Combining seed dressing and foliar applications of phosphorus fertiliser can give similar crop growth and yield benefits to soil applications together with greater recovery rates

Davey L. Jones[1, 2*], Peter J. Talboys[3], John R. Healey[4], Paul J. Withers[5], Tiina Roose[6], Anthony C. Edwards[7], Paulo S. Pavinato[8]

[1]School of Natural Sciences, Bangor University, United Kingdom, [2]School of Agriculture and Environment, Faculty of Science, University of Western Australia, Australia, [3]Bangor University, United Kingdom, [4]Bangor University, School of Natural Sciences, United Kingdom, [5]Lancaster Environment Centre, Lancaster University, United Kingdom, [6]University of Southampton, United Kingdom, [7]Scotland's Rural College, United Kingdom, [8]University of São Paulo, Brazil

Submitted to Journal:
Frontiers in Agronomy

Specialty Section:
Plant-Soil Interactions

Article type:
Original Research Article

Manuscript ID:
605655

Received on:
12 Sep 2020

Revised on:
14 Nov 2020

Frontiers website link:
www.frontiersin.org

Conflict of interest statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest

Author contribution statement

PJT, JRH, PJAW and DLJ designed the research. PJT conducted the research. PJT and DLJ collected and analysed the data. PJT wrote the first draft of the manuscript. All authors contributed to the final version of the manuscript. The seed treatment was potassium phosphate, the soil treatments were granules of TSP (triple super phosphate) and DAP (diammonium phosphate).

Keywords

crop nutrition, Foliar feeding, Food security, Integrated nutrient management, precision agriculture, fertiliser management, Phosphorus use efficiency (PUE)

Abstract

Word count: 216

Phosphorus (P) fertilisers have a dramatic effect on agricultural productivity, but conventional methods of application result in only limited recovery of the applied P. Given the increasing volatility in rock phosphate prices, more efficient strategies for P fertiliser use would be of economic and environmental benefit in the drive for sustainable intensification. This study used a combination of controlled-environment experiments and radioisotopic labelling to investigate the fertiliser use efficiency of a combination of seed (grain) dressing and foliar applications of P to spring wheat (Triticum aestivum L.). Radioisotopic labelling showed that the application of foliar P in the presence of photosynthetic light substantially increased both P-uptake into the leaf and P-mobilisation within the plant, especially when an adjuvant was used. When compared with soil application of inorganic P buried into the rooting zone, a combination of 3 µmol seed dressings and three 46.3 µmol plant-1 foliar applications were far more efficient at providing P fertilisation benefits in P-limiting conditions. We conclude that a combination of seed dressing and foliar applications of P is potentially a better alternative to conventional soil-based application, offering greater efficiency in use of applied P both in terms of P-uptake rate and grain yield. Further work is required to evaluate whether these results can be obtained under a range of field conditions.

Contribution to the field

The primary aim of this study was to evaluate whether P-fertiliser recovery and crop yield could be improved by replacing conventional soil-fertiliser use with a combined fertilization strategy that uses early and later growth stage P application, with minimum fertiliser contact with the soil: a combination of seed dressing and foliar application. Our second aim was to investigate the optimal timing and dose of seed dressing and foliar applications to maximise its contribution to plant P uptake. The combination of approaches is the novel angle of this manuscript.

Funding statement

The authors would like to thank the UK Department for Environment, Food and Rural Affairs, Biotechnology and Biological Sciences Research Council and Scottish Government for funding this work as a component of the Sustainable Arable LINK project (LK09136).

Ethics statements

Studies involving animal subjects

Generated Statement: No animal studies are presented in this manuscript.

Studies involving human subjects

Generated Statement: No human studies are presented in this manuscript.

Inclusion of identifiable human data

Generated Statement: No potentially identifiable human images or data is presented in this study.

Data availability statement

Generated Statement: The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Combining seed dressing and foliar applications of phosphorus fertiliser can give similar crop growth and yield benefits to soil applications together with greater recovery rates

Peter J. Talboys[1], John R. Healey[1], Paul J.A. Withers[1,2], Tiina Roose[3], Anthony C. Edwards[4], Paulo S. Pavinato[5] and Davey L. Jones[1,6]*

[1]School of Natural Sciences, Deiniol Road, Bangor, Gwynedd, LL57 2UW, UK, [2]Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK, [3]Faculty of Engineering and Environment, University of Southampton, University Road, Southampton, SO17 1BJ, UK, [4]Crop & Soil Systems, SRUC Aberdeen Campus, Craibstone Estate, Aberdeen, AB21 9YA, UK, [5]College of Agriculture Luiz de Queiroz-ESALQ-USP, Av. Pádua Dias, 11, Piracicaba-SP 13418-900, Brazil, [6]UWA School of Agriculture and Environment, University of Western Australia, Crawley, WA 6009, Australia

[*]Correspondence: Davey Jones. *d.jones@bangor.ac.uk*

Keywords: Crop nutrition, Foliar feeding, Food security, Integrated nutrient management, Precision agriculture, Phosphorus use efficiency

Abstract. Phosphorus (P) fertilisers have a dramatic effect on agricultural productivity, but conventional methods of application result in only limited recovery of the applied P. Given the increasing volatility in rock phosphate prices, more efficient strategies for P fertiliser use would be of economic and environmental benefit in the drive for sustainable intensification. This study used a combination of controlled-environment experiments and radioisotopic labelling to investigate the fertiliser use efficiency of a combination of seed (grain) dressing and foliar applications of P to spring wheat (*Triticum aestivum* L.). Radioisotopic labelling showed that the application of foliar P in the presence of photosynthetic light substantially increased both P-uptake into the leaf and P-mobilisation within the plant, especially when an adjuvant was used. When compared with soil application of inorganic P buried into the rooting zone, a combination of a 3 µmol seed dressing and three successive 46.3 µmol plant^{-1} foliar applications were far more efficient at providing P fertilisation benefits in P-limiting conditions. We conclude that a combination of seed dressing and foliar applications of P is potentially a better alternative to conventional soil-based application, offering greater efficiency in use of applied P both in terms of P-uptake rate and grain yield. Further work is required to evaluate whether these results can be obtained under a range of field conditions.

Introduction

Due to its low mobility in soil phosphorus (P) availability to plants is often limited, with corresponding constraints upon growth and yield. Low P availability can also negatively affect root growth (Drew, 1975; Li et al., 2020), with concurrent consequences for the acquisition of water and other nutrients (Takahashi and Anwar, 2007). Agriculture has compensated for this by applying high quantities of soluble inorganic P fertilisers, which has produced a significant positive effect on agricultural productivity, but often results in a negative effect on environmental quality (Zhang et al., 2015; Withers et al., 2020). This is particularly prevalent in wheat production systems where over fertilisation of the soil leads to excessive P losses to surface and groundwater via surface run-off and leaching (Dodd and Sharpley, 2015). Strategies are therefore needed to use P fertiliser more efficiently in wheat cropping systems and to retain P in the soil after removal of the crop, for example, through the use of cover crops and residue management (Liu et al., 2019).

Conventional P-fertiliser strategies aim to maintain high levels of plant-available P in soil, ensuring that P does not become limiting during crop growth and development (Tunney et al., 1997; Moody 2007; Valkama et al., 2011). This entails the application of the entire predicted plant P-offtake in a single dose before sowing to ensure that the soil P content is maintained above critical levels during all stages of crop growth (Syers et al., 2008). However, due in part to the ability of crop plants to acquire native and residual soil P, less than half of the applied fertiliser P is typically acquired by the current season's crop (Wang et al., 2016). The remainder is either immobilised in the soil (Stutter et al., 2012) or lost to the environment through leaching or run-off (Withers et al., 2001a, 2014). Whilst rock P prices remained low this inefficiency was not a significant issue for agriculture, however, with rock P prices both increasing and becoming far more volatile in recent years, this current approach to P fertiliser use appears to be unsustainable (Lyon et al., 2020). An alternative strategy of targeted P-fertilisation has been proposed, whereby smaller quantities of P are applied with greater precision to meet crop demand (Simpson et al., 2011; Withers et al., 2014). Maximising the recovery of residual or legacy soil P also helps to reduce the losses both to the soil and watercourses, thus improving the financial efficiency of the process, while reducing the risk of pollution.

One method of P fertilisation that has exhibited potentially large gains in recovery of applied P within the crop over conventional soil fertilisation is direct application to the leaf (Silberstein and Wittwer, 1951; Bindranan et al., 2020). The temporal flexibility of foliar P application relative to incorporating or placing P in the soil at the time of sowing offers the potential for P to be more accurately matched to the plant's increasing demand for P later in the growing season (Sutton et al., 1983; Allison et al., 2002). The benefits of foliar feeding, however, remain controversial, especially in terms of its impact on final grain yield (McBeath et al., 2020).

Foliar applied P is proposed to enter the leaf through direct stomatal penetration and through cuticular pores, although opinion differs as to their relative contributions (Noack et al., 2010). Stomatal entry requires that plant water status and atmospheric conditions maintain stomatal opening, but potentially promoted rapid P uptake. Movement though cuticular pores is a more complex process, with aqueous pores of less than 1 nm diameter formed around trichomes and cuticular ledges allowing the limited exchange of water and dissolved salts the environment (Schönherr, 2006). This process is far slower than stomatal penetration (Schönherr, 2006; Xie et al., 2020). The formulation of the foliar P product (especially pH, counter-ion, and adjuvant content) also has a major effect on its rate of uptake into the plant. Low solution pH increases the potential uptake rate achievable by reducing ionisation of the orthophosphate molecule (pKa_1 2.12; pKa_2 7.21; pKa_3 12.67), thus increasing its capacity to penetrate the leaf (Bouma, 1969). The identity of the cation used as the counter-ion to the P form has been suggested to affect the P uptake potential by altering the ability of the formulation to retain moisture (Koontz and Biddulph, 1957). Increasing the amount of time that the P is in solution on the leaf surface has been considered key to improving the rate of P uptake by changes in formulation of foliar P fertilisers (Koontz and Biddulph, 1957; Fernández and Brown, 2013). The major strategy for this has been the use of different types of adjuvants to increase the spread of droplets and increase retention of moisture; they may also have the benefit of increasing the permeability of the cuticle to P (Holloway, 1994). While these adjuvants have been shown to greatly increase foliar uptake of P, their phytotoxicity in high concentrations means care is required for their optimal use (Stein and Storey, 1986; Appah et al., 2020).

Having entered the leaf, foliar applied P is mobile throughout the plant, albeit to a lesser extent than that taken up by roots (Bastani and Hajiboland, 2017). Typically 30-40 % translocated from the leaf to which it was applied (Barrier and Loomis, 1957; Koontz and

Biddulph, 1957). Of particular importance is the translocation of foliar applied P to the meristematic tissues in both shoots and roots where high levels of nutrient consumption are essential for continued growth and development of the plant (Gordon-Weeks et al., 2003).

One difficulty in applying sufficient foliar P to satisfy plant demand is that all crop species are limited in the amount that can be applied in a single dose without scorching the leaf. This can reduce the plant's photosynthetic capacity and has particularly serious consequences in early growth stages (Gray, 1977; Barel and Black, 1979ab; Noack et al., 2010). Winter wheat grown without any soil P-fertiliser has been shown to have optimum foliar dose rates of 2 kg ha^{-1} P at GS32 (stem elongation), and 4 kg ha^{-1} P at GS39 (flag leaf emerged), with foliar fertilisation above these rates found to cause crop yield to decline to untreated control levels (Mosali et al., 2006). The benefit of repeated foliar applications of small amounts of P has also been demonstrated in other crops (Sohair et al., 2018).

Another major reason for past reluctance to use foliar P as a replacement for soil-applied P has been its failure, at the dosages used, to supply sufficient P at early growth stages to maximise a crop's yield potential. Such early supply of P to a crop has been shown to be essential to maximise both early growth and final yield (Grant et al., 2001). This negative effect can be compounded by low surface cover of the crop during early growth leading to a large proportion of applied foliar P falling straight onto the soil surface (Noack et al., 2010).

An approach to P that specifically addresses the need to supply P for early growth is the application of small quantities of P to the seed (grain) surface prior to sowing. This P is released very close to the developing root system, thus maximising the capture of the applied P by the plant. However, the seed surface can only be coated with limited quantities of P, meaning that such treatments have not always been shown to be beneficial to final yields (Peske et al., 2009; Valluru et al., 2010). Greater success has been found by combining seed treatment with other, more substantial P application methods (e.g. conventional soil-based P fertilisation). The application to the seed surface disproportionately reduces the plant's requirement for additional P-fertiliser and so significantly improves the overall efficiency of use (Sekiya and Yano, 2009).

The primary aim of this study was to evaluate whether P-fertiliser recovery and crop yield could be improved by replacing conventional soil-fertiliser use with a combined fertilization strategy that uses early and later growth stage P application, with minimum fertiliser contact with the soil: a combination of seed dressing and foliar application. Our second aim was to investigate the optimal timing and dose of seed dressing and foliar applications to maximise its contribution to plant P uptake.

MATERIALS AND METHODS

Seed Dressing of P Fertiliser

For the seed dressing trial, wheat (*Triticum aestivum* L., cv. Paragon; bread wheat) was grown in 8 cm diameter opaque pots filled with 300 g of sandy loam textured soil (Eutric Cambisol; FAO, 2015). The pots had aeration holes in the base. The soil was collected from the Henfaes Experimental Station, Abergwyngregyn, UK (53°14′21.3″N, 4°0′50.3″W; 10 m above sea level), and had a 0.5 M $NaHCO_3$ (pH 8.5) extractable P concentration (Olsen P) of 10 mg l^{-1} (Olsen et al., 1954). This is a potentially limiting level of plant available P in the soil according to the current UK soil assessment system for arable crops (Index 1 classification; AHDB, 2019). The same soil and wheat variety was used for all trials. Further details of the soil chemical, biological and physical properties can be found in Sánchez-Rodríguez et al. (2018). Seed dressings were applied to the seed coat using a micro-pipette and then air dried at 20°C for 2 h before planting. For this experiment, seeds were dressed with varying quantities (1, 2, 3, or 4 µmol P $seed^{-1}$; 31-62 µg P $seed^{-1}$) of a commercial potassium phosphate seed dressing solution (OMEX Agriculture Ltd., Lincoln, UK). In total 1.6 µl was added to the surface of each seed. The amount of K in each treatment was kept constant by adding the corresponding amount of KCl (for each K-PO_4 dose) so that each seed received 4.6 µmol K in total. Based on sowing density of 350 seeds m^{-2} (HGCA, 2000), this equates to a P application dose of 0.43 kg P ha^{-1}. For the positive controls, the readily soluble P-fertilisers diammonium phosphate (DAP) or triple super phosphate (TSP) were applied at 885 µmol P per pot based on 35 kg P ha^{-1} equivalent as per UK government recommendations for this soil (AHDB, 2019). The dose was scaled down to a 10 cm diameter circle to ensure standardisation of fertiliser input per plant with the other experiments where the pot diameter was different (see below). This fertiliser was placed in the soil at 3 cm below the depth of the planted seeds, and offset from the seed laterally by 1 cm. Three seeds were planted in each pot at 1 cm depth, and at emergence two seedlings were removed to leave only the largest seedling per pot. The pots were kept in a climate-controlled glasshouse with artificial lighting (light intensity = 260 µmol m^{-2} s^{-1} PAR) set to 20°C and minimum 16 h day length. Soil water holding capacity was measured according to the saturation-drainage method of Verheijen et al. (2019). The pots were placed in a completely randomised design ($n = 4$) and maintained at 80% of their water holding capacity by weighing the pots three times a week (Mon, Wed, Fri), measuring the weight loss due to evaporation and transpiration and then replacing the water lost. To ensure that P was the only limiting macronutrient, the equivalent of 60 kg ha^{-1} N (as NH_4NO_3) and 60 kg ha^{-1} K_2O (as KCl) were applied in solution form to each pot at seedling emergence. Other nutrients were controlled by the weekly application of 10 ml of a modified Hoagland's nutrient solution containing: 5 mM Ca; 3.87 mM Fe; 3.87 µM Na; 765 µM Zn; 2 mM SO_4; 320 nM Cu; 46.3 nM B; 500 µM Mo; 9.1 nM Mn; 18 µM Cl; 38.7 µM EDTA (Talboys et al., 2014). At 25 d after planting, the whole plant was extracted from the pot, and the root systems washed free from soil using a stainless steel mesh and a stream of deionised-water (Paudel et al., 2018). The soil-free root systems were then floated in water-filled transparent plastic trays, and scanned using a flatbed scanner

(Perfection 4990 Photo; Epson Electronics America Inc., San Jose, CA, USA). The resulting image was processed using WinRhizo® software (Regent Instruments Inc., Chemin Ste-Foy, Quebec, Canada) to determine the length of seminal and lateral root for each plant. The boundary conditions used by the software were that roots ≥0.350 mm in diameter were classified as seminal roots, and < 0.350 mm were classed as lateral roots (Heppell et al., 2014). The plants were then dried at 85°C overnight, weighed, and dry-ashed (550°C, 16 h). The residue was dissolved in 0.5 M HCl and then their P content determined using the ascorbate / molybdate blue method of Murphy and Riley (1962).

Foliar Application of Radioisotopically Labelled P Fertiliser

Wheat seedlings were grown in the same growth conditions as described above, but with no seed dressing. The pots were placed in a completely randomised design (n = 5). Once they had three leaves (GS13) they were laid horizontally with one leaf lightly affixed to a clean bench surface using electrical tape. A 16 mm^2 square was then marked out using petroleum jelly on either the underside or the top leaf surface. 3 μl of a commercial ammonium phosphate foliar fertiliser (6.62 M P; OMEX Agriculture Ltd.) labelled with 22.2 MBq ml^{-1} ^{33}P (American Radiolabeled Chemicals Inc., St Louis, MO, USA) was then applied to the leaf surface, either mixed with 0.1% (v/v) of the adjuvant IA-500 (Interagro Ltd., Braintree, UK) or without, and left for 16 h with artificial illumination (light intensity = 260 μmol m^{-2} s^{-1} PAR representative of a cloudy day in the UK summer). Experiments to assess the effect of daylight were conducted in the same manner, but all treatments had 0.1% (v/v) IA-500 and dark treatments were covered to eliminate the presence of light and the level of replication was n = 3. After 16 h, the seedlings were dried at 80°C and the ^{33}P distribution in the plant imaged using a Cyclone Plus phosphor imaging system (Perkin-Elmer Inc., Waltham, MA, USA) with an exposure time of 15 min. The dried plants were then dry-ashed (550°C, 16 h), the residue dissolved in 0.5 M

HCl and the ^{33}P content of the resulting solution quantified using a Wallac 1404 scintillation counter (Perkin-Elmer Inc.).

Effects of Seed and Foliar P Fertilisation of Plants Grown to Maturity

For an experiment in which wheat plants were grown to mature grain harvest, seeds were planted in either 11 cm diameter, 30 cm deep pots containing 3 kg of sandy loam textured soil (as described previously but with an Olsen P value of 29 mg l^{-1}; national Index 3; AHDB, 2019), or in 10 cm diameter pots, 8.5 cm deep pots containing 500 g of the original sandy loam soil (Olsen P 10 mg l^{-1}; national Index 1; AHDB, 2019). Based on the Olsen P values and national guidelines (AHDB, 2019), these two experiments provided both extreme P limiting (500 g pots) and P-sufficient (3 kg pots) environmental conditions. For the seed dressing treatment, potassium phosphate (3.0 µmol P seed^{-1}; OMEX Agriculture Ltd.) was applied to the seed coat as described above. In all other treatments, the seeds received KCl so that the addition of K was the same (3.45 µmol K seed^{-1}) for both the P-treated and P-untreated seeds. For the positive controls, diammonium phosphate (DAP) or triple super phosphate (TSP) was applied at 885 µmol P per pot at a rate equivalent to 35 kg P ha^{-1}. The fertiliser addition and plant growth conditions are as described in Section 2.1. To ensure that P was the only limiting macronutrient, the equivalent of 60 kg ha^{-1} N (as NH_4NO_3) and 100 kg ha^{-1} K_2O (as KCl) was applied in liquid form to each pot at seedling emergence, with another 60 kg ha^{-1} N applied at the stem extension growth stage (GS30). Micronutrients were controlled by the weekly application of 10 ml of Hoagland's solution as used in the seed dressing experiments detailed above. The pots were placed in a completely randomised design (n = 4) and maintained on a self-watering bench with capillary matting to ensure that soil moisture was never limiting.

Foliar applications were performed at Zadoks growth stages GS13 (three leaf), GS31 (stem extension) and GS39 (flag leaf) (Zadoks et al., 1974). These applications were pipetted onto the leaves of each plant using a micro-pipette, and manually spread such that they covered as much leaf as possible. A spray was not used so that we could be certain that all the applied P dose remained on the surface of the leaves. Equal quantities were applied to the top and bottom of the leaf, and applications were conducted in the morning so that there was a minimum of 8 h of photosynthetic light directly afterwards to maximise initial uptake rates. Treatments were either the ammonium phosphate solution described above (OMEX Agriculture Ltd.) for the P treatments or an NH_4Cl solution control for all other plants to ensure equal application of foliar NH_4^+, both mixed with 0.1% (v/v) of the adjuvant IA-500 (Interagro Ltd.). Each dose consisted of 70 µmol N plant^{-1} and for the P treatments 46.3 µmol P plant^{-1} with the amount applied following commercial recommendations (Omex, 2020). Based on a final field establishment of 275 plants m^{-2} (HGCA, 2000), this equates to a P dose of 4 kg P ha^{-1}. Once the grains had hardened, they were judged mature, and the entire aerial portion of each plant was harvested and the grain removed. The fresh weight of the grain yield and total biomass were then determined before drying at 85°C overnight. The dried tissue was then re-weighed, dry-ashed (550°C, 16 h), the residue dissolved in 0.5 M HCl and then their P content determined using the ascorbate / molybdate blue method of Murphy and Riley (1962). In the results section all masses are quoted as dry weight.

Statistical Analysis

P recovery (% of P applied) was calculated as plant P content of the treated plants minus the average P content of the control (zero P) plants, divided by the amount of fertiliser P applied. All the growth and fertiliser experiments had a completely randomised design and replicated at $n = 3$ or greater. Statistical testing was performed using Student's unpaired t-test in Microsoft Excel (Microsoft Corp., Redwood City, CA) or by one-way or two-way ANOVA with Tukey post-hoc pairwise comparisons using Minitab v17 (Minitab Inc., State College, PA). $p < 0.05$ was used as the cut-off value for statistical significance.

RESULTS

Seed Dressing with P is an Efficient Way to Promote Early Growth and Uptake

Seed dressing with 2, 3 or 4 µmol P per seed showed significant benefits in total P uptake by 25 d (of 59-108%) over control plants that had received no P addition (Fig. 1A). For the 3 and 4 µmol P dosages there was no significant difference in P uptake compared with plants grown in soil to which 885 µmol P (35 kg P ha^{-1}) had been added in the form of TSP or DAP. Seed dressing at rates of 1, 3 and 4 µmol P seed^{-1} also produced significantly greater total lateral root length (by 52 - 79 %) over no-P controls, although data for 2 µmol P dosages were not significant (Fig. 1B). All four seed treatment doses produced lateral root lengths that did not differ significantly from the soil DAP/TSP treatments (they ranged from 14 % to 28 % lower than the average of the TSP and DSP treatments). For seminal root lengths, only the soil DAP / TSP treatments produced significant increases over the controls. As a consequence of the much lower P doses per plant applied in the seed dressings than the soil application treatments, the rate of recovery of applied P was much greater in the seed coat treatments; it did not show a linear response with dose: 90% for 1 µmol, 207 % for 2 µmol, 252 % for 3 µmol and 185% for 4 µmol (compared with 1.23 % for TSP and 1.16 % for DAP). These recovery rates suggest considerable soil immobilisation of fertiliser P in the TSP and DAP treatments.

Foliar P Entry is Enhanced by Adjuvant and Photosynthetic Activity

The amendment of the foliar P solution with the adjuvant IA-500 resulted in a significant increase in the rate at which P was capable of entering the plant through the top surface of the leaf for plants grown for 16 h in the light (Fig. 2). There was, however, no significant difference in the entry rate of P applied to the leaf underside when using IA-500 compared to when it was absent. Grain yield in t ha^{-1} was estimated by scaling up the pots to the field scale according to HGCA (2000).

Illumination of seedlings with 260 µmol m^{-2} s^{-1} PAR for 16 h, following application of foliar P formulations incorporating the adjuvant IA-500 to the leaf underside, significantly increased both the uptake of P through the lower leaf surface into the whole plant (Fig. 3A), and the subsequent translocation of the applied P through the plant (Fig. 3B, C), compared with seedlings incubated in the dark.

Combining Seed Dressing and Foliar Applications can Replicate the P-Uptake and Grain Yield Achieved With Placed Soil Fertilisation and Improve P Recovery

In the two pot experiments in which the wheat plants were grown to grain yield maturity, the use of the two forms of readily soluble, soil-applied P-fertilisers (TSP and DAP respectively) at a rate equivalent to 35 kg P ha^{-1} produced significant increases (by ≥ 79 %) in total plant P uptake over the no-P addition controls (Fig. 4A, 5A). In comparison to the control, an increase in P-uptake (by ≥ 104 %) was also observed in both experiments when P seed dressings of 3 µmol seed^{-1} were combined with 3 foliar applications of 46.3 µmol plant^{-1}; this treatment also produced uptake rates not significantly different from the soil applied P treatment in both experiments (Fig. 4A, 5A). In the experiment using a smaller soil volume (and less intrinsic soil P), there was also a significant increase (by 119 %) in P uptake over the no-P controls for the treatment with the three foliar P applications without seed P dressing (Fig. 4A), whereas this was not the case for the experiment using the larger soil volume with a greater soil P concentration (Fig. 5A).

In the smaller soil volume, grain yield was significantly greater than the no-P controls for the treatments using soil applied P (TSP), seed dressing combined with 3 foliar applications and 3 foliar applications alone respectively (Fig. 4B). There were no significant differences in grain yield for any of the treatments in the larger soil volume. Applications of foliar P at a single growth stage produced no significant increases in P uptake or grain yield over the no-P controls in either experiment.

In both experiments, the recovery rate of P in the whole plant as a percentage of the amount of applied P was much greater (by ≥ 240%) in both the treatments with three foliar P applications alone and with seed dressing combined with the three foliar applications over the soil applied P treatments (Fig. 4C, 5C). In the smaller soil volume the seed dressing combined with three foliar applications treatment produced a significantly greater P recovery rate (by 87%) than the three foliar applications alone treatment, whereas this difference was not significant in the larger soil volume.

DISCUSSION

Evidence from ^{33}P Labelling Allows Optimisation of Foliar P Application Strategy

Most previous studies on P foliar fertilisers have relied on increases in growth and leaf ^{31}P content to measure the success of different foliar treatments. Using a combination of ^{31}P and ^{33}P isotopes, this study has provided direct evidence that the use of an adjuvant in foliar P formulations causes an increase in P uptake following application to the upper leaf surface, confirming its value for promoting P uptake rates into the leaf (Noack et al., 2010). We also showed that the applied P has the ability to penetrate the cuticle of the upper leaf surface, and especially the lower leaf surface, even without amendment with an adjuvant. Our result contrasts strongly with that of Peirce et al. (2014) who found that more P uptake occurred when fertiliser was applied to the leaf surface. In our case, we attribute foliar entry to the presence of stomata which are present on both sides of *T. aestivum* leaves at similar densities (Zhu et al., 2018). Trichomes are a significant barrier to leaf surface penetration, reducing the contact area of droplets with the leaf surface (Brewer et al., 1991). The increased uptake rates on the lower side of the leaf we observed can be attributed to *T. aestivum* leaves having a lower density of trichomes here compared to the upper surface (Fernández et al., 2014). In addition, our results are consistent with photosynthesis and transpiration rates being higher in stomata on the underside of cereal leaves (Driscoll et al., 2006). The important role of stomatal conductance in transfer of foliar applied P into the plant can also be inferred from the positive effect of growing plants in photosynthetic light (compared with the dark); stomata are known to open in response to light (Dietrich, 2001). Growing plants in photosynthetic light also increased the mobility of the foliar applied P within the plant, which is likely to be linked to the increased flux of organic compounds into the phloem observed during active photosynthesis (Giaquinta, 1978). Phosphorus could be carried into the phloem this way either via increased esterification of applied P or through simple mass flow delivering the P to the vicinity of vascular tissues. It is unclear whether the increased P mobilisation from the leaf enhances the rate of P entry into the leaf tissue through maintaining a stronger concentration gradient, or vice versa. Nonetheless, given that foliar scorch has been attributed to high nutrient imbalance at the area of foliar fertiliser application (Marschner, 1995), high mobilisation rates of foliar P from the leaf may enable higher dosage applications. Our results also indicate that foliar sprays may work better when applied in the early morning to maximise uptake, although clearly this needs further testing at the field scale. It should be noted that there is no overall consensus in the literature on the optimal timing for foliar applications with the optimal response window in the day being dependent on crop type, prevailing weather conditions and nutrient (Fageria et al., 2009). However, results with other nutrients (e.g. N, Se) have indicated maximal uptake rates in the morning or evening in comparison to the middle of the day (Kyllingsbaek, 1980; Liu et al., 2012).

Uptake Efficiency of a Combination of Seed Dressing and Foliar Applications is Greater Than for Soil Applied P Fertiliser

Application of P as a seed dressing at any of the doses used in the experiment increased lateral root production to a similar extent as did its application in the soil at ≥ 221 times the dose rate. However, seed application tended not to have the same magnitude of benefit to soil application in seminal root growth. The enhancement of lateral root growth is likely to be particularly important in enabling the exploitation of reserves of P and other mineral nutrients in a larger soil volume (Zhu and Lynch, 2004). This benefit is likely to be especially important for uptake of P because of its low mobility in the soil, and given the increase in P uptake over controls is greater than the quantity applied as a seed dressing, a high proportion of P taken up by the plants in the experiment is likely to have come from soil reserves. These effects of enhanced early root production, and concurrent enhancements in P uptake are consistent with the findings of previous studies in other plant species (Valluru et al., 2010), and point to seed dressings being a valuable tool in increasing P-fertiliser use efficiency.

The combination of a P seed dressing and three subsequent foliar applications resulted in high rates of P uptake (equivalent to those achieved with much larger doses of soil applied fertiliser) in both pot experiments. The added advantage of combining seed with foliar application was, however, not consistent between the two experiments. The benefit over foliar application alone was clear when plants were grown in a smaller soil volume (500 g per plant) with low intrinsic soil P reserves. However, when plants were grown in a larger soil volume with a much higher available P reserves, the combined seed and foliar application was better than the seed-only application but did not lead to a significantly greater P uptake than the foliar-only treatment. When *T. aestivum* seedlings are grown under severe P stress, they have been shown to have a markedly reduced ability to acquire P from foliar applications (Fernández et al., 2014). This could possibly explain our results, where seed dressing P was required to maintain the plants' ability to uptake foliar P when grown in small soil volumes, but in larger soil volumes, P supply was maintained by the higher soil P status regardless of seed treatments.

The effectiveness of seed plus foliar or foliar applications alone was greatly enhanced in the P-limiting conditions of a small volume of low P soil (Fig. 4) compared to the P-sufficient conditions of a large volume of high P soil (Fig. 5). In P-sufficient conditions, foliar applications enhanced total plant uptake of P (Fig. 5A) with greater efficiency than soil fertilisation (Fig. 5C), but consistent with other studies in high P soils (Bai et al., 2013), there was no effect of P application on grain yield (Fig. 5B)(McBeath et al., 2020). We attribute this to the P in the high P soil becoming available progressively during the growing period due to the mineralization of organic P reserves in the soil and greater exploitation of native soil P reserves as the root system develops.

The pot experiments were all performed using foliar P loading rates of 46.3 µmol plant^{-1} for each application at GS13, GS31 and GS39. Previous work by Mosali et al. (2006) has shown that under field conditions, winter wheat had higher optimal dose rates at an equivalent to our experiments of 50.7 µmol plant^{-1} dosage^{-1} at GS32 and 101.3 µmol plant^{-1} dosage^{-1} at GS39. These applications did not include an adjuvant in the formulation. The total quantity of foliar P applied per plant combining all three applications in our experiments (138.9 µmol) is just 8.6% less than the optimal dose for two applications found by Mosali et al. (2006) in their field experiment (152.0 µmol). In reality, the quantity applied to the leaf surface is likely to have been much greater in our experiment as all of the foliar P was applied directly to the leaves together with an adjuvant, rather than being sprayed onto the crop where a proportion can fall onto the soil without contacting the crop. Our plants showed no negative effects of applying such quantities of P early in the growing season. This indicates that our combination of adjuvant supplementation and application of foliar P at the beginning of the day, to maximise initial uptake rates, appeared to prevent any negative effects related to foliar scorch. In addition, the addition of IA-500 into the formulation will have considerably reduced the ability of leaf trichomes to suspend droplets above the leaf surface. This presumably also reduced the already limited possibilities for optically produced foliar scorch, as this is caused by such droplets rather than the solution in contact with the leaf surface (Egri et al., 2010).

Limits to the level of P-fertilisation possible though foliar application, due to the constraints of foliar scorch, have previously limited their usefulness to situations where other factors such as environmental conditions have depressed yields to sub-optimal levels, with crop P demand reduced concurrently to a level that foliar P can satisfy (Mosali et al., 2006; Noack et al., 2010). That we have demonstrated the capacity to apply larger quantities of P to leaves resulting in grain yields not significantly different from those obtained by conventional soil fertilisation illustrates that foliar application of P may be a more versatile strategy than previously thought.

In our experiments, a much higher dose of soil applied P fertiliser produced no advantage over the other treatments in terms of grain yield. Important evidence to explain this result is that the rate of recovery in the plant of applied P was significantly much larger in the foliar, and especially the combined seed with foliar, applications than for the soil application. When correcting for the amount of P uptake by untreated control plants, the rate of fertiliser recovery for the seed dressings with foliar applications is consistently close to 100% in both experiments. It is also notable that the combination of seed and foliar application produced a higher mean P recovery rate than foliar application alone in both experiments, significantly so in the larger-soil volume experiment. The advantage of direct and precise application of much smaller doses of P to the seed and leaves over conventional soil application is a reduction in the quantity of P immobilised in the soil for long periods of time. This advantage of this precision is likely to be both spatial and temporal: the specific targeting of P application to times of greatest plant demand is expected to have enhanced the ability of the plant to it take up and utilise it (Withers et al., 2014).

The capacity of crops to take up larger quantities of P than that applied in fertiliser during the current growing season, which was demonstrated by this study, is important for strategies to increase the sustainability of food production. The study demonstrated that precise application of small quantities of P fertiliser to seed and leaves led to a much greater magnitude of P uptake from soil P reserves. While we have no evidence about the chemical form of soil P accessed by the plants, their enhanced rate of lateral root growth is likely to have been important for this outcome. Direct effects of organic acids exuded from these roots (Ström et al., 2002) or indirect effects via rhizosphere microbes (Rodríguez and Fraga, 1999) or mycorrhizal fungi (Smith et al., 2011) can play an important role in enabling plant uptake of insoluble forms of P that have been immobilised in the soil matrix (Withers et al., 2014). Through such mechanisms, these soil P reserves can maintain a gradually diminishing supply of plant-available P for over a century (Blake et al., 2003). The importance of such a low dose seed and foliar P fertilisation strategy for more sustainable production over the medium-term is particularly important in countries such as the UK, where high levels of historical P fertiliser application to agricultural soils have built up large P reserves in excess of immediate crop nutritional requirements (Withers et al., 2001b). Even when this eventually reduces soil P reserves, or if novel crop varieties are produced that have a greater P demand, this strategy has the potential to be adapted to increase the rate of P supply. This could be achieved by increasing the number of P foliar applications per growing season, or by its combination with application of more sustainable sources of slow-release P fertiliser to the soil, such as struvite (Massey et al., 2009).

CONCLUSION

This study provides evidence that a combination of seed dressing and foliar applications could be an effective alternative P-fertilisation strategy for spring wheat. The combination of a seed dressing dosage that promotes early vigour with foliar P applications which include an adjuvant produced a P nutrition response comparable to conventional soil P fertilisation at much smaller (≤ 16%) rates of P application. This approach minimises the contact of fertiliser P with the soil, and thus minimises soil immobilisation into less available forms of P, with potential benefit for increased fertiliser P-use efficiency and reduced risk of pollution. In addition, it promotes crop use of intrinsic soil P reserves. This strategy therefore has the potential to increase the efficiency of both future use of fertiliser P resources and the exploitation of the soil legacy of past P fertilization in agriculture, and so can play an important role in the sustainable intensification of food production. Further work is now required to evaluate whether these results can be obtained under a range of field conditions (e.g. soil, crop and weather combinations).

CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

AUTHOR CONTRIBUTIONS

PJT, JRH, PJAW and DLJ designed the research. PJT conducted the research. PJT and DLJ collected and analysed the data. PJT wrote the first draft of the manuscript. All authors contributed to the final version of the manuscript.

ACKNOWLEDGEMENTS

We would like to thank Roger Sylvester-Bradley (ADAS), Robin Walker (SRUC) and Alison Rollett (ADAS) for their scientific input to the work and Ian Elliot and David Booty at Omex Agriculture Ltd for the provision of the fertiliser products. This manuscript has been released as a report at https://ahdb.org.uk/improving-the-sustainability-of-phosphorus-use-in-arable-farming-targeted-p, (AHDB, 2016).

FUNDING

The authors would like to thank the UK Department for Environment, Food and Rural Affairs, Biotechnology and Biological Sciences Research Council and Scottish Government for funding this work as a component of the Sustainable Arable LINK project (LK09136).

REFERENCES

AHBD (2016) Improving the sustainability of phosphorus use in arable farming – 'Targeted P'. Project Report PR569. Agriculture and Horticulture Development Board, Kenilworth, UK.

AHDB (2019) Nutrient Management Guide (RB209). Agriculture and Horticulture Development Board, Kenilworth, UK.

Allison MF, Fowler JH, Allen EJ (2002) Effects of soil- and foliar-applied phosphorus fertilizers on the potato (*Solanum tuberosum*) crop. *Journal of Agricultural Science* 137, 379-395.

Appah S, Jia WD, Ou MX, Wang P, Asante EA (2020) Analysis of potential impaction and phytotoxicity of surfactant-plant surface interaction in pesticide application. *Crop Protection* 127, 104961.

Bai Z, Li H, Yang X, Zhou B, Shi X, Wang B, Li D, Shen J, Chen Q, Qin W, Oenema O, Zhang FS (2013) The critical soil P levels for crop yield, soil fertility and environmental safety in different soil types. *Plant and Soil* 372, 27-37.

Barel D, Black CA (1979a) Foliar application of P. I. Screening of various inorganic and organic P compounds. *Agronomy Journal* 71, 15-21.

Barel D, Black CA (1979b) Foliar application of P. II. Yield responses of corn and soybeans sprayed with various condensed phosphates and P-N compounds in greenhouse and field experiments. *Agronomy Journal* 71, 21-24.

Barrier GE, Loomis WE (1957) Absorption and translocation of 2,4-dichlorophenoxyacetic acid and P by leaves. *Plant Physiology* 32, 225-231.

Bastani S, Hajiboland R (2017) Uptake and utilization of applied phosphorus in oilseed rape (*Brassica napus* L. cv. Hayola) plants at vegetative and reproductive stages: Comparison of root with foliar phosphorus application. *Soil Science and Plant Nutrition* 63, 254-263.

Bindraban PS, Dimkpa CO, Pandey R (2020) Exploring phosphorus fertilizers and fertilization strategies for improved human and environmental health. *Biology and Fertility of Soils* 56, 299-317.

Blake L, Johnston AE, Poulton PR, Goulding KWT (2003) Changes in soil phosphorus fractions following positive and negative phosphorus balances for long periods. *Plant and Soil* 254, 245-261.

Bouma D (1969) The response of subterranean clover (*Trifolium subterraneum* L.) to foliar applications of phosphorus. *Australian Journal of Agricultural Research* 20, 435-445.

Brewer CA, Smith WK, Vogelmann TC (1991) Functional interaction between leaf trichomes, leaf wettability and the optical properties of water droplets. *Plant, Cell & Environment* 14, 955-962.

Dietrich P (2001) The role of ion channels in light-dependent stomatal opening. *Journal of Experimental Botany* 52, 1959-1967.

Dodd RJ, Sharpley AN (2015) Recognizing the role of soil organic phosphorus in soil fertility and water quality. *Resources Conservation and Recycling* 105, 282-293.

Drew MC (1975) Comparison of the effects of a localised supply of phosphate, nitrate, ammonium and potassium on the growth of the seminal root system, and the shoot in Barley. *New Phytologist* 75, 479-490.

Driscoll SP, Prins A, Olmos E, Kunert KJ, Foyer CH (2006) Specification of adaxial and abaxial stomata epidermal structure and photosynthesis to CO_2 enrichment in maize leaves. *Journal of Experimental Botany* 57, 381-390.

Egri A, Horváth A, Kriska G, Horváth G (2010) Optics of sunlit water drops on leaves, conditions under which sunburn is possible. *New Phytologist* 185, 979-87.

Fageria NK, Barbosa Filho MP, Moreira A, Guimarães CM (2009) Foliar fertilization of crop plants. *Journal of Plant Nutrition* 32, 1044-1064.

FAO (2015). World Reference Base for Soil Resources 2014, update 2015 International soil classification system for naming soils and creating legends for soil maps. IUSS Working Group WRB World Soil Resources Reports No. 106. FAO, Rome

Fernández V, Brown PH (2013) From plant surface to plant metabolism, the uncertain fate of foliar-applied nutrients. *Frontiers in Plant Science* 4, 289.

Fernández V, Guzmán P, Peirce CAE, McBeath TM, Khayet M, McLaughlin MJ (2014) Effect of wheat phosphorus status on leaf surface properties and permeability to foliar-applied phosphorus. *Plant and Soil* 384, 7-20.

Giaquinta R (1978) Source and sink leaf metabolism in relation to phloem translocation. *Plant Physiology* 61, 380-385.

Gordon-Weeks R, Tong YP, Davies TGE, Leggewie G (2003) Restricted spatial expression of a high-affinity phosphate transporter in potato roots. *Journal of Cell Science* 116, 3135-3144.

Grant CA, Flaten DN, Tomasiewicz DJ, Sheppard SC (2001) The importance of early season phosphorus nutrition. *Canadian Journal of Plant Science* 81, 211-224.

Gray RC (1977) Foliar fertilization with primary nutrients during the reproductive stage of plant growth. *Proceedings of the Fertilizer Society* 164, 1-23.

Heppell J, Talboys P, Payvandi S, Zygalakis KC, Fliege J, Jones DL, Withers PJA, Roose T (2014) How changing root system architecture can help tackle a reduction in soil phosphate (P) levels for better plant P acquisition. *Plant, Cell & Environment* 38, 118-128.

HGCA (2000) Optimum winter wheat plant population. Topic Sheet 32. Home-Grown Cereals Authority, London, UK.

Holloway PJ (1994) Physicochemical factors influencing the adjuvant-enhanced spray deposition and coverage of foliage-applied agrochemicals. In: Holloway PJ, Rees RT, Stock D, eds. pp 83-106. Interactions Between Adjuvants, Agrochemicals and Target Organisms, Ernst Schering Research Foundation Workshop volume 12, Springer-Verlag, Berlin.

Koontz H, Biddulph O (1957) Factors affecting absorption and translocation of foliar applied phosphorus. *Plant Physiology* 32, 463-470.

Kyllingsbaek A (1980) Absorption of urea by barley plants after foliar fertilization at different times during the day and night. *Tidsskrift for Planteavl* 84, 343-348.

Li CH, Wang JD, Zhang YC (2020) Root growth and phosphorus efficiency among sweet potato genotypes under low phosphorus. *Journal of Plant Nutrition* 43, 1320-1330.

Liu J, Macrae ML, Elliott JA, Baulch HM, Wilson HF, Kleinman PJA (2019) Impacts of cover crops and crop residues on phosphorus losses in cold climates: A review. *Journal of Environmental Quality* 48, 850-868.

Liu CJ, Liu FG, Chen W, Zhu DY, Li DJ, Liu CQ, Wu HH (2012) Effects of selenium foliar spraying on its accumulation in fresh corn. *Jiangsu Journal of Agricultural Sciences* 28, 713-716.

Lyon C, Cordell D, Jacobs B, Martin-Ortega J, Marshall R, Camargo-Valero MA, Sherry E (2020) Five pillars for stakeholder analyses in sustainability transformations: The global case of phosphorus. *Environmental Science & Policy* 107, 80-89.

Marschner H (1995) Mineral Nutrition of Higher Plants. Academic Press, London, UK.

Massey MS, Davis JG, Ippolito J, Sheffield RE (2009) Effectiveness of recovered magnesium phosphates as fertilizers in neutral and slightly alkaline soils. *Agronomy Journal* 101, 323-329.

McBeath TM, Facelli E, Peirce CAE, Arachchige VK, McLaughlin MJ (2020) Assessment of foliar-applied phosphorus fertiliser formulations to enhance phosphorus nutrition and grain production in wheat. *Crop & Pasture Science in press*.

McKenzie RH, Bremer E, Kryzanowski L, Middleton AB, Solberg ED, Heaney D, Coy G, Harapiak J (2003) Yield benefit of phosphorus fertilizer for wheat, barley and canola in Alberta. *Canadian Journal of Soil Science* 83, 431-441.

Moody PW (2007) Interpretation of a single-point P buffering index for adjusting critical levels of the Colwell soil P test. *Australian Journal of Soil Research* 45, 55-62.

Mosali J, Desta K, Teal RK, Freeman KW, Martin KL, Lawles JW, Raun WR (2006) Effect of foliar application of phosphorus on winter wheat grain yield, phosphorus uptake, and use efficiency. *Journal of Plant Nutrition* 29, 2147-2163.

Murphy J, Riley JP (1962) A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta* 27, 31-36.

Noack SR, McBeath TM, McLaughlin MJ (2010) Potential for foliar phosphorus fertilisation of dryland cereal crops: a review. *Crop and Pasture Science* 61, 659-669.

Omex (2020) Foliar and Specialty Product Guide. OMEX Agriculture Ltd King's Lynn Norfolk UK.

Olsen SR, Cole CV, Watanabe FS, Dean LA (1954) Estimation of available phosphorus in soils by extraction with sodium bicarbonate. Circular 939, United States Department of Agriculture, Washington DC, USA.

Paudel I, Bar-Tal A, Rotbart N, Aphrath A, Cohen S (2018) Water quality changes seasonal variations in root respiration, xylem CO_2, and sap pH in citrus orchards. *Agricultural Water Management* 197, 147-157.

Peske FB, Baudet L, Peske ST (2009) Yield of soybean plants derived from seeds coated with phosphorus. *Revista Brasileira de Sementes* 31, 95-101.

Peirce CAE, McBeath TM, Fernandez V (2014) Wheat leaf properties affecting the absorption and subsequent translocation of foliar-applied phosphoric acid fertiliser. *Plant and Soil* 384, 37-51.

Rodríguez H, Fraga R (1999) Phosphate solubilizing bacteria and their role in plant growth promotion. *Biotechnology Advances* 17, 319-339.

Sánchez-Rodríguez AR, Carswell AM, Shaw R, Hunt J, Saunders K, Cotton J, Chadwick DR, Jones DL, Misselbrook TH (2018) Advanced processing of food waste based digestate for mitigating nitrogen losses in a winter wheat crop. *Frontiers in Sustainable Food Systems* 2, 35.

Schönherr J (2006) Characterization of aqueous pores in plant cuticles and permeation of ionic solutes. *Journal of Experimental Botany* 57, 2471-2491.

Sekiya N, Yano K (2009) Seed P-enrichment as an effective P supply to wheat. *Plant and Soil* 327, 347-354.

Silberstein O, Wittwer SH (1951) Foliar applications of phosphatic fertilizers to vegetable crops. *Proceedings of the American Society for Horticultural Science* 58, 179-180.

Simpson RJ, Oberson A, Culvenor RA, Ryan MH, Veneklaas EJ, Lambers H, Lynch JP, Ryan PR, Delhaize E, Smith FA, Smith SE, Harvey PR, Richardson AE (2011) Strategies and agronomic interventions to improve the phosphorus-use efficiency of farming systems. *Plant and Soil* 349, 89-120.

Smith SE, Jakobsen I, Grønlund M, Smith FA (2011) Roles of arbuscular mycorrhizas in plant phosphorus nutrition, interactions between pathways of phosphorus uptake in arbuscular mycorrhizal roots Have important implications for understanding and manipulating plant phosphorus acquisition. *Plant Physiology* 156, 1050-1057.

Sohair EDE, Abdall AA, Amany MA, Houda AR (2018) Effect of nitrogen, phosphorus and potassium nano fertilizers with different application times, methods and rates on some growth parameters of Egyptian cotton (*Gossypium barbadense* L.). *Bioscience Research* 15, 549-564.

Stein LA, Storey JB (1986) Influence of adjuvants on foliar absorption of nitrogen and phosphorus by soybeans. *Proceedings of the American Society for Horticultural Science* 111, 829-832.

Ström L, Owen AG, Godbold DL, Jones DL (2002) Organic acid mediated P mobilization in the rhizosphere and uptake by maize roots. *Soil Biology & Biochemistry* 34, 703-710.

Stutter MI, Shand CA, George TS, Blackwell MSA, Bol R, Mackay RL, Richardson AE, Condron LM, Turner BL, Haygarth PM (2012) Recovering phosphorus from soil, a root solution? *Environmental Science & Technology* 46, 1977-1978.

Sutton PJ, Peterson GA, Sander DH (1983) Dry matter production in tops and roots of winter wheat as affected by phosphorus availability during various growth stages. *Agronomy Journal* 75, 657-663.

Syers JJK, Johnston AE, Curtin D (2008) Efficiency of soil and fertilizer phosphorus use. Food and Agriculture Organization of the United Nations, Rome, Italy.

Takahashi S, Anwar MR (2007) Wheat grain yield, phosphorus uptake and soil phosphorus fraction after 23 years of annual fertilizer application to an Andosol. *Field Crops Research* 101, 160-171.

Talboys PJ, Owen DW, Healey JR, Withers PAW, Jones DL (2014) Auxin secretion by *Bacillus amyloliquefaciens* FZB42 both stimulates root exudation and limits phosphorus uptake in *Triticum aestivum*. *BMC Plant Biology* 14, 51.

Tunney H, Breeuwsma A, Withers PJA, Ehlert PAI (1997) Phosphorus fertilizer strategies, present and future. In: Tunney H, Carton OT, Brookes PC, Johnston AE (eds), pp. 177-203. Phosphorus loss from soil to water. CAB International, Wallingford,UK.

Valkama E, Uusitalo R, Turtola E (2011) Yield response models to phosphorus application: a research synthesis of Finnish field trials to optimize fertilizer P use of cereals. *Nutrient Cycling in Agroecosystems* 91, 1-15.

Valluru R, Vadez V, Hash CT, Karanam P (2010) A minute P application contributes to a better establishment of pearl millet (*Pennisetum glaucum* (L.) R. Br.) seedling in P deficient soils. *Soil Use and Management* 26, 36-43.

Verheijen FGA, Zhuravel A, Silva FC, Amaro A, Ben-Hur M, Keizer JJ (2019) The influence of biochar particle size and concentration on bulk density and maximum water holding capacity of sandy vs sandy loam soil in a column experiment. *Geoderma* 347, 194-202.

Wang FM, Rose T, Jeong K, Kretzschmar T, Wissuwa M (2016) The knowns and unknowns of phosphorus loading into grains, and implications for phosphorus efficiency in cropping systems. *Journal of Experimental Botany* 67, 1221-1229.

Withers PJA, Clay S, Breeze V (2001a) Phosphorus transfer in runoff following application of fertilizer, manure, and sewage sludge. *Journal of Environment Quality* 30, 180-188.

Withers PJA, Edwards AC, Foy RH (2001b) Phosphorus cycling in UK agriculture and implications for phosphorus loss from soil. *Soil Use & Management* 17, 139-149.

Withers PJA, Sylvester-Bradley R, Jones DL, Healey JR, Talboys PJ (2014) Feed the crop not the soil: rethinking phosphorus management in the food chain. *Environmental Science & Technology* 48, 6523-6530.

Withers PJA, Forber KG, Lyon C, Rothwell S, Doody DG, Jarvie HP, Martin-Ortega J, Jacobs B, Cordell D, Patton M, Camargo-Valero MA, Cassidy R (2020) Towards resolving the phosphorus chaos created by food systems. *Ambio* 49, 1076-1089.

Xie RH, Zhao JQ, Lu LL, Brown P, Guo JS, Tian SK (2020) Penetration of foliar-applied Zn and its impact on apple plant nutrition status: in vivo evaluation by synchrotron-based X-ray fluorescence microscopy. *Horticulture Research* 7, 147.

Zadoks JC Chang TT, Konzak CF (1974) A decimal code for the growth stages of cereals. *Weed Research* 14, 415-421.

Zhang XN, Guo QP, Shen XX, Yu SW, Qiu GY (2015) Water quality, agriculture and food safety in China: Current situation, trends, interdependencies, and management. *Journal of Integrative Agriculture* 14, 2365-2379.

Zhu J, Lynch JP (2004) The contribution of lateral rooting to phosphorus acquisition efficiency in maize (*Zea mays*) seedlings. *Functional Plant Biology* 31, 949-958.

Zhu XC, Cao QJ, Sun LY, Yang XQ, Yang WY, Zhang H (2018) Stomatal conductance and morphology of arbuscular mycorrhizal wheat plants response to elevated CO_2 and NaCl stress. *Frontiers in Plant Science* 9, 1363.

Figure Legends

Fig. 1. Micro-molar concentration P seed dressings enhance root production and P uptake in *Triticum aestivum*. Panel A shows total length of seminal and lateral roots per plant, after 25 d when using seed P dressings or placed soil P fertiliser compared with an untreated control. Placed fertiliser treatments equated to 885 µmol P plant^{-1}. Panel B shows total plant P uptake of the plants reported in Panel A, expressed as total P acquired per plant. $n = 4$ for each treatment except for the 4 µmol seed dressings where $n = 3$. Lower case letters indicate values that differ significantly at the $p < 0.05$ level (one-way ANOVA). Error bars are standard errors of the mean (SEM). The seed treatment was potassium phosphate, the soil treatments were granules of TSP (triple super phosphate) and DAP (diammonium phosphate).

Fig. 2. Effect of the adjuvant IA-500 upon the uptake rate of foliar P into *Triticum aestivum* leaves in photosynthetic light. Average uptake rates into the whole plant of ^{33}P after application to a 16 mm^2 area of either the bottom or top surface of one leaf over 16 h. Treatments incorporated either no adjuvant (dark bars) or 0.1 % v/v IA-500 (light bars). $n = 5$ for each treatment, lower case letters mark values significantly different from each other at the $p < 0.05$ level (two-way ANOVA). Error bars are standard errors of the mean (SEM).

Fig. 3. Effect of photosynthetic light upon the uptake rate of foliar P into *Triticum aestivum* leaves. Panel A shows the average uptakes rates of ^{33}P into the whole plant ($n = 3$). Panels B and C show images of the distribution of ^{33}P in whole wheat seedlings displaying the mobility of ^{33}P following its application to a 16 mm^2 area of the bottom surface of one leaf over 16 h when placed in either the light (Panel B) or dark (Panel C). Scale bars are 2 cm. Lower case letters mark values significantly different from each other at the $p < 0.05$ level (unpaired t-test). Error bars are standard errors of the mean (SEM).

Fig. 4. Combining foliar P application with seed P dressing can produce comparable yields of *Triticum aestivum* to soil P fertilisation with greater P recovery rates over the untreated control in P-limiting conditions. Panel A: Total P content of soil grown wheat plants grown to maturity with P-fertilisation regimes of untreated control; triple super phosphate (TSP) granules placed in soil (885 µmol P plant^{-1}); single or triple applications of foliar P (46.3 µmol P plant^{-1} application^{-1}); and seed dressing (3 µmol P plant^{-1}) combined with three foliar applications (46.3 µmol P plant^{-1} application^{-1}). Panel B: Grain yields scaled to t ha^{-1} for the treatments reported in A. Panel C: Recovery rates of all the applied P in the whole plant for the treatments that produced significant differences to the control in A. Values represent means ± SEM (n = 4) with lowercase letters showing significant differences between treatments ($p < 0.05$; one-way ANOVA).

Fig. 5. Combining foliar P application with seed P dressing can produce comparable yields of *Triticum aestivum* to soil P fertilisation with greater P recovery rates over the untreated control in P-sufficient conditions. Panel A: Total P content of wheat plants grown to maturity in 3 kg sandy loam soil. P-fertilisation treatments were untreated controls, di-ammonium phosphate (DAP) granules placed in soil (885 µmol P plant^{-1}); single or triple applications of foliar P (46.3 µmol P plant^{-1} application^{-1}); seed dressings (3 µmol P plant^{-1}) combined with three foliar applications (46.3 µmol P plant^{-1} application^{-1}). Panel B: Grain yields scaled to t ha^{-1} for the treatments reported in A. Panel C: Recovery rates of the applied P in the whole plant for the treatments that produced significant differences to the control in A. Values represent means ± SEM (n = 4) with lowercase letters showing significant differences between treatments (p < 0.05; one-way ANOVA).

740

Figure 1

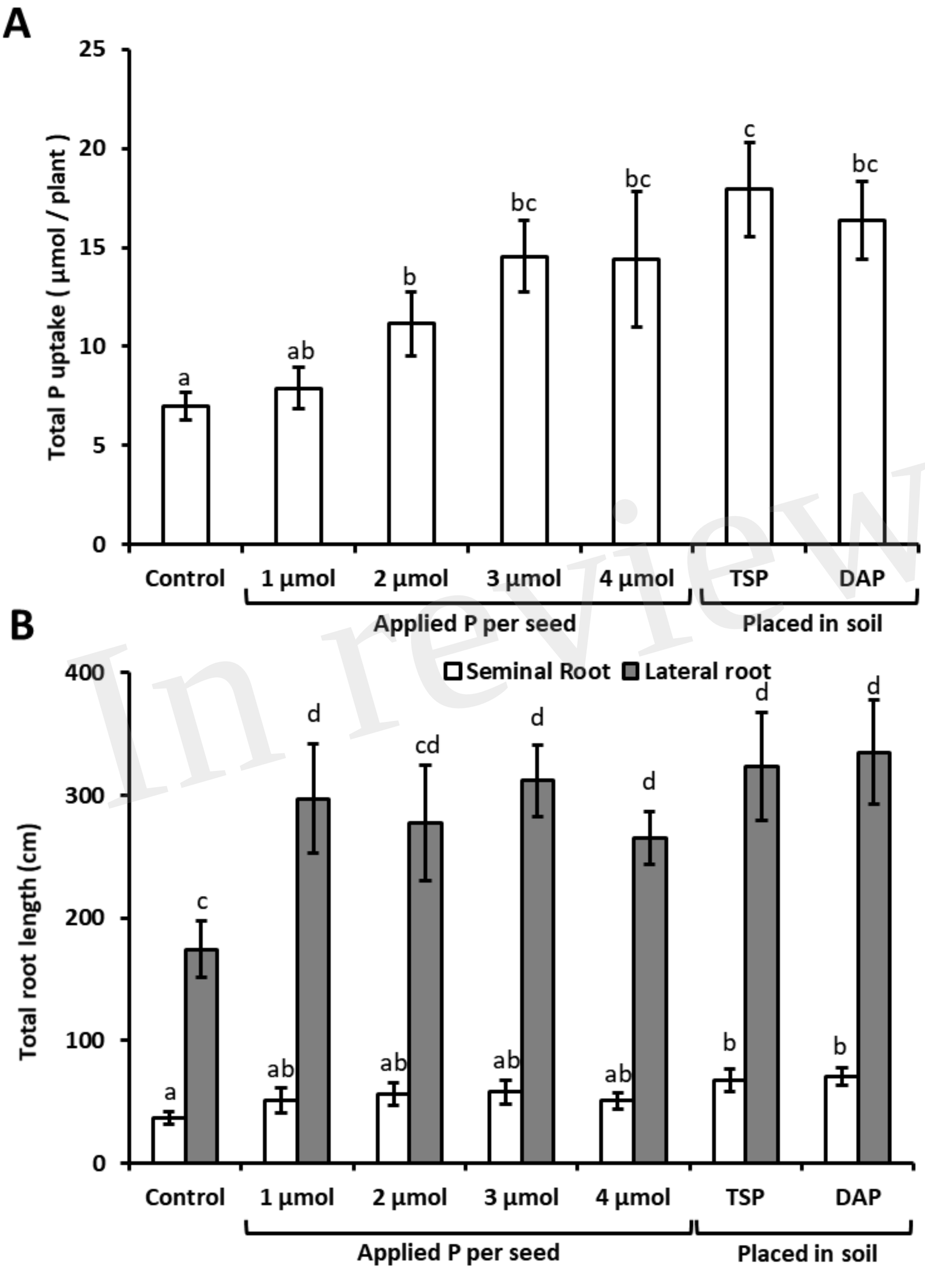

A
Total P uptake (µmol / plant)
0
5
10
15
20
25
a
ab
b
bc
bc
c
bc
Control
1 µmol
2 µmol
3 µmol
4 µmol
TSP
DAP
Applied P per seed
Placed in soil
B
Total root length (cm)
0
100
200
300
400
Seminal Root
Lateral root
a
c
ab
d
ab
cd
ab
d
ab
d
b
d
b
d
Control
1 µmol
2 µmol
3 µmol
4 µmol
TSP
DAP
Applied P per seed
Placed in soil

Figure 2

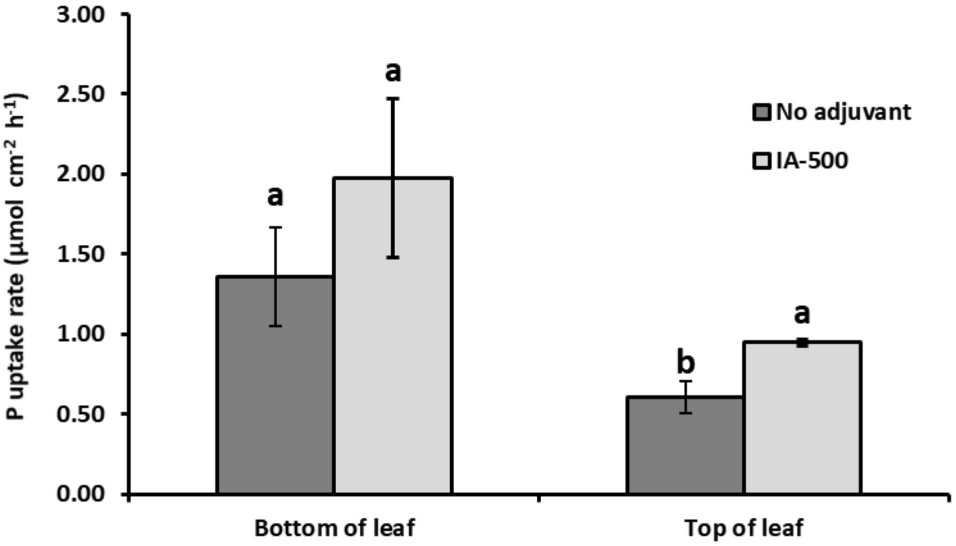

3.00
2.50
2.00
1.50
1.00
0.50
0.00
P uptake rate (µmol cm-2 h-1)
a
a
b
a
No adjuvant
IA-500
Bottom of leaf
Top of leaf

Figure 3

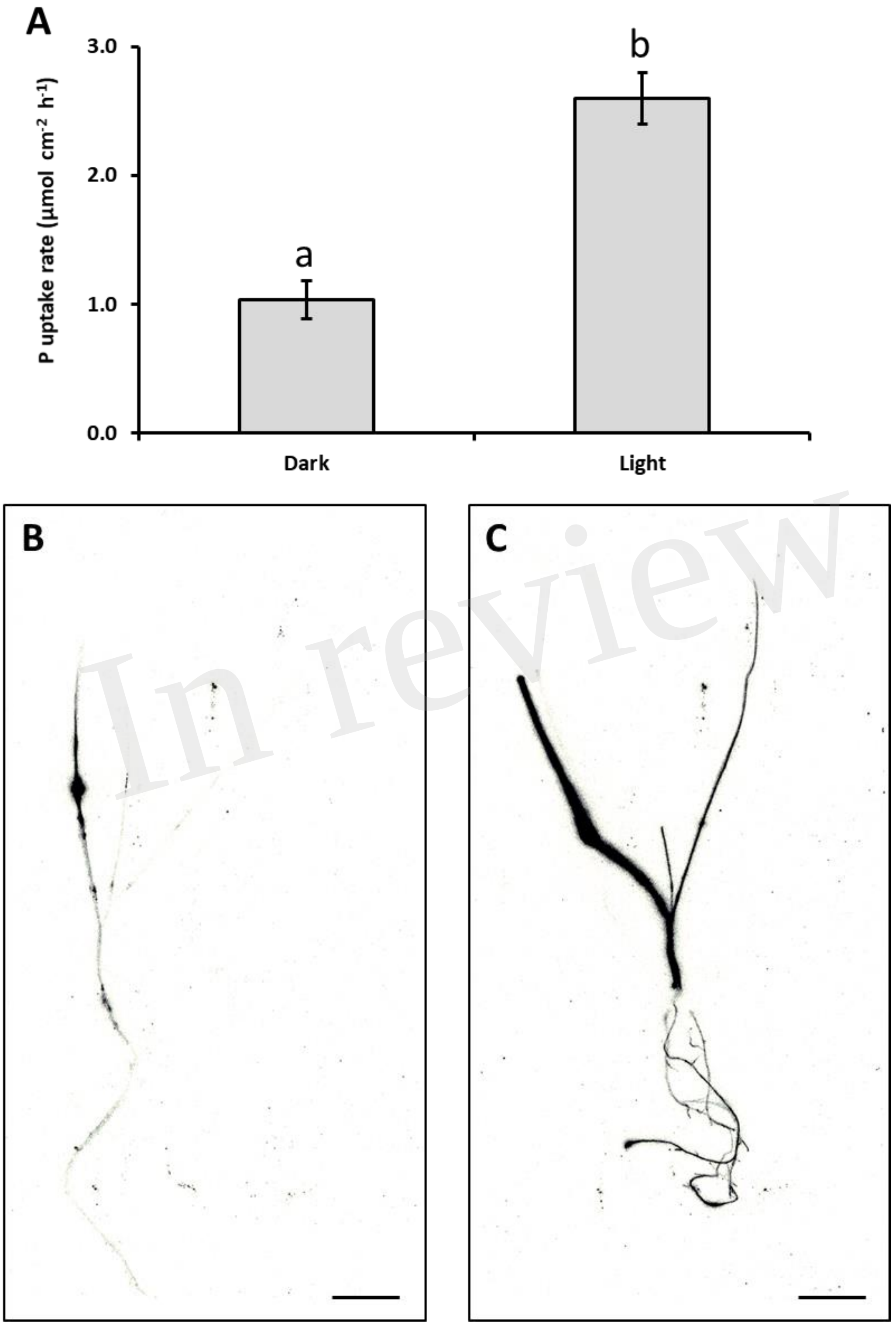


Figure 4

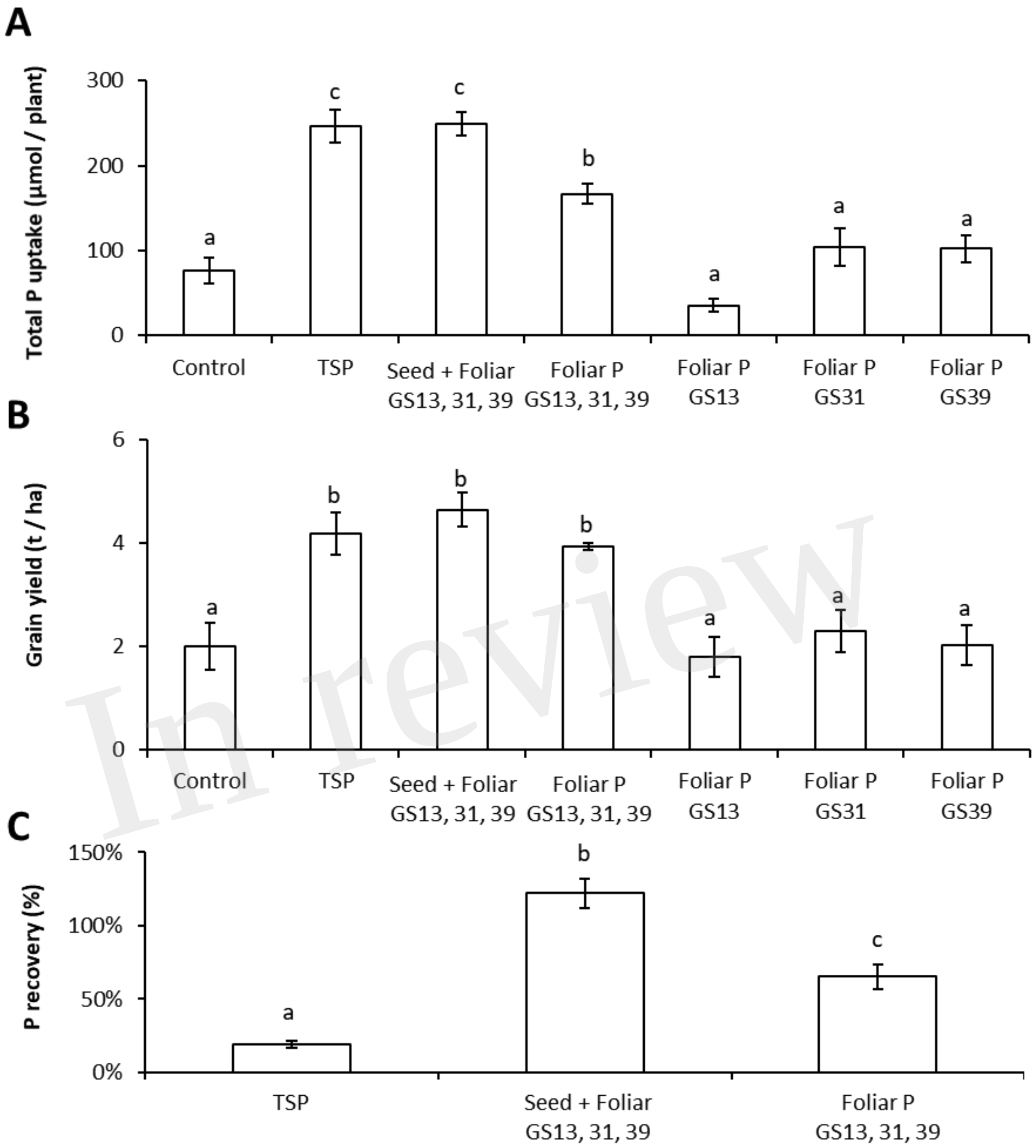
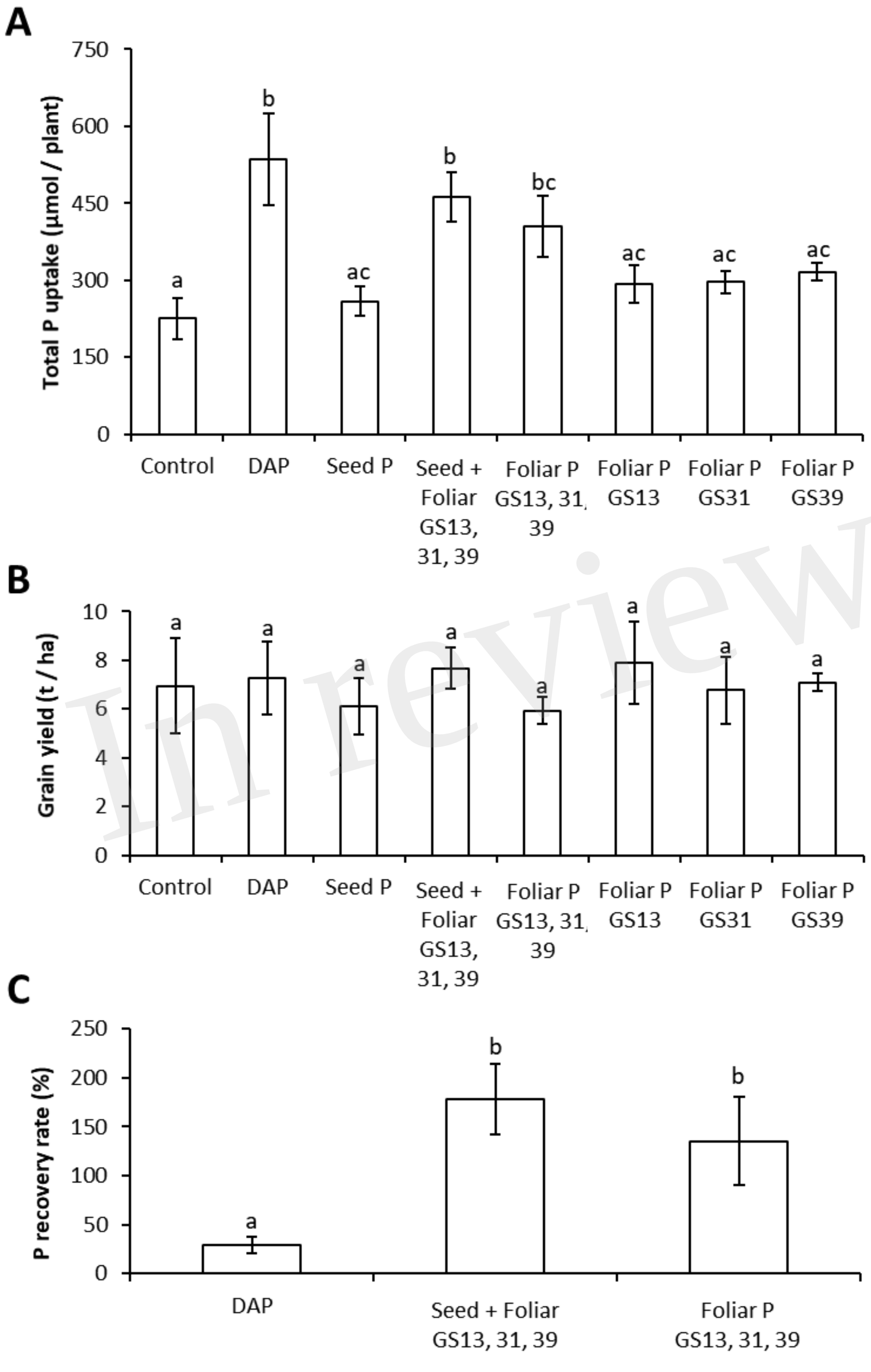

A
Total P uptake (µmol / plant)
300
200
100
0
c
c
b
a
a
a
a
Control
TSP
Seed + Foliar GS13, 31, 39
Foliar P GS13, 31, 39
Foliar P GS13
Foliar P GS31
Foliar P GS39
B
Grain yield (t / ha)
6
4
2
0
b
b
b
a
a
a
a
Control
TSP
Seed + Foliar GS13, 31, 39
Foliar P GS13, 31, 39
Foliar P GS13
Foliar P GS31
Foliar P GS39
C
P recovery (%)
150%
100%
50%
0%
b
c
a
TSP
Seed + Foliar GS13, 31, 39
Foliar P GS13, 31, 39

Figure 5


A
Total P uptake (µmol / plant)
0
150
300
450
600
750
a
b
ac
b
bc
ac
ac
ac
Control
DAP
Seed P
Seed + Foliar GS13, 31, 39
Foliar P GS13, 31, 39
Foliar P GS13
Foliar P GS31
Foliar P GS39
B
Grain yield (t / ha)
0
2
4
6
8
10
a
a
a
a
a
a
a
a
Control
DAP
Seed P
Seed + Foliar GS13, 31, 39
Foliar P GS13, 31, 39
Foliar P GS13
Foliar P GS31
Foliar P GS39
C
P recovery rate (%)
0
50
100
150
200
250
a
b
b
DAP
Seed + Foliar GS13, 31, 39
Foliar P GS13, 31, 39