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Seed Phosphorus Effects on Rice Seedling Vigour in Soils Differing in Phosphorus Status

Terry J. Rose * and **Carolyn A. Raymond**

Southern Cross Plant Science, Southern Cross University, Lismore, NSW 2480, Australia; carolyn.raymond@scu.edu.au

* Correspondence: terry.rose@scu.edu.au; Tel.: +61-2-66203457

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Abstract: A key driver of the current unsustainable global phosphorus (P) cycle is the removal of P from fields in harvested grains. Minimising the concentration of P in grains of staple cereal crops would contribute towards addressing the issue, but it is possible that reducing grain P concentration may impact the vigour of subsequent seedlings. We used a hydroponic method to obtain low- and high-P rice (*Oryza sativa* L.) seeds from plants grown under near-identical conditions, so that any differences in subsequent seedling growth were likely due to differences in seed P concentrations rather than other seed quality differences that may arise from growing mother plants under different conditions. Seedling biomass production and P uptake were then investigated using high- and low-P seed of four rice genotypes in a P-rich soil and a P-deficient soil in a pot study in a glasshouse. In the P-rich soil, with a history of P fertilisation, with P fertiliser banded below seeds at sowing at 20 kg P ha^{-1} on a pot surface area basis, seedling biomass and P uptake were significantly affected by genotype ($p < 0.05$) but not by seed P concentration. In the P-deficient Ferralsol, main effects of seed P concentration, genotype and P fertiliser treatment (nil P, banded P fertiliser, broadcast and incorporated P fertiliser) on seedling biomass were all significant ($p < 0.01$) with, a significant genotype × P fertiliser treatment interaction. Overall, low-P seed produced less biomass than high-P seed (0.059 vs. 0.067 g plant^{-1}) and nil P fertiliser (0.057 g plant^{-1}) resulted in less biomass than banded P fertiliser and broadcast P fertiliser (0.064 and 0.068 g plant^{-1}, respectively). When two genotypes were re-grown in the P-deficient Ferralsol with P fertiliser banded under the seed at 20 kg P ha^{-1} there was a significant effect of genotype on shoot biomass ($p < 0.001$) but only a trend towards lower seedling biomass with low P seed compared to high P seed ($p = 0.128$). Overall, the results suggest that seed P concentration does not affect seedling vigour when external soil P fertility is sufficiently high, but in P-deficient soils seedling biomass production and P uptake can be reduced by 10–20%. Further research is required to determine whether agronomic interventions including seed P priming or biological seed dressings can mitigate any impacts of lower seed P concentration on seedling vigour in P-deficient soils.

Keywords: ferralsol; phosphorus deficiency; seed quality

1. Introduction

Early vigour is a desirable trait in field crops to enhance water and nutrient uptake and to provide competitiveness against weeds. As such, there is increased interest in selecting for seedling vigour in breeding programs for major crop species [1,2]. While seedling vigour is in part driven by genetics, it is also affected by the growing environment, and in infertile soils, by the mineral composition of seeds [3]. In particular, it has been suggested that seed phosphorus (P) reserves are critical for rapid root development and nutrient acquisition, with consequences for seedling shoot vigour and crop yields [4].

In natural ecosystems where soil bioavailable P levels are low, the enrichment of seeds with high concentrations of P suggests that higher seed P levels may provide an evolutionary advantage [5]. Studies on the staple cereal crop rice (*Oryza sativa* L.) have also found that the P harvest index (PHI; the proportion of total aboveground P located in the grains) is substantially higher than the respective biomass harvest indices (HI; the proportion of total aboveground biomass located in the grains) across a range of cultivars [6], and that variation in grain P levels among genotypes is driven predominantly by the growing environment with limited genetic contribution [7,8]. These results suggest that seed P loading is a trait that has been highly conserved during the evolution of rice, which in turn supports the idea that higher seed P levels may confer a competitive advantage in natural ecosystems.

In agricultural systems where soil P deficiency is often corrected by the application of P fertilisers or amendments, the necessity of high seed P levels is less clear. Studies on agricultural soils low in bioavailable P have suggested that seedling vigour is reduced in crops grown with low seed P concentrations [9–12]). However, the negative effects became less pronounced in rice seedlings with increasing soil P fertility [11] and, in an Andosol supplemented with P fertiliser, Rose et al. [13] found no negative effect of low seed P concentrations on rice seedling growth. Indeed, soil P status appears to be a major driver of rice seedling vigour and seedling P uptake, regardless of the cultivar grown [14,15]. Hydroponic studies with maize [16] and rice [17] seedlings also suggest that external P supply is the primary driver of P uptake in young plants. As such, it is possible that seed P levels may have no effect on seedling vigour when seeds are sown into fertile soils or soils amended with P fertiliser, owing to the dominant effect of exogenous P supply on vigour.

While a number of studies have reported impaired seedling vigour in agricultural crop species when seed low in P was sown, it has been argued previously that the results of many of these studies need to be interpreted cautiously due to the methods used to generate low-P seed [13,14]. Where low P seeds have been obtained from plants grown in highly P-deficient soils (e.g., [9,18–20]), the low-P seeds were often smaller [18,20] and may have suffered from other issues associated with P-deficiency stress suffered by the mother plants. More recent studies have sourced low- and high-P seeds from growing environments that differ in P status and yield potential, but are not inherently P deficient [13,14,21]. However, it is acknowledged that even in these recent studies the sourcing of seeds from different growing environments could still lead to confounding effects in subsequent seedling vigour studies. In light of this, a hydroponic method was developed to produce rice seeds that differ in seed P concentration where parent plants were grown under near-identical conditions in the glasshouse. Using seeds generated with the hydroponic method, the hypothesis that seed P concentration would have no effect on seedling vigour in fertilised soils with a history of P fertilisation under typical farmer practice of applying P fertiliser at sowing was tested. The hypothesis that seed P concentration would have an effect on seedling vigour in soils low in bioavailable P, but this would be mitigated with the application of P fertiliser at sowing, was also tested.

2. Materials and Methods

2.1. High- and Low-P Seed Material

To avoid issues with low- and high-P seed being obtained from different growing environments, we used a hydroponic method that capitalised on our recent finding that around 70% of total P in rice grains in paddy systems (i.e., flooded soils) comes from P taken up from the soil during grain filling [22]. We therefore grew plants under identical hydroponic conditions until mid-grain filling when yield components (tiller number, panicle length and grains per spikelet) had been established, before increasing the nutrient solution P supply to plants used to produce high-P seed.

An earlier hydroponic study with multiple P dose rates found the biomass and grain yield plateau of cv. IR64 was reached when plants were grown in full strength (minus P) Yoshida nutrient solution [23] in 5 L containers supplemented with a pipetted dose of KH_2PO_4 solution twice per week, equivalent to 0.75 mg P day^{-1} [24]. At higher P dose rates, biomass and grain yields did not increase but grain P concentrations increased.

In the present study, seeds of four rice cultivars—IR64, Kasalath, Dular and Seratus Hari—were germinated and cultivated with a P dose equivalent to 0.75 mg P day^{-1} as per Jeong et al. [24]. Plants were grown in a temperature controlled-glasshouse at Southern Cross University (Lismore, New South Wales, Australia) from January to April 2016, where temperatures in the glasshouse ranged from 16.8–38.8 °C and humidity from 40–98%. For each of the four cultivars, six 5 L containers containing two plants each were randomly positioned across three 1 m × 1.5 m benches. Containers were re-randomised on each occasion that P was pipetted into the nutrient solution.

In flooded soils, rice plants can take up around 70% of their final P content during the grain filling period, with a large proportion of P taken up in this period accumulating in grains between 8–15 days after anthesis [22]. To increase grain P concentrations in half of the plants, three containers of each cultivar received the equivalent of 10 mg P day^{-1} from 8–15 days after anthesis, pipetted into containers daily as KH_2PO_4 solution. Control plants continued to receive two P applications per week equivalent to 0.75 mg P day^{-1}. No new tillers emerged as a result of the introduction of higher P nutrition, but leaves on existing tillers remained a darker green colour than in control plants for the remainder of the growth period.

Grain was harvested from plants at 33 days after anthesis in all cultivars and grain from the three containers of low-P seeds or high-P seeds were pooled for each cultivar before being air-dried in a laboratory at ambient temperature for 1 week to around 14% moisture. A subsample of 100 high-P seeds and 100 low-P seeds of each cultivar were individually weighed to assess seed mass. Mean seed biomass differed by genotype but not P level, hence 300 high- and low-P seeds ± 1 mg of the mean weight for each genotype were then selected for subsequent seedling vigour studies. A subsample of 50 of these seeds was then oven-dried for 5 day at 60 °C and finely ground for determination of seed nutrient concentrations. Nitric acid (2.5 mL) was added to a 0.2 g subsample of ground material for digestion in a MARS Xpress microwave oven (CEM Corporation, Matthews, NC, USA). The volume of the digest was brought up 10 mL using milliQ water, and the concentrations of Mg, Ca, P, K, Zn, Mn, Fe, and Cu in the solutions were quantified using inductively coupled plasma optical emission spectroscopy (ICP-OES 4300D, Perkin Elmer, Waltham, MA, USA). Concentrations of N and S in samples were measured using a LECO TruMAC CNS analyser. Mean seed biomass and P parameters for each cultivar and P level are shown in Table 1.

Table 1. Mean biomass, P concentration and P content of low- and high-phosphorus seeds used in all experiments.

Genotype	Seed P Level	Mean Seed Biomass (mg)	Seed P Concentration (mg g^{-1})	Seed P Content (μg Seed^{-1})
IR64	High	27.5	1.77	48.6
	Low	26.9	1.29	34.8
Dular	High	27.8	1.92	53.4
	Low	28.2	0.98	27.7
Kasalath	High	20.7	1.47	30.5
	Low	21.2	0.82	17.4
Seratus Hari	High	24.9	1.81	45.1
	Low	24.2	1.35	32.6

2.2. *Experiment 1—Effect of Seed P Levels on Seedling Growth in a Soil with High P Fertility*

The soil was collected from the top 0–100 mm layer of a field on a commercial farm near Woodburn, NSW, Australia, where sugarcane (*Saccharum officinarum* L.), soybean (*Glycine max*) and aerobic rice are grown in rotation. The soil was classified as a Gleysol [25] and the field had received regular applications of nitrogen (N) and P fertiliser over the past 30 years. Key chemical properties of the soil were measured at the Environmental Analysis Laboratory, Lismore, NSW, Australia using methods of Rayment and Lyons [26], and are shown in Table 2. After the soil was air-dried and sieved to 2 mm, boxes 0.36 m wide × 0.56 long × 0.26 m high were filled with the soil to within 80 mm of the rim. Nitrogen (as urea), and potassium (K; as muriate of potash), were mixed into the soil at rates of 50 kg N ha^{-1} and 50 kg K ha^{-1} on a pot surface area basis. Phosphorus fertiliser (triple superphosphate) was then banded directly below the seeding line at a rate of 20 kg P ha^{-1} on a pot surface area basis. A further 5 cm layer of soil was then added, and rice seeds were sown to a depth of 20 mm (i.e., 30 mm above the P fertiliser band). Seeds of each genotype were sown in rows of 10, with rows of high- and low-P seeds of the four rice genotypes completely randomised within a box. The three replicate boxes were then placed on benches in the same glasshouse used to produce high and low-P seed (above) in November 2016.

The soil was watered to drainage after sowing then every 3 day for the duration of the experiment. Rice seedlings were harvested at 25 days after sowing (DAS), approximately 20–22 days after emergence depending on genotype, by severing shoots at ground level. Glasshouse temperature ranged from 15.2–38.8 °C and humidity from 32–90%.

Table 2. Selected physiochemical chemical properties of the 0–100 mm layer of the Gleysol (experiment 1) and Ferralsol (experiments 2 and 3).

Property	Gleysol	Ferralsol
Basic texture	clay loam	loam
Total carbon (%)	2.29	3.97
Total nitrogen (%)	0.18	0.32
KCl extractable ammonium (mg kg^{-1})	9.9	20
KCl extractable nitrate (mg kg^{-1})	0.9	47
pH (1:5 water)	5.57	5.04
EC (dS m^{-1})	0.04	0.18
Bray 2 P (mg kg^{-1})	92	32
Cation exchange capacity (cmol^{+} kg^{-1})	27.34	5.57
Base cations (cmol^{+} kg^{-1})		
Calcium	14.8	4.13
Magnesium	10.1	0.43
Potassium	0.63	0.39
Sodium	0.37	0.22
Aluminium	0.88	0.28

2.3. Experiment 2—Effect of Seed P Levels and P Fertiliser on Seedling Growth in a Soil with Low P Fertility

The soil was collected from the top 0–100 mm layer of a field at Wollongbar Primary Industries Institute, Wollongbar, New South Wales, Australia. The soil is highly P-fixing Ferralsol [25] and cereal growth is significantly reduced in the absence of P fertiliser [27]. Selected physiochemical properties of the 0–100 mm layer of the soil are shown in Table 2.

After the soil was air-dried and sieved to 2 mm, the soil was added to within 80 mm of the rim the same boxes, with the same additions of N and K fertiliser, as experiment 1. In one treatment (banded P), triple superphosphate was banded below seeds as per experiment 1 at 20 kg P ha^{-1} on a pot surface area basis. In a second treatment (broadcast and incorporated P), triple superphosphate was mixed at 20 kg P ha^{-1} into the top 50 mm layer of soil which was then placed above the existing soil. The third P fertiliser treatment was a nil-P control where the top 50 mm layer of soil was added on top of the existing soil with no addition of P fertiliser. Seeds of each genotype × seed P level combination were then sown in rows of 10 as per experiment 1 (i.e., four genotypes × two seed P levels randomised within a box). The 12 boxes (three fertiliser treatments x four replicate boxes) were laid out in a completely randomised design in the glasshouse in January 2017.

The soil was watered to drainage immediately after sowing then every 3 day for the duration of the experiment. Rice seedlings were harvested at 25 DAS as per experiment 1. Glasshouse temperature over the duration of the experiment ranged from 20.3–39.7 °C and humidity ranged from 45–96%.

2.4. Experiment 3—Reconfirmation of Results from Experiment 2

Given that the results of experiment 2 were contrary to our expectations (i.e., the addition of P fertiliser did not overcome the effects of low seed P content), we sought to confirm the results in a subsequent experiment with a greater number of seedlings per row and in slightly cooler conditions in early autumn. The same Ferralsol used in experiment 2 was added to the same boxes. In April 2017 high- and low-P seeds of genotypes Kasalath and Dular were sown 10 mm deep in lines of 15 seeds (2 genotypes × 2 seed P levels randomised within as box) above a P fertiliser band, as described in experiment 2.

The soil was watered to drainage after sowing then every 3 day until 25 DAS, when rice seedlings were harvested as per earlier experiments. Glasshouse temperature over the duration of the experiment ranged from 16.7–30.5 °C and humidity ranged from 49–97%.

2.5. Shoot Biomass and P Concentration Measurements

All shoot material was oven-dried for 5 day at 60 °C and weighed. The dried material was then finely ground and a 0.2 g subsample digested with nitric acid and P concentration in digestate quantified by ICP-OES as described above. The P content of shoots was calculated by multiplying the biomass by the respective P concentration. All rice shoot biomass and P content data were expressed on a per plant (seedling) basis.

2.6. Statistical Analyses

Shoot biomass and P content data from experiment 1, and shoot biomass data in experiment 3, were subject to a 2-way ANOVA fitting genotype, seed P level (high or low) and their interaction as factors, while in experiment 2 data were subject to a 3-way ANOVA fitting genotype, seed P level and P fertiliser treatment and their interactions as factors. Significance of genotype differences in biomass and P uptake was tested using Duncan's multiple range test.

3. Results

3.1. Experiment 1

There was a significant effect of genotype on seedling biomass and P content (IR64 > Dular > Kasalath = Seratus Hari), but no effect of seed P or any genotype × seed P interaction (Table 3). The magnitude of differences between genotypes was greater for shoot P content, where IR64 (0.234 mg plant^{-1}) had more than double the shoot P content of both Kasalath (0.092 mg plant^{-1}) and Seratus Hari (0.101 mg plant^{-1}).

Table 3. ANOVA results for shoot biomass and shoot P content in Experiment 1 (Gleysol). Treatments that share a common letter within a column in the main effect of "genotype" are not significantly different at $p \leq 0.05$.

Effect	Shoot Biomass	Shoot P Content
	p-value	
Genotype (G)	<0.001	<0.001
Seed P (SP)	0.491	0.351
G × SP	0.599	0.254
Genotype	g plant^{-1}	mg plant^{-1}
Dular	0.067 b	0.168 b
IR64	0.087 c	0.234 c
Kasalath	0.057 a	0.092 a
Seratus Hari	0.051 a	0.101 a

3.2. Experiment 2

Seedling biomass was significantly affected ($p \leq 0.05$) by the main effects of genotype, seed P level and P fertiliser treatment, while shoot P content was significantly affected by genotype and P fertiliser treatment (Table 4). Overall, low-P seed produced less biomass than high-P seed (0.059 vs. 0.067 g plant^{-1}), genotypes IR64 and Kasalath (both 0.068 g plant^{-1}) produced more biomass than Seratus Hari and Dular (0.056 and 0.059 g plant^{-1}, respectively) and nil P fertiliser (0.057 g plant^{-1}) produced less biomass than banded P fertiliser and broadcast P fertiliser (0.064 and 0.068 g plant^{-1}, respectively).

Shoot P content was in the order of IR64 > Seratus Hari > Dular = Kasalath, while broadcast P resulted in significantly higher shoot P content (0.235 mg plant^{-1}) than nil P (0.174 mg plant^{-1}) and banded P fertiliser (0.193 mg plant^{-1}) (Table 4).

There was also a significant interaction for genotype × P fertiliser treatment, but none of the interactions with seed P level were significant (Table 4). There was no significant difference between genotypes for shoot biomass under the nil P fertiliser treatment but significant effects were observed between genotypes when P fertiliser was applied either as a band or broadcast and incorporated (Figure 1). Shoot P content was higher in Seratus Hari than Kasalath or Dular in the nil P treatment but was similar in the banded P treatment. In contrast, IR64 had significantly higher shoot P content than all other genotypes for the banded P treatment (Figure 1). IR64 also had significantly higher shoot P content than all other genotypes under the broadcast P treatment.

Table 4. ANOVA results for shoot biomass and shoot P content in Experiment 2 (Ferralsol). Treatments that share a common letter within a column in the main effect of "seed P" are not significantly different at $p \leq 0.05$.

Effect	Shoot Biomass	Shoot P Content
		p value
Genotype (G)	0.002	<0.001
Fertiliser P (FP)	0.003	<0.001
Seed P (SP)	0.003	0.056
G × FP	0.050	0.031
G × SP	0.673	0.849
FP × SP	0.504	0.512
FP × SP × G	0.916	0.613
	g plant^{-1}	mg plant^{-1}
Genotype		
Seratus Hari	0.056 a	0.213 b
Dular	0.059 a	0.169 a
IR64	0.068 b	0.242 c
Kasalath	0.068 b	0.179 a
Seed P		
Low P seed	0.059 a	0.192 *
High P seed	0.067 b	0.210
Fertiliser P		
Nil P	0.057 a	0.174 a
Banded P	0.064 b	0.193 a
Broadcast P	0.068 b	0.235 b

* means should not technically be compared as *p* value was 0.056.

3.3. Experiment 3

There was a significant effect of genotype on shoot biomass ($p < 0.001$) where shoot biomass in Dular (mean of 0.103 g plant^{-1}) was higher than Kasalath (mean of 0.059 g plant^{-1}). There was no significant effect of seed P level ($p = 0.128$) or genotype × seed P interaction ($p = 0.520$) on shoot biomass at 25 DAS.

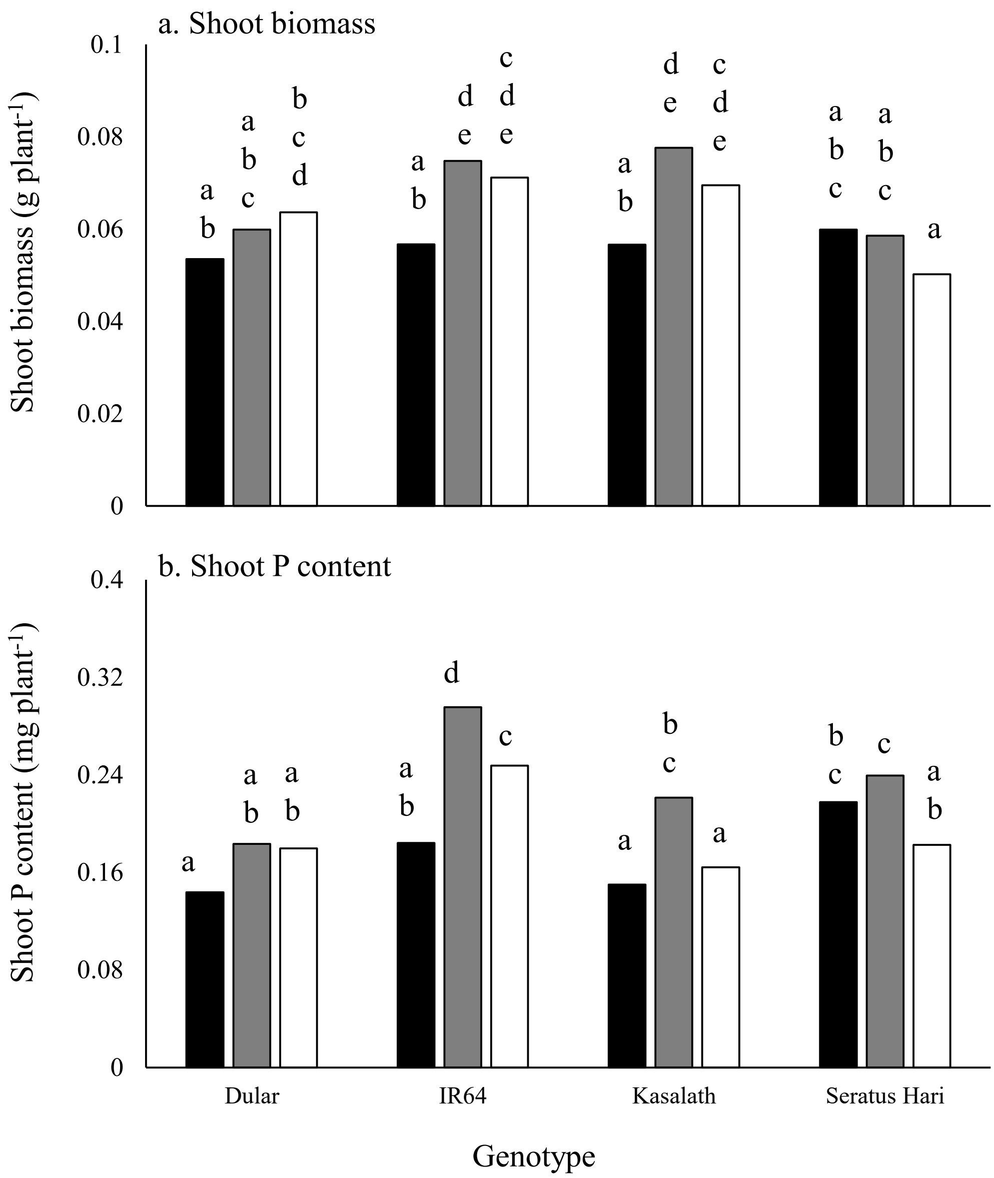

Figure 1. Effect of genotype and phosphorus fertiliser treatment on (**a**) shoot biomass and (**b**) shoot P content of 25-day-old rice seedlings grown in a high-phosphorus-fixing Ferralsol. Black bars represent nil P fertiliser, grey bars represent broadcast phosphorus fertiliser and white bars represent banded phosphorus fertiliser. Bars that do not share a common letter are significantly different at $p \leq 0.05$.

4. Discussion

While a number of papers have examined vigour of seedlings produced from seeds differing in P concentration (see [13] and references therein), the seeds are typically obtained from plants grown under different levels of P stress (e.g., [9,18,20]) or from plants grown in vastly different environments (e.g., [14]). The results of these studies may therefore be influenced by seed quality attributes other than P concentration. In the present study, low-P and high-P seeds were obtained from plants grown under near-identical conditions, where the only difference was higher P supply in the nutrient solution in one set of plants from 8–15 days after anthesis. Having minimised potential differences in seed quality attributes due to different growing environments or stress levels suffered by mother plants, we suggest any difference in seedling performance between plants grown from low-P and high-P seeds is most likely due to differences in seed P concentration.

In direct-seeded rice systems in developed nations, where P fertilisers are readily available, P fertiliser is typically applied at sowing in a band near the seed [28,29]. Data from experiment 1 suggest that in these systems, which have relatively fertile soils owing to a history of P fertilisation, seed P levels appear to have little effect on rice seedling biomass or P accumulation at 25 days after sowing in the typical scenario where P fertiliser is banded near the seed. This is consistent with reports in both maize [16] and rice [17] where external P concentration appears to be the key driver of early seedling vigour rather than the inherent seed P levels.

However, many rice-growing soils across the globe suffer from P-deficiency owing to a lack of total P in the soil or a lack of bioavailable P [30], and many of these soils are "upland" rice soils where the crop is direct-seeded. In the low-P Ferralsol in experiment 2, it is unsurprising that biomass and P uptake were lower with low seed P levels where no P fertiliser was applied because exogenous P levels (i.e., levels of bioavailable P in the soil) were low, and would thus be unable to compensate for lower levels of P in seeds. However, seedling growth and P uptake were affected by seed P level even when 20 kg P ha^{-1} was applied. It is also worth noting that Ferralsols have the highest P fixing capacities of any Australian soils [31]), and the 20 kg P ha^{-1} applied may simply have been insufficient to provide enough exogenous P to seedlings to overcome the lower levels of P in the seeds. Further, the greater seedling biomass and P uptake in the Ferralsol in experiment 2 where P fertiliser was broadcast and incorporated compared to when P fertiliser was banded under the seed was unexpected. On high P-fixing soils, fertiliser P availability is typically greatest with minimum mixing with the soil, where high P concentrations in the fertiliser band can saturate soil P sorption sites to render some P bioavailable [32]. One possibility is that any improvements in P availability in the band were negated by the small volume of soil that was fertilised, with the developing fibrous rice root system unable to exploit the localised P source.

Ultimately, the results concur with those of Bolland and Baker [9], where the application of P fertiliser to a highly P deficient soil (total P of 58 mg kg^{-1}) could not mitigate the effects of low seed P on seedling vigour. Field studies with rice also indicated that P fertiliser could not always overcome the impact of low seed P levels on seedling vigour, but any potential for P fertiliser to mitigate the effects depended on genotype [14]. In the present study, genotype had a significant effect on seedling vigour in all experiments, but there was no interaction with seed P levels in any experiment. Interestingly, when genotypes Dular and Kasalath were trialled in experiment 3 in autumn in the same Ferralsol, seed P levels did not have a significant impact on seedling biomass, although there was a trend towards lower biomass with low P seeds ($p = 0.128$). Notably, in experiment 2 Kasalath produced more biomass than Dular in the banded P fertiliser treatment (Figure 1), yet under the same Ferralsol and P banding regime in experiment 3 in Autumn with reduced day length and lower temperatures, Dular produced significantly more biomass than Kasalath (0.103 vs. 0.059 g plant^{-1}). The differences in the results observed between the experiments highlight the confounding effects of genotype × environment interactions on results, but are consistent with other studies where low P seeds can, but do not always, lead to a reduction in seedling vigour in P-deficient soils [14].

5. Conclusions

Low seed P levels appear to have a limited impact on seedling vigour in soils with adequate P fertility when P fertiliser is applied at sowing, and as such, breeding a low grain P trait may be beneficial in developed countries where the use of P fertiliser is commonplace. Many developing nations in the tropics have negative P budgets [33], and would therefore benefit from a low grain P trait to reduce the export of P from fields at harvest. Further, micronutrient deficiencies in humans can also occur in these regions, and a reduction in rice grain P, and therefore the antinutrient phytate [34], may benefit human nutrition in these regions. However, owing to the negative P budgets many of these same regions have P-deficient soils [30], and thus direct sowing of low P seed may increase the risk of poor seedling vigour. Further work is needed to investigate whether agronomic interventions such as seed P priming or other biological seed dressings can mitigate any impacts of lower seed P levels on seedling vigour in P-deficient soils.

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