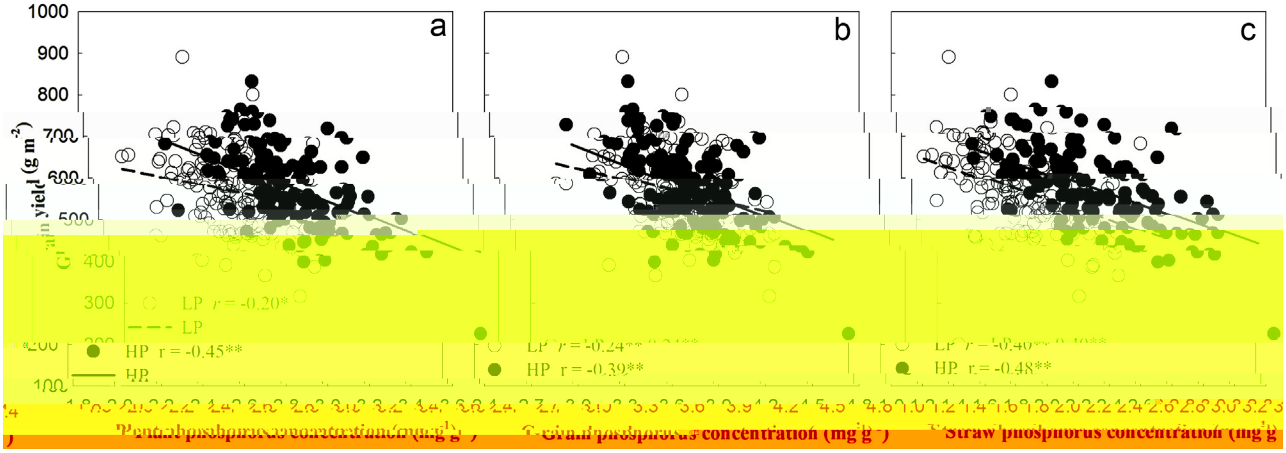

Fig. 1. Correlations of grain yield with plant P concentration (a), grain P concentration (b) and straw P concentration (c) under low P (LP) and high P (HP) conditions. * and ** indicate significance at $p < 0.05$ and $p < 0.01$ (n = 127), respectively.

Table 2
Relationship of P concentrations with yield components and harvest index under low P (LP) and high P (HP) conditions.

Trait	Panicles (No. m^{-2})	Spikelets $panicle^{-1}$	Spikelets (No. m^{-2})	Grain filling percentage (%)	1000 Grain weight (mg)	Harvest index (%)
LP						
Grain	0.04	−0.13	−0.12	−0.09	−0.09	−0.17
Straw	0.04	−0.07	−0.04	−0.38**	−0.01	−0.47**
Plant	0.20*	−0.15	0.02	−0.15	−0.11	−0.06
HP						
Grain	0.17	−0.21*	−0.11	−0.20*	−0.17	−0.16
Straw	0.03	−0.13	−0.15	−0.36**	−0.03	−0.49**
Plant	0.18*	−0.21*	−0.11	−0.27**	−0.16	−0.24**

* and ** indicate significance at $p < 0.05$ and $p < 0.01$ (n = 127), respectively.

Table 3
Relationships of P accumulations with yield components and harvest index under low P (LP) and high P (HP) conditions.

Trait	Panicles (No. m^{-2})	Spikelets $panicle^{-1}$	Spikelets (No. m^{-2})	Grain filling percentage (%)	1000 Grain weight (mg)	Harvest index (%)
LP						
Grain	−0.01	0.07	0.09	0.72**	0.17	0.62**
Straw	−0.20*	0.05	−0.12	−0.23**	0.18*	−0.69**
Plant	−0.17	0.09	−0.02	0.37**	0.28**	−0.06
HP						
Grain	0.06	0.01	0.09	0.72**	0.13	0.68**
Straw	−0.25**	−0.01	−0.23**	−0.24**	0.22*	−0.73**
Plant	−0.21*	0.01	−0.16	0.28**	0.30**	−0.22*

* and ** indicate significance at p < 0.05 and p < 0.01(n = 127), respectively.

dition (Fig. 1a); similar trends were also found between the grain P concentration and grain yield (Fig. 1b). In comparison with the whole plant and grain P concentrations, the straw P concentration showed a stronger negative correlation with grain yield under both P conditions (Fig. 1c). It is noteworthy that the correlation coefficients for the relationships between P concentrations and grain yield were generally low, regardless of significance. Moreover, straw P concentration was strongly and negatively correlated with grain filling percentage and harvest index under both P conditions (Table 2). These results show that exposure to a high straw P concentration adversely affected yield formation in the tested RILs.

3.3. Relationships between P accumulations and grain yield-related traits

Under both P conditions, the total P accumulation at maturity showed a significant positive correlation with grain yield (Fig. 2a). Strong positive correlations were observed between grain P accumulation and grain yield, with correlation coefficients of 0.91 under both P conditions (Fig. 2b). However, the straw P accumulation was negatively correlated with grain yield under both P conditions with low correlation coefficients (Fig. 2c). For the correlations between P accumulation and yield components, the total plant P accumulation was positively correlated with grain filling percentage and grain weight (Table 3). The grain P accumulation was significantly and positively correlated with the grain filling percentage and harvest index under both P conditions. It is noteworthy that the straw P accumulation was significantly and negatively correlated with the grain filling percentage and harvest index under both P conditions. These findings also demonstrate the adverse effects of high P accumulation in straw on yield formation by the tested RILs.

3.4. Effects of growth duration on P concentrations and accumulations

Under LP and HP conditions, P accumulations in grain, straw, and whole plants were significantly correlated with growth duration before heading; however, the PHI and PTE were negatively correlated with growth duration (Table 4). Growth duration had no effect on any P concentration under the LP condition; however,

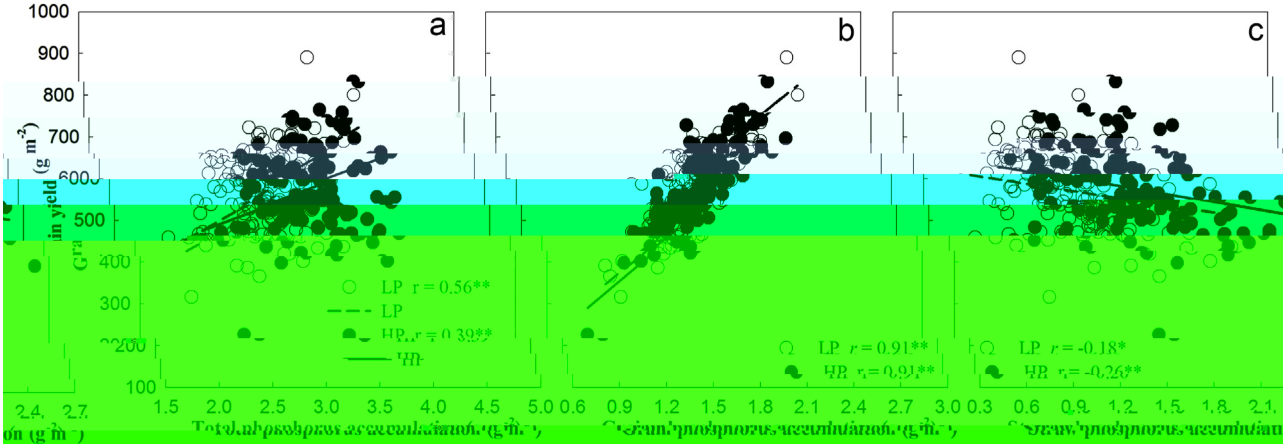

Fig. 2. Correlations of grain yield with total P accumulation (a), grain P accumulation (b) and straw P accumulation (c) under low P (LP) and high P (HP) conditions. * and ** indicate significance at $p < 0.05$ and $p < 0.01$ ($n = 127$), respectively.

Table 4
Relationships of growth duration before heading (days) with P concentration and accumulation and use efficiency under low P (LP) and high P

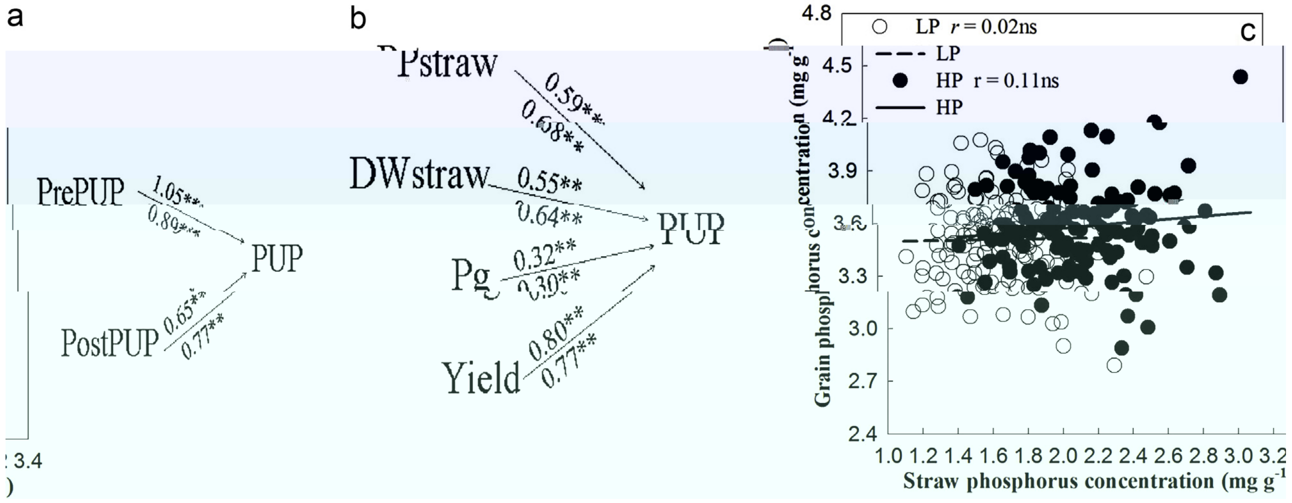

Fig. 4. Direct effects of pre anthesis (PrePUP) and post anthesis (PostPUP) P accumulations, straw and grain P concentrations (Pstraw, Pg), and straw biomass (DWstraw) and grain yield (Yield) on total P accumulation (PUP) under low P (above the

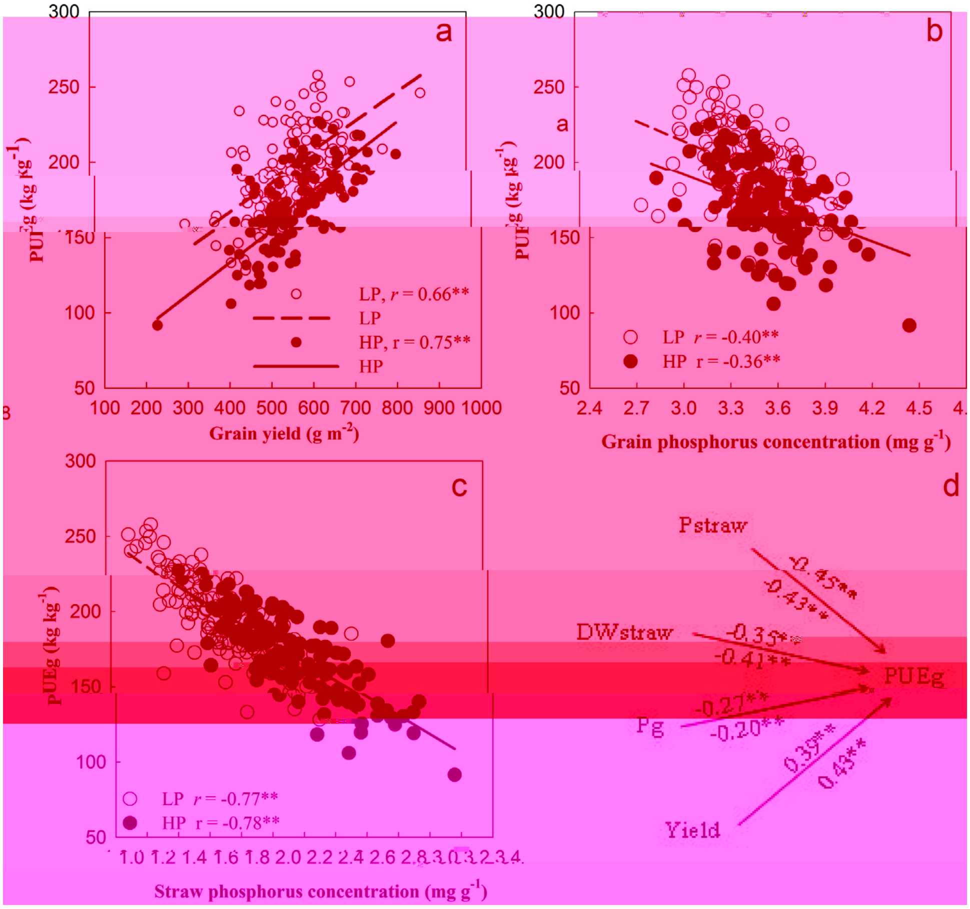

Fig. 5. Correlations of P use efficiency (PUEg) with straw and grain P concentrations (Pstraw, Pg) and grain yield, and direct effects of straw biomass (DW straw) and grain yield (Yield), Pstraw and Pg on PUEg under low P (above the arrow) and high P (below the arrow) conditions. * and ** indicate significance at $p < 0.05$ and $p < 0.01$, respectively.

In comparison with the relationship between the grain P concentration and grain yield, there was a much stronger and negative relationship between the straw P concentration and grain yield (Fig. 1c). A low straw concentration had positive impacts on the grain filling percentage and harvest index under both P conditions (Table 2). Therefore, our study and previous reports suggest that grain and straw P concentrations are closely associated with P efficiency, and it is possible for a genotype with relatively low P concentrations in particular parts of the plant, especially straw, to achieve high P efficiency. Although the P concentrations in grain and straw were found to be negatively correlated with grain yield, the negative correlation did not imply that low grain and straw P concentrations led to higher grain yield.

In contrast to the P concentration, the total plant P accumulation and grain P accumulation were positively correlated with grain yield (Fig. 2a and b). Similar results have been reported in rice and wheat (Calderini et al., 1995; Rose et al., 2010). However, straw P accumulation was negatively and weakly associated with grain yield (Fig. 2c). Generally, grain P accumulation showed significant positive correlations with the grain filling percentage and harvest index under LP and HP conditions, in contrast with the negative correlations between the grain P concentration and grain filling percentage under HP condition (Tables 2 and 3). Therefore, these findings suggest that the contributions of P accumulations in various plant parts to yield formation are different from those of P concentrations to some extent. Interestingly, high P distribution in the straw was associated with impaired yield formation. Taken together with the results described above, these findings suggest that a genotype yielding relatively more grain may show relatively high grain P accumulation and relatively low grain and straw P concentrations.

The straw P concentration showed large genotypic variation, as shown by analysis of the coefficients of variance of the RILs (Table 1). However, the analysis revealed a highly positive correlation between grain P accumulation and grain yield (Fig. 2b), highly negative correlations between grain yield and the straw P concentration (Fig. 1c)/straw P accumulation (Fig. 2c), no relationship between the straw and grain P concentrations (Fig. 4c), a small coefficient of variance for the grain P concentration (Table 1), and a negative correlation between the straw P concentration/accumulation and the two yield components (grain filling percentage and harvest index, Tables 2 and 3). These findings show that the grain P concentration was relatively stable across RILs, whereas the straw P concentration showed considerable genetic variation. Therefore, a low straw P concentration, which may be beneficial for yield formation, can be used as a criterion for estimation of high P use efficiency during the selection of genotypes for breeding programs.

4.3. Phosphorus concentrations and accumulations with PUEg

In this study, P concentrations in grain and straw were negatively correlated with PUEg (Fig. 5b and c) under both P conditions. Additionally, in comparison with the grain P concentration, the straw P concentration showed a stronger negative correlation and larger negative direct effects on PUEg (Fig. 5c and d). These results strongly suggest that the straw P concentration has a considerable influence on PUEg in comparison with that of the grain P concentration, implying that genotypes with low straw P concentrations are likely to have high PUEg. However, different relationships were observed between grain and straw P accumulations and PUEg in the present study. Grain P accumulation was positively correlated with PUEg ($r = 0.49$ under the LP condition and 0.64 under HP condition, $p < 0.01$), while straw P accumulation was negatively correlated with PUEg ($r = -0.78$ under the LP condition and -0.79 under the HP condition, $p < 0.01$). A low grain P concentration has been proposed as a trait that may improve P efficiency (Rose et al., 2010; Vandamme et al., 2016a). By considering the negative associations of P concentrations with grain yield (Fig. 1) and PUEg (Fig. 5), simultaneous improvement in P use efficiency and grain yield should be achievable in future breeding programs by reducing the straw P concentration. Additionally, a low straw P concentration may increase the P efficiency of a crop system by reducing the amount of P removed from fields at harvest, as has been reported for a low grain P concentration (Rose et al., 2010; Vandamme et al., 2016a). However, the critical and optimal grain and straw P concentrations with regard to increasing PUEg have not been identified and merit further study.

It is often argued that a low whole plant P concentration can be achieved by reducing the concentration of inorganic P in vacuoles or by enhancing internal P reutilization (Richardson et al., 2011). Phosphorus efficient plants with low P concentrations usually remobilize P from metabolically inactive sites to active sites in non-mature tissues, and this strategy is adopted by some plants to tolerate low P supply (Ahmad et al., 2001; Akhtar et al., 2008; Richardson et al., 2011). The studies of Dordas (2009) and Horst et al. (1993) also revealed that P re-translocation from vegetative tissues to reproductive tissues is important for grain development, as confirmed by the positive relationship between the PHI and grain yield in the present study (Fig. 3a). PUEg can also be calculated by dividing the PHI by the grain P concentration. In our study, significant positive correlations were observed between the PHI and PUEg ($r = 0.87$ under the LP condition and $r = 0.90$ under the HP condition, $p < 0.01$). Therefore, increased P translocation to grains was associated with an increased PHI, which in turn may have increased PUEg. Our results indicate that high PTE may increase the PHI and reduce the straw P concentration (Fig. 3b and c). The straw P concentration was significantly and negatively correlated with PT ($r = -0.29$ under the LP condition and -0.45 under the HP condition, $p < 0.01$) and the PHI ($r = -0.81$ under the LP condition and -0.80 under the HP condition, $p < 0.01$). Therefore, a lower straw P concentration may be partly attributed to more PT, higher PTE, and a higher PHI. These results suggest that, when P fertilizer application is slightly reduced, sufficient P may be accumulated in grains for yield formation by transferring straw P to grains, and high PUEg may be achieved.

As shown in Table 4, a long duration of growth may increase P accumulation and P translocation; however, growth duration had no effect, or a negative effect, on the P concentration, PHI, and PTE. Interestingly, we observed that growth duration had no effect on PUEg under either P application condition. These findings suggest that genotypes with growth periods of short duration may show reduced plant

Conflict of interest

The authors have no conflict of interest.

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