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META-ANALYSIS

# Quantitative evaluation of the grain zinc in cereal crops caused by phosphorus fertilization. A meta-analysis

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## Abstract

Zinc (Zn) deficiency is a well-documented worldwide problem for crops and humans. Although phosphorus (P) fertilizer application achieves high grain yield in intensive agricultural systems, it can reduce Zn availability in cereal grains. Therefore, a quantitative evaluation of the P–Zn antagonism is needed. A global meta-analysis of 51 publications with wheat, maize, and rice was performed to quantitatively analyze the effect of P application on grain Zn concentration. Phosphorus application reduced grain Zn concentration by 16.6% for wheat, 20.2% for maize, and 0% for rice. Phosphorus application did not affect soil available Zn concentration but, averaged across the three crops, significantly decreased root Zn concentration by 9.94%; the reduction was associated with a reduction in colonization of roots by arbuscular mycorrhizal fungi. Phosphorus application did not affect shoot-to-root or grain-to-straw ratios of Zn concentration, indicating that Zn translocation and remobilization within the plant were not reduced by P application. Especially for wheat and maize, the P–Zn antagonism was explained by a "dilution effect" and the suppression of Zn uptake efficiency by roots rather than by a suppression of translocation and remobilization. In addition to partially explaining the cause of the P–Zn antagonism, this is the first study using meta-analysis method to quantitatively demonstrate a P–Zn antagonism for Zn concentration in wheat and maize. Biofortification for increasing the grain Zn concentration may benefit from an increased understanding of how P application affects rhizosphere and root processes.

**Keywords** Phosphorus supply · Zinc concentration · Grain · Cereal crops · Meta-analysis · Rhizosphere

## 1 Introduction

As an essential micronutrient, zinc (Zn) is required for the health of both crops and humans, but Zn deficiency is currently a widespread problem in human nutrition (Stein 2010; Cakmak and Hoffland 2012; Gibson 2012). This is especially true for the populations in developing countries, who rely on cereal grains as staple foods (Rengel et al. 1999; Palmgren et al. 2008; Cakmak 2009). Achieving a sufficient Zn intake from consumption of cereal grains is therefore important. Phosphorus (P) fertilizer application has increased cereal grain yield in the last few decades (Roy et al. 2016), but has globally reduced grain Zn concentration irrespective of crop species (Christensen and Jackson 1981; Verma and Minhas 1987; Biswapati and Mandal 1990; Abbas et al. 2007; Amanullah 2016; Chen et al. 2017; Zhang et al. 2017a). As a consequence, any attempts to increase grain Zn availability should consider the potentially negative effect of P fertilizer.

Previous studies have evaluated the influence of P fertilizer application on cereal grain Zn concentrations, usually with specific conditions and single experiments (Friesen et al. 1980; Debnath et al. 2015; Drissi et al. 2015; Dang et al. 2016; Coetzee et al. 2017; Iqbal et al. 2017; Sánchez-Rodríguez et al. 2017). The conclusions regarding the P–Zn relationship have sometimes been quite different. Besides finding an antagonistic effect of P on cereal grain Zn concentrations, researchers have found a non-effect (Su et al. 2018) or a slightly synergistic effect (Iqbal et al. 2017; Naeem et al. 2018), and these differences might be due to variation in soil texture, pH, or other soil properties (Haldar and Mandal 1981; Goh et al. 1997; Grant et al. 2002; Gao et al. 2011; Ghasemi-Fasaei and Mayel 2012; Hagh et al. 2016). In recent years, a

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number of studies on the effects of P application on cereal grain Zn have greatly increased. This increase has made it feasible to use a meta-analysis to quantify the negative/positive effect of P application on grain Zn concentration and to identify the underlying mechanisms.

Many studies have focused on the P–Zn antagonism and have proposed various mechanisms to explain the antagonism (Ragab 1980; Singh et al. 1986; Totawat and Saeed 1990; Zhao et al. 2007; Zan 2012; Vafaei and Sarraf 2014; Smith et al. 2017). These proposed mechanisms include reductions in Zn availability in soil, Zn concentration by roots, Zn translocation from roots to other tissues, and Zn remobilization from vegetative organs to grain (Fig. 1a). As the main cereal crops, wheat, maize, and rice play an important role in providing dietary Zn intake for human (Fig. 1 b, c, and d). Some studies found that Zn availability in soil was reduced by P application (Adnan 2016) because P fertilizer additions enhanced Zn adsorption by increasing the negative charges on the surface of the iron and aluminum oxides (Saeed and Fox 1979). Other reports showed, however, that Zn availability in soil was not affected or was even slightly enhanced by P fertilizer application (Takkar et al. 1976; Reddy and Yadav 1994; Zhang et al. 2012). In a pot experiment, the rate of Zn uptake per unit fresh weight of maize roots was reduced by P application (Safaya 1976). Grain Zn accumulation is also affected by the translocation and remobilization of Zn within the plant (Haslett et al. 2001; Pearson and Rengel 1994). Our previous field studies with wheat and maize on the North China Plain indicated that root-to-shoot Zn translocation and shoot-to-grain Zn remobilization efficiency from source to sink tissues were not affected by P application (Zhang et al. 2015, 2016). Overall, these results suggest that a clear understanding of the effects of P application on Zn uptake, translocation, and remobilization is still missing.

Root concentration of Zn has been considered a key process determining the Zn concentration in aboveground plant parts (Zhang et al. 2017b). Root morphology and rhizosphere processes can affect Zn acquisition. Zinc uptake efficiency in rice cultivars, for example, is closely associated with root length, root volume, and root surface area (Chen et al. 2009). In addition, a quantitative meta-analysis clearly showed that root colonization by arbuscular mycorrhizal fungi (AMF) can greatly increase crop Zn concentrations (Lehmann et al. 2014). The mycorrhizal pathway of Zn uptake by roots contributes to Zn accumulation in wheat grain (Coccina et al. 2019; Watts-Williams et al. 2015; Watts-Williams et al. 2014). Under P deficiency in maize, root exudation of organic

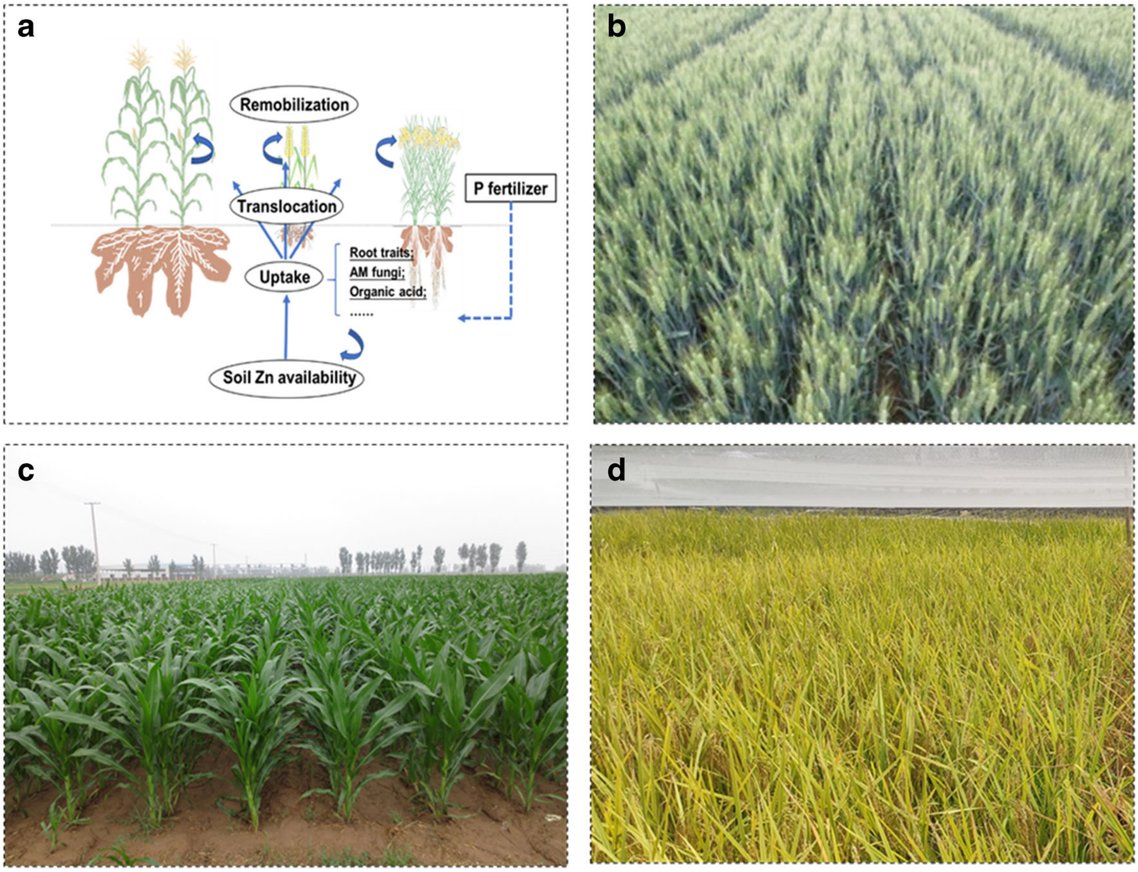

**Fig. 1** The possible mechanism of P affecting Zn transportation from soil to grain (**a**) in cereal crops: winter wheat (**b**), summer maize (**c**), and rice (**d**). The crops of winter wheat and summer maize are planted in Quzhou county in China, and rice is planted in Chongqing in China. Photographs by Wei Zhang

acids increased (Gaume et al. 2001; Hinsinger et al. 2003), which can increase soil Zn availability (Duffner et al. 2012). In contrast, a higher P fertilizer application, which exceeded the critical P application for maximal value of root morphology, can decrease root dry weight, root length, and root surface area (Wen et al. 2017), as well as rhizosphere processes including root colonization by AMF (Deng et al. 2017) and root exudation (Shen et al. 2002; Gaume et al. 2001). It remains unclear whether P application induces changes in root morphology and physiology that further influence the uptake and accumulation of Zn in the grain of cereal crops.

Crop species markedly differ in their capacity for Zn uptake in response to P fertilizer addition perhaps because the effect of P fertilization on root and rhizosphere properties differs among crops. On a P-deficient soil, for example, a high rate of root colonization by AMF increased P uptake by maize (Itoh & Barber 1983; Jemo et al. 2014; Lyu et al. 2016; Deng et al. 2017; Wen et al. 2017), whereas a large amount of root dry weight was more important for P uptake by rice (Chin et al. 2011). These root and rhizosphere traits in different crops may further influence P and Zn uptake by roots. A quantitative evaluation of the effect of P application on the Zn nutrition of the major cereal crops is therefore necessary.

In the current study, we conducted a meta-analysis to test two hypotheses: (1) P fertilizer application does not affect Zn translocation efficiency or remobilization efficiency but reduces Zn uptake efficiency by roots and (2) especially in wheat and maize, P fertilizer application reduces root Zn uptake efficiency in part by reducing AMF colonization of roots. To test these hypotheses, we conducted a meta-analysis in order to quantitatively evaluate the effects of P fertilizer application on grain Zn of the main cereal crops (wheat, maize, and rice). We also used the analysis to explore the possible mechanisms controlling Zn mobilization from soil to grain and to explore the possible reasons for differences among the three crops in P–Zn antagonism.

## 2 Materials and methods

### 2.1 Literature search

We conducted a literature search using the ISI Web of Knowledge (http://apps.webofknowledge.com) and the China National Knowledge Infrastructure database (CNKI, http://www.cnki.net) to collect the peer-reviewed journal articles published before March 2019. By using search terms phosphorus* AND zinc* AND (wheat OR maize OR corn OR rice), we collected a total of 51 articles (46 in English and 5 in Chinese), which were conducted at 43 locations globally. Among the 51 articles, 25, 16, and 6 solely concerned wheat, maize, and rice crops, respectively; 3 considered both wheat and maize crops; and 1 considered both rice and wheat crops. Our analysis included reports concerning all types of wheat (spring wheat, winter wheat, and durum wheat), maize, and rice and reports from both field and reports greenhouse experiments. Among the 51 articles, 28 described field studies, 22 described greenhouse studies, and 1 described a field and greenhouse study. Data were further scrutinized and extracted using the following inclusion criteria: (1) studies should include pair-wise control (no P fertilizer application) and P treatments (P fertilizer added) such that the P treatments have the same indicators as the control; (2) crop species were wheat, maize, or rice; (3) if one paper reported multiple independent experiments (e.g., two experiments at separate locations, years, and crops), each was considered an individual study and was incorporated as an independent observation in our dataset; and (4) Zn concentration in grain, straw, shoots, or roots was reported. Zn and P concentrations in grain, straw, and roots were measured as mg Zn $\mathrm{kg}^{-1}$ and g P $\mathrm{kg}^{-1}$, respectively. In this report, Zn "content" is equal to Zn concentration multiplied by the dry weight of the indicated plant part. Data, i.e., means, standard deviations, standard errors, and number of replicates were collected from tables and figures by using GetData Graph Digitizer (version 2.25).

The following information was documented for each study: crop; Zn concentrations and dry weights in grain, straw, and roots; Zn content in grain and straw; AMF colonization; organic acid exudation; experiment site; experiment type; year; soil type; soil P concentration (Olsen-P, Bray-P, total P); soil Zn concentration (DTPA-Zn, total Zn, and water soluble Zn); and Zn application. The term "shoot" refers to aboveground plant parts. The term "shoot Zn content" refers to the sum of the aboveground Zn content in grain and straw at crop maturity.

In this study, root Zn concentration was considered an indicator of Zn uptake efficiency, and the shoot-to-root Zn ratio and grain-to-straw Zn ratio are used to calculate the translocation efficiency of Zn from roots to shoots and the remobilization efficiency of Zn from straw to grain as shown below:

$$\begin{aligned}&\text{shoot}-\text{to}-\text{root Zn ratio}\\&\quad=\text{shoot Zn concentration}/\text{root Zn concentration}\end{aligned}$$

$$\begin{aligned}&\text{grain}-\text{to}-\text{straw Zn ratio}\\&\quad=\text{grain Zn concentration}/\text{straw Zn concentration}\end{aligned}$$

ΔGrain Zn concentration and Δsoil Zn concentration (DTPA-Zn, total Zn, and water soluble Zn) are calculated by the following equations in order to analyze the change in values caused by P application compared to the control:

$$\begin{aligned}&\Delta\text{grain Zn concentration}\\&\quad=\text{grain Zn concentration with P application}-\text{grain Zn}\\&\qquad\text{concentration without P application}\end{aligned}$$

$$\begin{aligned}\Delta\text{soil available Zn concentration} \\ = \text{soil available Zn concentration with P application} - \\ \text{soil available Zn concentration without P application}\end{aligned}$$

### 2.2 Data analysis

In the meta-analysis, the natural logarithm of the response ratio (lnR) is calculated as the effect size (Hedges et al., 1999), i.e., the effect of P treatments on Zn concentration in crops, using the following equations:

$$R = \frac{Xt}{Xc}$$

$$\ln R = \ln\left(\frac{Xt}{Xc}\right) = \ln(Xt) - \ln(Xc)$$

where Xt is the mean of Zn concentration in grain, straw, or roots for the P treatment and Xc is the mean of those concentrations for the no P control. Mean effect sizes and bias-corrected 95% confidence intervals (CIs) were generated using a bootstrapping procedure (4999 iterations). To facilitate the interpretation, the percentage of change in Zn concentration of crops in the P treatment relative to no P control is calculated by the following equation:

$$\text{Change in Zn concentration } (\%) = (R - 1) \times 100\%$$

$$= \left(\frac{Xt - Xc}{Xc}\right) \times 100\%$$

A positive value indicated an increase in Zn concentration of crops under P treatment relative to the control, while a negative value indicated a decrease. The mean percentage change was considered significantly positive or negative when the 95% CI did not overlap with zero. In addition, the frequency distributions of effect sizes were plotted to reflect the distribution regularities of individual studies. The frequencies of effect sizes were also fitted to a Gaussian distribution function to test the homogeneity of observations. The effect of P fertilizer application was considered significant if the 95% CI did not overlap with zero. Means of categorical variables were considered significantly different if their 95% CIs did not overlap with each other.

### 2.3 Statistical analysis

The effect sizes fit a normal distribution (range from − 1.28 to 0.44, $P > 0.05$) according to Kolmogorov-Smirnov analysis, suggesting that the data were suitable for a meta-analysis. Mean effect size, changes in Zn concentration, and corrected bias (i.e., the 95% confidence intervals [CI]) for each category generated using bootstrapping (10,000 iterations) were calculated using a mixed-effect model with SPSS 13.0 (SPSS Inc., Chicago, IL, USA) and SigmaPlot 12.5 (Systat, San Jose, CA, USA) software. One-way analyses of variance (ANOVAs) were conducted to evaluate the treatment effect in each figure, and means were compared using the least significant difference (LSD) at a 5% level of probability, using SPSS 13.0 (SPSS Inc., Chicago, IL, USA).

## 3 Results and discussion

### 3.1 Effect of P application on dry weight and Zn concentration in grain, straw, and roots

Phosphorus application increased the dry weight of grain, straw, and roots (Fig. 2). Averaged across the three crops, P application increased the dry weight relative to the control by 32.8% for grain, 39.2% for straw, and 49.5% for roots. For grain dry weight, the increase caused by P application was 35.7% for wheat, 25.8% for maize, and 14.7% for rice (Fig. 2a). The increase in straw and root dry weight was greater for wheat and maize than for rice (Fig. 2 b and c).

Table 1 showed that P fertilizer application decreased Zn concentration in all tissues. The grain Zn concentrations were

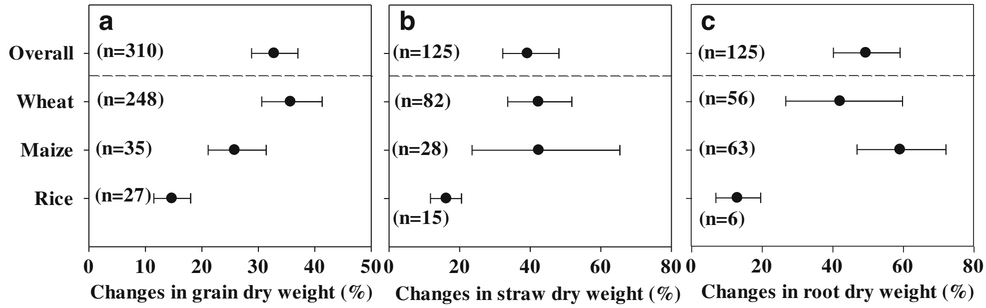

**Fig. 2** Changes in the dry weight of grain (**a**), straw (**b**), and roots (**c**) of three cereal crops in response to P application compared to the control. The values are means with 95% bootstrap confidence intervals, and sample sizes are in parentheses. The zero point indicates no effect in dry weight of grain, straw, and root of crops under P treatment relative to the control. Means with confidence intervals that do not overlap zero indicate that the dry weight was significantly affected by P application

**Table 1** Effects of No P and P application on Zn concentrations in grain, straw, and root of wheat, maize, and rice

| Characteristics | Unit | No P | | | P application | | |
|---|---|---|---|---|---|---|---|
| | | Minimum | Maximum | Mean | Minimum | Maximum | Mean |
| Grain Zn | | | | | | | |
| Wheat | mg $kg^{-1}$ | 17.8 | 60.4 | 37.7 | 8.2 | 50.3 | 30.8 |
| Maize | mg $kg^{-1}$ | 18.3 | 62.2 | 36.3 | 12.8 | 56.3 | 25.2 |
| Rice | mg $kg^{-1}$ | 14.9 | 38.4 | 22.0 | 15.6 | 35.9 | 20.6 |
| Straw Zn | | | | | | | |
| Wheat | mg $kg^{-1}$ | 5.61 | 66.9 | 23.4 | 4.1 | 46.0 | 15.1 |
| Maize | mg $kg^{-1}$ | 11.9 | 54.5 | 33.8 | 6.2 | 46.4 | 20.7 |
| Rice | mg $kg^{-1}$ | 24.1 | 74.3 | 45.4 | 25.7 | 48.2 | 33.0 |
| Root Zn | | | | | | | |
| Wheat | mg $kg^{-1}$ | 15.2 | 97.9 | 41.7 | 13.5 | 100.2 | 36.5 |
| Maize | mg $kg^{-1}$ | 3.52 | 53.0 | 33.5 | 3.33 | 55.0 | 19.2 |
| Rice | mg $kg^{-1}$ | 36.7 | 89.5 | 63.3 | 27.1 | 59.3 | 44.1 |

reducing from 37.7, 36.3, and 22.0 mg $kg^{-1}$ under no P application to 30.8, 25.2, and 20.6 mg $kg^{-1}$ under P application of wheat, maize, and rice, respectively. In terms of the Zn reduction degree, across all 51 studies, we found an overall negative effect of P application on grain Zn concentration (− 16.0%, CI = − 17.8% to − 14.2%; Fig. 3a). The reduction in grain Zn concentration caused by P application was 16.6% for wheat and 20.2% for maize; P application, however, did not significantly affect the grain Zn concentration in rice. Phosphorus application reduced straw Zn concentration by an average of 21.9% across the three crops; the reduction was 24.2% for wheat and 28.2% for maize (Fig. 3b), but the P application did not significantly affect straw Zn concentration in rice. The reduction in root Zn concentration caused by P application was 15.8% for wheat and 8.22% for maize (Fig. 3c), and once again, P application did not significantly affect the root Zn concentration for rice. P application increased Zn content in grain, straw, and root of wheat and rice, but had no effect or slightly decreasing tendency on Zn content of maize (Fig. 3 d, e, and f). Compared with the control, P application resulted in an overall increase of 6.75% in shoot Zn content for all crops; the increase was 12.5% for wheat and 10.8% for rice (Fig. 3g); P application had no effect on shoot Zn content for maize.

This global-scale meta-analysis provided quantitative evidence that despite increasing grain yield, P application reduced cereal grain Zn concentration. This negative effect of P fertilizer application potentially hinders Zn biofortification progress worldwide, especially for wheat and maize, for which the reduction in grain Zn was greater than for rice. The difference between rice and the other two crops has several potential explanations. First, the mobilization of P and Zn is greater in paddy soil than in dryland soil (Faye et al. 2006). Second, the decrease in AMF colonization due to P application was greater for maize and wheat roots than for rice roots. A previous study indicated that colonization of rice roots by AMF is rare due to the anoxic environment under the flooded conditions (Ilag et al. 1987).

To our knowledge, this is the first study to use meta-analysis method to quantitatively evaluate Zn concentration reduction extent due to P fertilizer application in grain of wheat, maize, and rice crops. We speculate that the reduction in grain Zn concentration for wheat, maize, and rice by P application may be influencing human health because high inputs of P fertilizer have been extensively reported for the intensive production of these three crops (Vitousek et al. 2009; MacDonald et al. 2011; Conley and Likens 2009). This concern with human health is particularly relevant for people who rely on wheat or maize as staple crops. In the case of wheat, it is reported that an adult human could consume 300 g grain $d^{-1}$, and that only 20% of whole grain Zn will be finally absorbed by the human intestine (Rosado et al., 2009). On the basis of grain Zn concentration in the present study (Table 1), 300 g $d^{-1}$ of wheat grain with no P application treatment could provide 2.26 mg Zn $d^{-1}$; however, humans who eat wheat grain from crops receiving P fertilizer as main food only obtain 1.84 mg Zn $d^{-1}$. This suggests that P fertilizer application indirectly decreases human Zn intake by 19% compared to no P application. The study therefore indicates that production areas with high rates of P fertilizer application should pay close attention to P–Zn antagonism. With respect to human nutrition and health, the consumption of wheat flour as a staple food may result in higher risk of low Zn intake than the consumption of rice.

### 3.2 Which factors determine grain Zn concentration?

Phosphorus application had no effect on the grain-to-straw Zn ratio (Fig. 4 a, b, c, and d) or shoot-to-root Zn ratio (Fig. 4 e, f, g, and h) for any of the three crops. Compared to the control, P

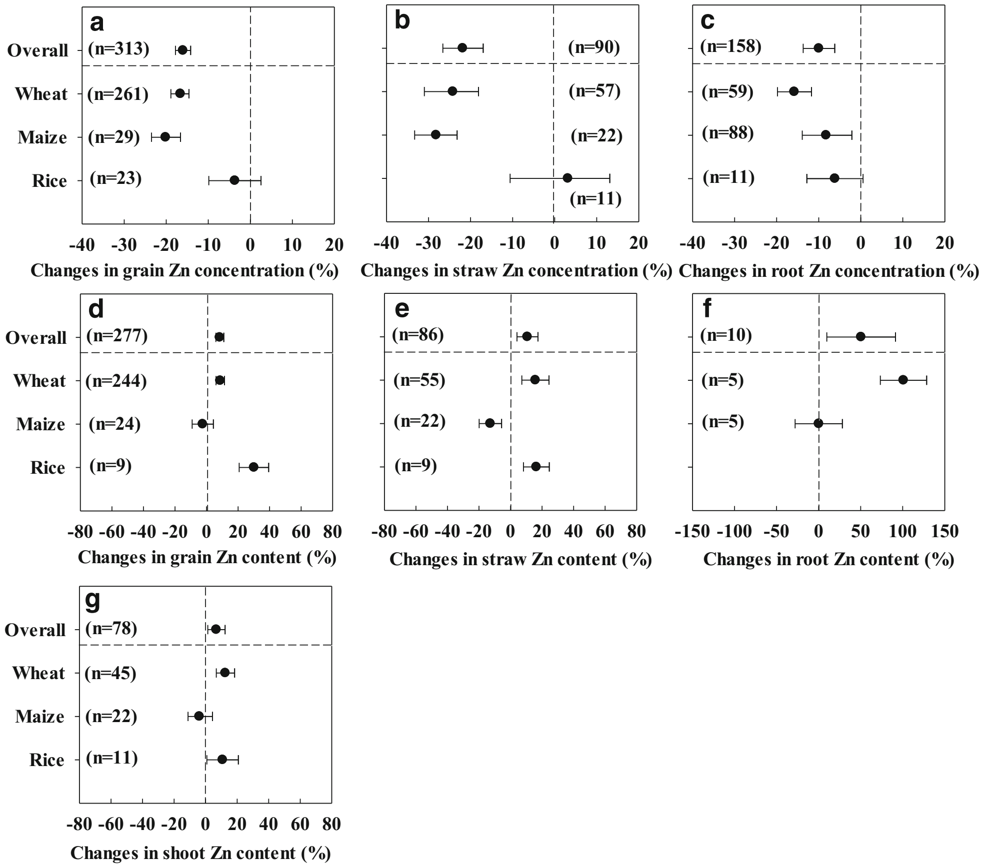

**Fig. 3** Changes in grain Zn concentration (**a**) and content (**d**), straw Zn concentration (**b**) and content (**e**), root Zn concentration (**c**) and content (**f**), and shoot Zn content (**g**) of the three cereal crops in response to P application compared to the control. The shoot Zn content includes the total Zn content of grain and straw at crop maturity; as explained in the text, Zn content is determined by multiplying the dry weight of the plant component by the concentration of Zn in the plant component. Values are means with 95% bootstrap confidence intervals, and sample sizes are in parentheses. The zero point indicates no effect in Zn concentration and content of crops under P treatment relative to the control. Means with confidence intervals that do not overlap zero indicate that the Zn concentration or content was significantly affected by P application. No data is available for rice in (**f**)

application also had no effect on the soil available Zn concentration for any of the three crops (Fig. 4 i, j, k, and l). P application, however, reduced root colonization by AMF by 31.5% for wheat and by 41.5% for maize, but did not affect AMF colonization of rice (Fig. 5a). Phosphorus application generally did not affect root exudation of organic acids (Fig. 5b).

For all crops, Δgrain Zn concentration was not related to Δsoil available Zn concentration (Fig. 6a), Δshoot-to-root Zn ratio (Fig. 6c), or Δgrain-to-straw Zn ratio (Fig. 6d). In contrast, Δgrain Zn concentration in wheat and maize increased linearly with Δroot Zn concentration (Fig. 6b).

Previous attempts to explain the P–Zn relationship focused on four processes affecting the movement of Zn from soil to grain: availability of soil Zn, Zn uptake efficiency by roots, Zn translocation from roots to shoots, and Zn remobilization from vegetative organs to grain (Lambert et al. 1979; Lu and Miller 1989; Jain and Dahama 2006; Kizilgoz and Sakin 2010; Jin et al. 2014; Khan et al. 2014; Imran et al. 2015; Li et al. 2015). The interaction between P and Zn in the soil did not explain the negative effect of P fertilizer on cereal grain Zn concentration in the current global-scale meta-analysis. The level of soil available Zn was not affected by P application (Fig. 4 i, j, k, and l), which was consistent with previous individual study (Bogdanovic et al. 1999). In fact, the results indicated that the soil P levels in the present agricultural systems were far lower than the level required to decrease soil available Zn (Chen et al. 2019). Consistent with results of Zhang et al. (2016), our meta-analysis revealed that P fertilizer application did not affect the root-to-shoot transport of Zn, i.e., Zn transport from roots to shoots does not appear to contribute to the decline of grain Zn concentration in response to P application. The grain-to-straw ratio of Zn was also not affected by P application, indicating that P application did not affect Zn remobilization. That result was consistent with our previous finding that Zn remobilization efficiency was not affected by P application rate (Zhang et al. 2015).

In addition, in regarding to the reasons of P–Zn antagonistic, the "dilution effect" also causes decrease in Zn concentration (Racz and Haluschak 1974; Moraghan 1984; Orabi et al. 1985; Maftoun and Moshiri. 2010; Lu et al. 2011; Mai et al. 2011a; Mai et al. 2011b; Zhang et al. 2017c). This study showed that the dry weight and Zn contents were slightly increasing with increasing P application, while Zn concentration was continually decreasing (Fig. 3). Under the low available P in soil, increasing P fertilizer rapidly enhances crops' biomass or yield, and the "dilution effect" maybe plays an important role in reduction of Zn concentrations, especially when the amount of P fertilizer increases from less to

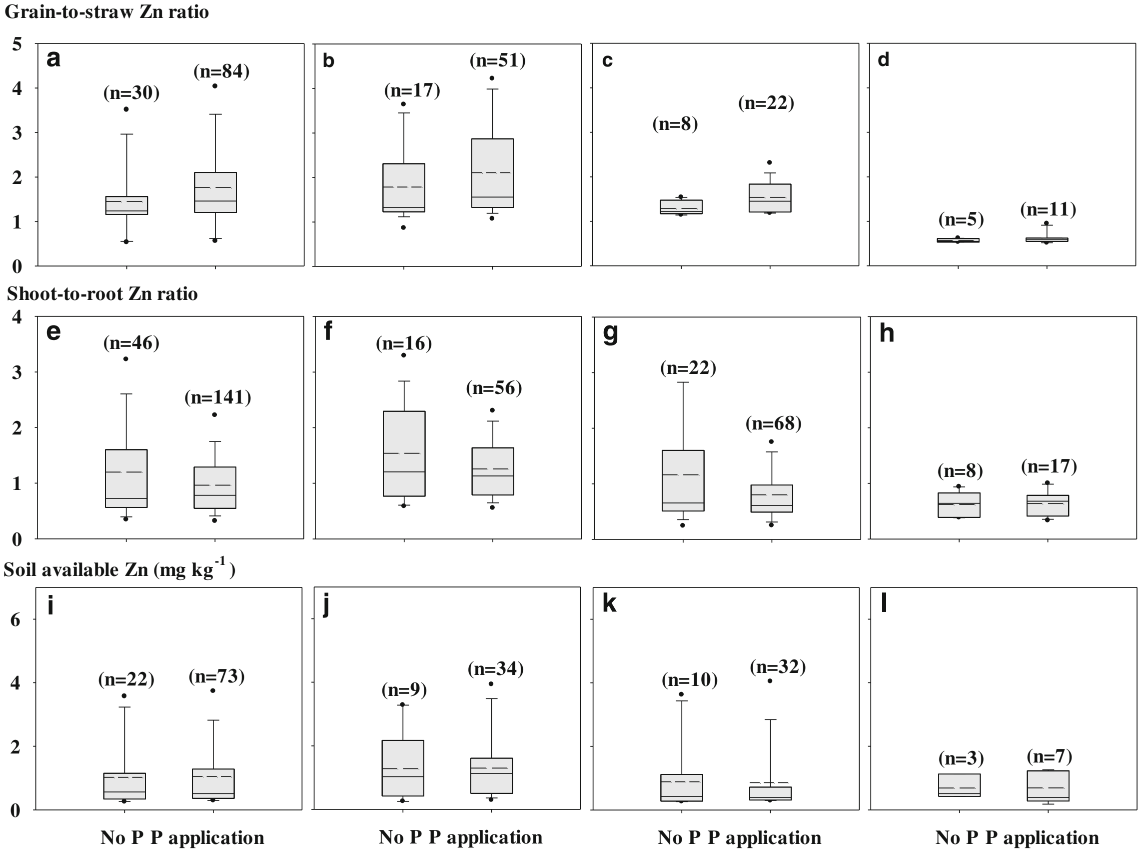

**Fig. 4** Effects of P application on grain-to-straw Zn ratio (**a** overall; **b** wheat; **c** maize; **d** rice), shoot-to-root Zn ratio (**e** overall; **f** wheat; **g** maize; **h** rice), and soil available Zn (**i** overall; **j** wheat; **k** maize; **l** rice). Sample sizes are in parentheses. The solid line through the box indicates the median, and the dotted line indicates the mean. Box boundaries indicate upper and lower quartiles, whisker caps indicate 95th and 5th percentiles, and black circles indicate outliers

appropriate, whereas increasing P fertilizer from optimal to excessive has little or no effect on further improvement of crops biomass or yield, but Zn concentration is continuous declination (Zhang et al. 2012). Meanwhile, the increased yield was associated with different trends in the concentrations of Fe, Cu, and Mn in grain compared to Zn concentrations (Zhang et al. 2012). This meant that it could not be only explained by the "dilution effect" but the limitation of Zn acquisition capability by root. Together, these results indicate that the negative effect of P application on grain Zn concentration is not due to reductions in available soil Zn or to translocation or remobilization of Zn within plants.

Zinc concentrations in roots of wheat and maize were significantly decreased by P application. Compared to the no P

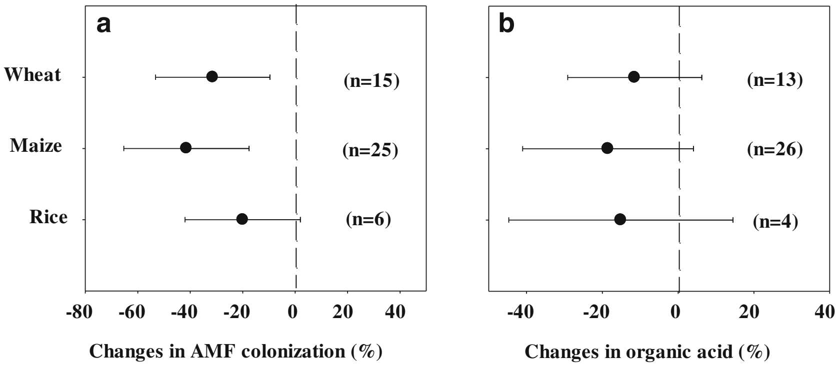

**Fig. 5** The effects of P application relative to the control on changes in AMF colonization (**a**) and on changes in root exudation of organic acid (**b**) for wheat, maize, and rice. Values are means with 95% bootstrap confidence intervals, and sample sizes are in parentheses. The zero point indicates no effect in AMF colonization and organic acid of crops under P treatment relative to the control. Means with confidence intervals that do not overlap zero indicate that the changes in AMF colonization or changes in root exudation of organic acid were significantly affected by P application

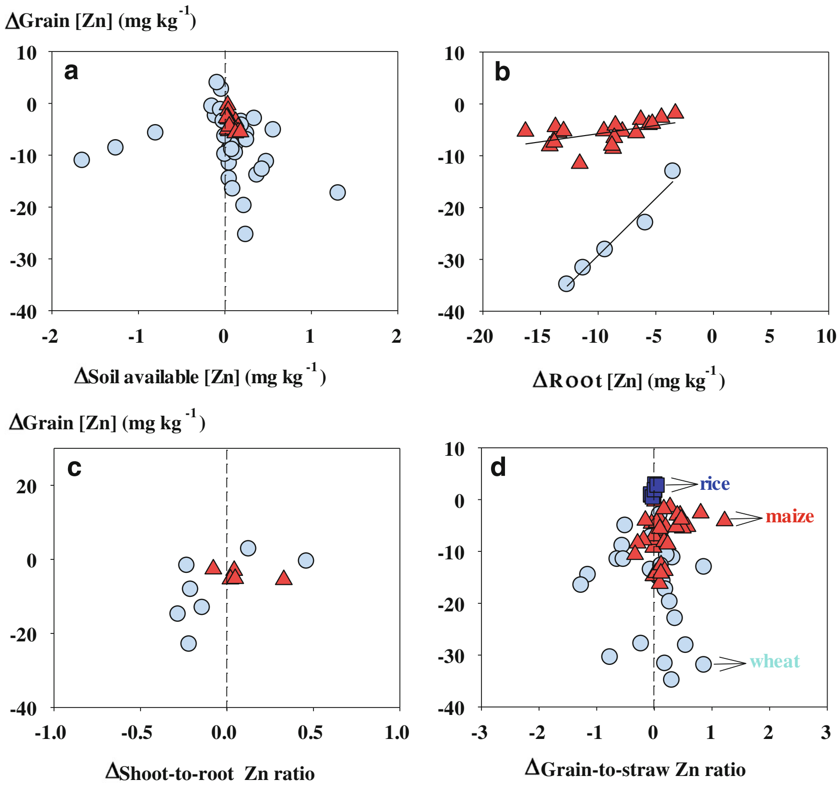

**Fig. 6** The relationship between Δ grain Zn concentration and **a** Δ soil available Zn concentration, **b** Δ root Zn concentration, **c** Δ shoot-to-root Zn ratio, and **d** grain-to-straw Zn ratio for wheat (circles), maize (triangles), and rice (squares). In (**b**), the regression equation is $y = -7.26 + 2.20*x$ ($R^2 = 0.96$) for wheat and $y = -2.59 + 0.32*x$ ($R^2 = 0.25$) for maize. No data is available for rice in (**a**), (**b**), and (**c**)

treatment, application of P fertilizer increased wheat grain dry weight by 35.7% and wheat shoot Zn content by 12.5%. Together, the decrease in Zn concentration in wheat roots, the substantial increase in wheat grain weight, and the smaller increase in wheat shoot Zn content suggest that Zn uptake efficiency by wheat roots is limited by P fertilizer application. The results confirm that the reduction in root Zn concentration caused by P application cannot be attributed to a restriction of root growth but instead can be attributed to the "dilution effect" (an increase in root biomass without a concomitant increase in root Zn content) and to a reduction in Zn uptake efficiency. A previous study also indicated that P application could restrict Zn concentration by roots (Zhang et al. 2016). Some physiological factors, including root dry weight, root colonization by AMF, and root exudation of organic acids, have been reported to indirectly affect Zn concentrations following P application (Hoffland et al. 2006; Lambers et al. 2006; Cavagnaro et al. 2010; Tian et al. 2012). The current global-scale meta-analysis is consistent with these previous reports.

Phosphorus application could potentially decrease root Zn concentration by decreasing root colonization by AMF and by decreasing root exudation of organic acids. Our meta-analysis indicated that P application reduced AMF root colonization, which is consistent with previous reports (Teng et al. 2013; Thompson et al. 2013). According to previous reports, AMF increase root uptake of P and metal elements (e.g., Zn, Cu, and Fe), which indicated that an increase in AMF root colonization can increase root uptake of Zn and P (Kothari et al. 1991; Smith 2003; Cavagnaro 2008; Ryan et al. 2008; Smith et al. 2011). A previous meta-analysis also reported that AMF increased Zn concentrations in various crops under P-deficient conditions (Lehmann et al. 2014). In wheat, P-deficient conditions caused the roots to increase their exudation of organic acids, which can increase P and Zn availability in the rhizosphere (Khademi et al. 2010). It is well indicated that organic acid exudation is able to mobilize Zn in soil. For instance, Rose et al. (2011) proposed that for rice, enhanced malate exudation was a response of Zn efficient rice genotypes to Zn deficiency. Another study also proved that carboxylates exuded by root increased Zn mobilization from a calcareous soil (Degryse et al., 2008), whereas the present study showed that P application reduced total organic acid exudation which was consistent with Shen et al. (2002). The results therefore indicated that P application could potentially affect rhizosphere processes and thereby decrease root Zn concentration.

### 3.3 Attaining both high grain yields and high grain Zn concentrations

We therefore suggest that the negative effect of P application on grain Zn concentration might be reduced by field management practices that alter root and rhizosphere properties, i.e., that increase root dry weight, AMF colonization, and organic acid exudation. In intensive agricultural production systems, the quantities of P fertilizer applied have frequently exceeded crop requirements in some regions (Vitousek et al. 2009). The quantity of P fertilizer applied, however, should be one that achieves both high grain yield and high grain Zn concentration. An optimal level of P fertilizer should be established based on soil P tests, crop requirements, and on data concerning the effects of P supply on crop roots and rhizosphere properties (Shen et al. 2013; Teng et al. 2013; Deng et al. 2017; Zhang et al. 2018). Teng et al. (2013) found that the optimal rate of P application for maximum grain yield was at or near the rate that began to negatively affect root and rhizosphere properties. In addition, crop breeding programs should attempt to improve root and rhizosphere properties (e.g., AMF colonization and organic acid exudation) so as to achieve both a high P-use efficiency (Hinsinger et al. 2005; Veneklaas et al. 2012) and a high grain Zn concentration. For instance, over-expression of *PSTOL1* (phosphorus-starvation tolerance 1), which increases early root growth in rice, significantly increases grain yield in P-deficient soil by enabling plants to acquire more P and other nutrients (Gamuyao et al. 2012). In another example, the genes *STOP1* (a transcription factor) and *ALMT1* (a malate transporter) underlie a malate exudation-dependent mechanism of Fe relocation in the root apical meristem and are essential for reprogramming root growth under low-P conditions (Mora-Macías et al. 2017). The current meta-analysis clearly shows that biofortification for increasing grain Zn concentration, whether via agronomic management or breeding, should account for the effects of P application on root and rhizosphere properties.

## 4 Conclusion

According to our meta-analysis, P fertilizer application resulted in an overall reduction of 16.0% in grain Zn concentration of wheat, maize, and rice. Zn content in grain, straw, and root of wheat and rice increased with increasing P application except for maize. Zinc mobilization processes, including soil available Zn, Zn translocation, and Zn remobilization, were not affected by P fertilizer supply and did not contribute to the reduction of grain Zn concentration. Root Zn concentration was substantially reduced by P fertilizer application and played an important role in decreasing grain Zn concentration. Our analysis indicated that P application decreased root Zn concentration by the "dilution effect" due to increasing root dry weight, and by altering root and rhizosphere properties including root colonization by AMF. P application increased wheat and maize biomass more than rice biomass, partly explaining why grain Zn concentration was reduced more in wheat and maize than in rice. Our meta-analysis is the first to assemble and assess quantitative data demonstrating a negative effect of P application on grain Zn concentration for wheat, maize, and rice. Our analysis is also the first to use meta-analysis to indicate that antagonism between P and Zn can be explained by the "dilution effect" and root and rhizosphere properties.

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**Data availability** The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

## Compliance with ethical standards

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## References

Adnan M (2016) Integrated effect of phosphorous and zinc on wheat quality and soil properties. Adv Environ Biol 10:40–45

Bogdanovic D, Ubavic M, Cuvardic M (1999) Effect of phosphorus fertilization on Zn and Cd contents in soil and corn plants. Nutr Cycl Agroecosyst 54:49–56. https://doi.org/10.1023/A:1009779415919

Cakmak I (2009) Enrichment of fertilizers with zinc: an excellent investment for humanity and crop production in India. J Trace Elem Med Biol 23:281–289. https://doi.org/10.1016/j.jtemb.2009.05.002

Cakmak I, Hoffland E (2012) Zinc for the improvement of crop production and human health. Plant Soil 361:1–2. https://doi.org/10.1007/s11104-012-1504-0

Cavagnaro TR (2008) The role of arbuscular mycorrhizas in improving plant zinc nutrition under low soil zinc concentrations: a review. Plant Soil 304:315–325. https://doi.org/10.1007/s11104-008-9559-7

Cavagnaro TR, Dickson S, Smith FA (2010) Arbuscular mycorrhizas modify plant responses to soil zinc addition. Plant Soil 329:307–313. https://doi.org/10.1007/s11104-009-0158-z

Chen WR, He ZL, Yang XE, Feng Y (2009) Zinc efficiency is correlated with root morphology, ultrastructure, and antioxidative enzymes in rice. J Plant Nutr 32:287–305. https://doi.org/10.1080/01904160802608627

Chen XP, Zhang YQ, Tong YP, Xue YF, Liu DY, Zhang W, Deng Y, Meng QF, Yue SC, Yan P, Cui ZL, Shi XJ, Guo SW, Sun YX, Ye YL, Wang ZH, Jia LL, Ma WQ, He MR, Zhang XY, Kou CL, Li YT, Tan DS, Cakmak I, Zhang FS, Zou CQ (2017) Harvesting more grain zinc of wheat for human health. Sci Rep-UK 7:7016. https://doi.org/10.1038/s41598-017-07484-2

Chen XX, Zhang W, Wang Q, Liu YM, Liu DY, Zou CQ (2019) Zinc nutrition of wheat in response to application of phosphorus to a calcareous soil and an acid soil. Plant Soil 434:139–150. https://doi.org/10.1007/s11104-018-3820-5

Chin JH, Gamuyao R, Dalid C, Bustamam M, Prasetiyono J, Moeljopawiro S, Wissuwa M, Heuer S (2011) Developing rice with high yield under phosphorus deficiency: Pup1 sequence to application. Plant Physiol 156:1202–1216. https://doi.org/10.1104/pp.111.175471

Coccina A, Cavagnaro TR, Pellegrino E, Ercoli L, McLaughlin MJ, Watts-Williams SJ (2019) The mycorrhizal pathway of zinc uptake contributes to zinc accumulation in barley and wheat grain. BMC Plant Biol 19:133. https://doi.org/10.1186/s12870-019-1741-y

Conley DJ, Likens GE (2009) Controlling eutrophication: nitrogen and phosphorus. Science 323:1014–1015. https://doi.org/10.1126/science.1167755

Degryse F, Verma VK, Smolders E (2008) Mobilization of Cu and Zn by root exudates of dicotyledonous plants in resin-buffered solutions and in soil. Plant Soil 306:69–84. https://doi.org/10.1007/s11104-007-9449-4

Deng Y, Feng G, Chen X, Zou C (2017) Arbuscular mycorrhizal fungal colonization is considerable at optimal Olsen-P levels for maximized yields in an intensive wheat-maize cropping system. Field Crop Res 209:1–9. https://doi.org/10.1016/j.fcr.2017.04.004

Duffner A, Hoffland E, Temminghoff E (2012) Bioavailability of zinc and phosphorus in calcareous soils as affected by citrate exudation. Plant Soil 361:165–175. https://xs.scihub.ltd/. https://doi.org/10.1007/s11104-012-1273-9

Faye I, Diouf O, Guissé A, Sène M, Diallo N (2006) Characterizing root responses to low phosphorus in pearl millet [*Pennisetum glaucum* (L.) R. Br.]. Agron J 98:1187–1194. https://doi.org/10.2134/agronj2005.0197

Gamuyao R, Chin JH, Pariasca-Tanaka J, Pesaresi P, Catausan S, Dalid C, Slamet-Loedin I, Tecson-Mendoza EM, Wissuwa M, Heuer S (2012) The protein kinase Pstol1 from traditional rice confers tolerance of phosphorus deficiency. Nature 488:535–539. https://xs.scihub.ltd/. https://doi.org/10.1038/nature11346

Gaume A, Mächler F, León CD, Narro L, Frossard E (2001) Low-P tolerance by maize (*Zea mays* L.) genotypes: significance of root growth, and organic acids and acid phosphatase root exudation. Plant Soil 228:253–264. https://xs.scihub.ltd/. https://doi.org/10.1023/A:1004824019289

Gibson RS (2012) Zinc deficiency and human health: etiology, health consequences, and future solutions. Plant Soil 361:291–299. https://xs.scihub.ltd/. https://doi.org/10.1007/s11104-012-1209-4

Haslett BS, Reid RJ, Rengel Z (2001) Zinc mobility in wheat: uptake and distribution of zinc applied to leaves or roots. Ann Bot 87:379–386. https://doi.org/10.1006/anbo.2000.1349

Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. Ecology 80:1150–1156. https://doi.org/10.1890/0012-9658(1999)080[1150:TMAORR]2.0.CO;2

Hinsinger P, Plassard C, Tang C, Jaillard B (2003) Origins of root-mediated pH changes in the rhizosphere and their responses to environmental constraints: a review. Plant Soil 248:43–59. https://xs.scihub.ltd/. https://doi.org/10.1023/A:1022371130939

Hinsinger P, Gobran GR, Gregory PJ, Wenzel WW (2005) Rhizosphere geometry and heterogeneity arising from root-mediated physical and chemical processes. New Phytol 168:293–303. https://doi.org/10.1111/j.1469-8137.2005.01512.x

Hoffland E, Wei CZ, Wissuwa M (2006) Organic anion exudation by lowland rice (*Oryza sativa* L.) at zinc and phosphorus deficiency. Plant Soil 283:155–162. https://xs.scihub.ltd/. https://doi.org/10.1007/s11104-005-3937-1

Ilag LL, Rosales AM, Elazegui FA, Mew TW (1987) Changes in the population of infective endomycorrhizal fungi in a rice-based cropping system. Plant Soil 103:67–73. https://xs.scihub.ltd/. https://doi.org/10.1007/BF02370669

Iqbal MM, Murtaza G, Mehdi SM, Naz T, Rehman A, Farooq O, Ali M, Sabir M, Ashraf M, Sarwar G (2017) Evaluation of phosphorus and zinc interaction effects on wheat grown in saline-sodic soil. Pak J Agric Sci 54:531–537. https://doi.org/10.21162/PAKJAS/17.4983

Itoh S, Barber SA (1983) Phosphorus uptake by six plant species as related to root hairs. Agron J 75:457–461. https://doi.org/10.2134/agronj1983.00021962007500030010x

Jemo M, Souleymanou A, Frossard E, Jansa J (2014) Cropping enhances mycorrhizal benefits to maize in a tropical soil. Soil Biol Biochem 79:117–124. https://doi.org/10.1016/j.soilbio.2014.09.014

Khademi Z, Jones DL, Malakouti MJ, Asadi F (2010) Organic acids differ in enhancing phosphorus uptake by *Triticum aestivum* L.-effects of rhizosphere concentration and counterion. Plant Soil 334:151–159. https://xs.scihub.ltd/. https://doi.org/10.1007/s11104-009-0215-7

Kothari SK, Marschner H, Römheld V (1991) Contribution of the VA mycorrhizal hyphae in acquisition of phosphorus and zinc by maize grown in a calcareous soil. Plant Soil 131:177–185. https://xs.scihub.ltd/. https://doi.org/10.1007/BF00009447

Lambers H, Shane MW, Cramer MD, Pearse SJ, Veneklaas EJ (2006) Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. Ann Bot-London 98:693–713. https://doi.org/10.1093/aob/mcl114

Lehmann A, Veresoglou SD, Leifheit EF, Rillig MC (2014) Arbuscular mycorrhizal influence on zinc nutrition in crop plants-a meta-analysis. Soil Biol Biochem 69:123–131. https://doi.org/10.1016/j.soilbio.2013.11.001

Lyu Y, Tang H, Li H, Zhang F, Rengel Z, Whalley WR, Shen J (2016) Major crop species show differential balance between root morphological and physiological responses to variable phosphorus supply. Front Plant Sci 7:1–15. https://doi.org/10.3389/fpls.2016.01939

MacDonald GK, Bennett EM, Potter PA, Ramankutty N (2011) Agronomic phosphorus imbalances across the world's croplands. P Natl Acad Sci USA 108:3086–3091. https://doi.org/10.1073/pnas.1010808108

Mora-Macías J, Ojeda-Rivera JO, Gutiérrez-Alanís D, Yong-Villalobos L, Oropeza-Aburto A, Raya-González J, Jiménez-Domínguez G, Chávez-Calvillo G, Rellán-Álvarez R, Herrera-Estrella L (2017) Malate-dependent Fe accumulation is a critical checkpoint in the root developmental response to low phosphate. P Natl Acad Sci USA 114:E3563–E3572. https://doi.org/10.1073/pnas.1701952114

Naeem A, Aslam M, Lodhi A (2018) Improved potassium nutrition retrieves phosphorus-induced decrease in zinc uptake and grain zinc concentration of wheat. J Sci Food Agric 98:4351–4356. https://doi.org/10.1002/jsfa.8961

Palmgren MG, Clemens S, Williams LE, Krämer U, Borg S, Schjørring JK, Sanders D (2008) Zinc biofortification of cereals: problems and solutions. Trends Plant Sci 13:464–473. https://doi.org/10.1016/j.tplants.2008.06.005

Pearson JN, Rengel Z (1994) Distribution and remobilization of Zn and Mn during grain development in wheat. J Exp Bot 45:1829–1835

Reddy DD, Yadav BR (1994) Zinc and phosphorus nutrition of wheat grown on a highly calcareous soil. Ann Arid Zone 33:233–237

Rengel Z, Batten GD, Crowley DE (1999) Agronomic approaches for improving the micronutrient density in edible portions of field crops. Field Crop Res 60:27–40. https://doi.org/10.1016/S0378-4290(98)00131-2

Rosado JL, Hambidge KM, Miller LV, Garcia OP, Westcott J, Gonzalez K, Conde J, Hotz C, Pfeiffer W, Ortiz-Monasterio I (2009) The quantity of zinc absorbed from wheat in adult women is enhanced by biofortification. J Nutr 139:1920–1925. https://doi.org/10.3945/jn.109.107755

Rose MT, Rose TJ, Pariasca-Tanaka J, Widodo WM (2011) Revisiting the role of organic acids in the bicarbonate tolerance of zinc-efficient rice genotypes. Funct Plant Biol 38:493–504. https://doi.org/10.1071/FP11008

Roy ED, Richards PD, Martinelli LA, Coletta LD, Lins SRM, Vazquez FF, Willig E, Spera SA, VanWey LK, Porder S (2016) The phosphorus cost of agricultural intensification in the tropics. Nat Plants 2: 1–6. https://xs.scihub.ltd/. https://doi.org/10.1038/nplants.2016.43

Ryan MH, McInerney JK, Record IR, Angus JF (2008) Zinc bioavailability in wheat grain in relation to phosphorus fertiliser, crop sequence and mycorrhizal fungi. J Sci Food Agric 88:1208–1216. https://doi.org/10.1002/jsfa.3200

Saeed M, Fox RL (1979) Influence of phosphate fertilization on zinc adsorption by tropical soils. Soil Sci Soc Am J 43:683–686. https://doi.org/10.2136/sssaj1979.03615995004300040011x

Safaya NM (1976) Phosphorus-zinc interaction in relation to absorption rates of phosphorus, zinc, copper, manganese, and iron in corn. Soil Sci Soc Am J 40:719–722. https://doi.org/10.2136/sssaj1976.03615995004000050031x

Sánchez-Rodríguez AR, Del Campillo MC, Torrent J (2017) Phosphorus reduces the zinc concentration in cereals pot-grown on calcareous Vertisols from southern Spain. J Sci Food Agric 97:3427–3432. https://doi.org/10.1002/jsfa.8195

Shen H, Yan X, Zhao M, Zheng S, Wang X (2002) Exudation of organic acids in common bean as related to mobilization of aluminum- and iron-bound phosphates. Environ Exp Bot 48:1–9. https://doi.org/10.1016/S0098-8472(02)00009-6

Shen J, Li C, Mi G, Li L, Yuan L, Jiang R, Zhang F (2013) Maximizing root/rhizosphere efficiency to improve crop productivity and nutrient use efficiency in intensive agriculture of China. J Exp Bot 64: 1181–1192. https://doi.org/10.1093/jxb/ers342

Smith SE (2003) Mycorrhizal fungi can dominate phosphate supply to plants irrespective of growth responses. Plant Physiol 133:16–20. https://doi.org/10.1104/pp.103.024380

Smith SE, Jakobsen I, Gronlund 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 Physiol 156:1050–1057. https://doi.org/10.1104/pp.111.174581

Stein AJ (2010) Global impacts of human mineral malnutrition. Plant Soil 335:133–154. https://xs.scihub.ltd/. https://doi.org/10.1007/s11104-009-0228-2

Su D, Zhou L, Zhao Q, Pan G, Cheng F (2018) Different phosphorus supplies altered the accumulations and quantitative distributions of phytic acid, zinc, and iron in rice (*Oryza sativa* l.) grains. J Agric Food Chem 66:1601–1611. https://doi.org/10.1021/acs.jafc.7b04883

Takkar PN, Mann MS, Bansal RL, Randhawa NS, Singh H (1976) Yield and uptake response of corn to zinc, as influenced by phosphorus fertilization. Agron J 68:942–946. https://doi.org/10.2134/agronj1976.00021962006800060024x

Teng W, Deng Y, Chen X, Xu X, Chen R, Lv Y, Zhao Y, Zhao X, He X, Li B (2013) Characterization of root response to phosphorus supply from morphology to gene analysis in field-grown wheat. J Exp Bot 64:1403–1411. https://doi.org/10.1093/jxb/ert023

Thompson JP, Clewett TG, Fiske ML (2013) Field inoculation with arbuscular-mycorrhizal fungi overcomes phosphorus and zinc deficiencies of linseed (*Linum usitatissimum*) in a vertisol subject to long-fallow disorder. Plant Soil 371:117–137. https://xs.scihub.ltd/. https://doi.org/10.1007/s11104-013-1679-z

Tian J, Wang X, Tong Y, Chen X, Liao H (2012) Bioengineering and management for efficient phosphorus utilization in crops and pastures. Curr Opin Biotechnol 23:866–871. https://doi.org/10.1016/j.copbio.2012.03.002

Veneklaas EJ, Lambers H, Bragg J, Finnegan PM, Lovelock CE, Plaxton WC, Price CA, Scheible WR, Shane MW, White PJ, Raven JA (2012) Opportunities for improving phosphorus-use efficiency in crop plants. New Phytol 195:306–320. https://doi.org/10.1111/j.1469-8137.2012.04190.x

Verma TS, Minhas RS (1987) Zinc and phosphorus interaction in a wheat-maize cropping system. Fertil Res 13:77–86. https://xs.scihub.ltd/. https://doi.org/10.1007/BF01049804

Vitousek PM, Naylor R, Crews T, David MB, Drinkwater LE, Holland E, Johnes PJ, Katzenberger J, Martinelli LA, Matson PA (2009) Nutrient imbalances in agricultural development. Science 324: 1519–1520. https://doi.org/10.1126/science.1170261

Watts-Williams SJ, Turney TW, Patti AF, Cavagnaro TR (2014) Uptake of zinc and phosphorus by plants is affected by zinc fertiliser material and arbuscular mycorrhizas. Plant Soil 376:165–175. https://xs.scihub.ltd/. https://doi.org/10.1007/s11104-013-1967-7

Watts-Williams SJ, Smith FA, McLaughlin MJ, Patti AF, Cavagnaro TR (2015) How important is the mycorrhizal pathway for plant Zn uptake? Plant Soil 390:157–166. https://xs.scihub.ltd/. https://doi.org/10.1007/s11104-014-2374-4

Wen Z, Li H, Shen J, Rengel Z (2017) Maize responds to low shoot P concentration by altering root morphology rather than increasing root exudation. Plant Soil 416:377–389. https://xs.scihub.ltd/. https://doi.org/10.1007/s11104-017-3214-0

Zhang Y, Deng Y, Chen R, Cui Z, Chen X, Russell Y, Zhang F, Zou C (2012) The reduction in zinc concentration of wheat grain upon increased phosphorus-fertilization and its mitigation by foliar zinc application. Plant Soil 361:143–152. https://xs.scihub.ltd/. https://doi.org/10.1007/s11104-012-1238-z

Zhang W, Liu D, Li C, Cui Z, Chen X, Russell Y, Zou C (2015) Zinc accumulation and remobilization in winter wheat as affected by phosphorus application. Field Crop Res 184:155–161. https://doi.org/10.1016/j.fcr.2015.10.002

Zhang W, Liu D, Liu Y, Cui Z, Chen X, Zou C (2016) Zinc uptake and accumulation in winter wheat relative to changes in root morphology and mycorrhizal colonization following varying phosphorus application on calcareous soil. Field Crop Res 197:74–82. https://doi.org/10.1016/j.fcr.2016.08.010

Zhang W, Liu D, Liu Y, Chen X, Zou C (2017a) Overuse of phosphorus fertilizer reduces the grain and flour protein contents and zinc bioavailability of winter wheat (*Triticum aestivum* L.). J Agric Food Chem 65:1473–1482. https://doi.org/10.1021/acs.jafc.6b04778

Zhang W, Chen X, Liu Y, Liu D, Chen X, Zou C (2017b) Zinc uptake by roots and accumulation in maize plants as affected by phosphorus application and arbuscular mycorrhizal colonization. Plant Soil 413: 59–71. https://xs.scihub.ltd/. https://doi.org/10.1007/s11104-017-3213-1

Zhang W, Chen X, Liu Y, Liu D, Du Y, Chen X, Zou C (2018) The role of phosphorus supply in maximizing the leaf area, photosynthetic rate, coordinated to grain yield of summer maize. Field Crop Res 219:113–119. https://doi.org/10.1016/j.fcr.2018.01.031

## References of the meta-analysis

Abbas AE, Hamad ME, Babiker HM, Nour AE (2007) Effects of phosphorus and zinc fertilizers on their contents in soil, plant and grains of corn. Gezira J Agric Sci 5:113–123

Amanullah I (2016) Residual phosphorus and zinc influence wheat productivity under rice-wheat cropping system. SpringerPlus 5:1–9. https://doi.org/10.1186/s40064-016-1907-0

Biswapati M, Mandal LN (1990) Effect of phosphorus application on transformation of zinc fraction in soil and on the zinc nutrition of lowland rice. Plant Soil 121:115–123. https://xs.scihub.ltd/. https://doi.org/10.1007/BF00013104

Chen X, Zhang W, Wang Q, Liu Y, Liu D, Zou C (2019) Zinc nutrition of wheat in response to application of phosphorus to a calcareous soil and an acid soil. Plant Soil 434:139–150. https://xs.scihub.ltd/. https://doi.org/10.1007/s11104-018-3820-5

Christensen NW, Jackson TL (1981) Potential for phosphorus toxicity in zinc-stressed corn and potato. Soil Sci Soc Am J 45:904–909. https://doi.org/10.2136/sssaj1981.03615995004500050017x

Coetzee PE, Ceronio GM, Preez CCD (2017) Effect of phosphorus and nitrogen sources on essential nutrient concentration and uptake by maize (*Zea mays* L.) during early growth and development. South African J Plant Soil 34:55–64. https://doi.org/10.1080/02571862.2016.1180714

Dang F, Wang W, Zhong H, Wang S, Zhou D, Wang Y (2016) Effects of phosphate on trace element accumulation in rice (*Oryza sativa* L.): a 5-year phosphate application study. J Soils Sediments 16:1440–1447. https://xs.scihub.ltd/. https://doi.org/10.1007/s11368-015-1342-9

Debnath S, Pachauri SP, Srivastava PC (2015) Improving use efficiency of applied phosphorus fertilizer by zinc fertilization in Basmati rice-wheat cropping system. Indian J Agric Res 49:414–420. https://doi.org/10.18805/ijare.v49i5.5803

Drissi S, Houssa A, Bamouh A, Coquant J, Benbella M (2015) Effect of zinc-phosphorus interaction on corn silage grown on sandy soil. Agriculture 5:1047–1059. https://doi.org/10.3390/agriculture5041047

Friesen DK, Miller MH, Juo ASR (1980) Liming and lime-phosphorus-zinc interactions in two Nigerian Ultisols: II. Effects on maize root and shoot growth. Soil Sci Soc Am J 44:1227–1232. https://doi.org/10.2136/sssaj1980.03615995004400060019x

Gao XP, Flaten DN, Tenuta M, Grimmett MG, Gawalko EJ, Grant CA (2011) Soil solution dynamics and plant uptake of cadmium and zinc by durum wheat following phosphate fertilization. Plant Soil 338:423–434. https://xs.scihub.ltd/. https://doi.org/10.1007/s11104-010-0556-2

Ghasemi-Fasaei R, Mayel S (2012) Influence of arbuscular mycorrhizal fungus, phosphorus and zinc on wheat grown on a calcareous soil. Int Res J Appl Basic Sci 3:1411–1416

Goh TB, Banerjee MR, Tu SH, Burton DL (1997) Vesicular arbuscular mycorrhizae-mediated uptake and translocation of P and Zn by wheat in a calcareous soil. Can J Plant Sci 77:339–346. https://doi.org/10.4141/P95-079

Grant CA, Bailey LD, Harapiak JT, Flore NA (2002) Effect of phosphate source, rate and cadmium content and use of Penicillium bilaii on phosphorus, zinc and cadmium concentration in durum wheat grain. J Sci Food Agric 82:301–308. https://doi.org/10.1002/jsfa.1034

Hagh ED, Mirshekari B, Ardakani MR, Farahvash F, Rejali F (2016) Optimizing phosphorus use in sustainable maize cropping via mycorrhizal inoculation. J Plant Nutr 39:1348–1356. https://doi.org/10.1080/01904167.2015.1086797

Haldar M, Mandal LN (1981) Effect of phosphorus and zinc on the growth and phosphorus, zinc, copper, iron and manganese nutrition of rice. Plant Soil 59:415–425. https://doi.org/10.1007/BF02184546

Imran M, Rehim A, Sarwar N, Hussain S (2015) Zinc bioavailability in maize grains in response of phosphorous-zinc interaction. J Plant Nutr Soil Sci 179:60–66. https://doi.org/10.1002/jpln.201500441

Jain NK, Dahama AK (2006) Phosphorus and zinc requirements of wheat under wheat (*Triticum aestivum*)-pearl millet (*Pennisetum glaucum*) cropping system. Arch Agron Soil Sci 52:645–653. https://doi.org/10.1080/03650340601036541

Jin JJ, Wang ZH, Dai J, Wang S, Gao YJ, Cao HB, Rong YU (2014) Effects of long-term N and P fertilization with different rates on Zn concentration in grain of winter wheat. J Plant Nutr Fertil 20:1358–1367 (In Chinese with English abstract)

Khan WD, Faheem M, Khan MY, Hussain S, Maqsood MA, Aziz T (2014) Zinc requirement for optimum grain yield and zinc biofortification depends on phosphorus application to wheat cultivars. Rom Agric Res 32:155–163

Kizilgoz I, Sakin E (2010) The effects of increased phosphorus application on shoot dry matter, shoot P and Zn concentrations in wheat (*Triticum durum* L.) and maize (*Zea mays* L.) grown in a calcareous soil. Afr J Biotechnol 9:5893–5896

Lambert DH, Baker DE, Cole H (1979) The role of mycorrhizae in the interactions of phosphorus with zinc, copper, and other elements. Soil Sci Soc Am J 43:976–980. https://doi.org/10.2136/sssaj1979.03615995004300050033x

Li M, Wang S, Tian X, Zhao J, Li H, Guo C, Chen Y, Zhao A (2015) Zn distribution and bioavailability in whole grain and grain fractions of winter wheat as affected by applications of soil N and foliar Zn combined with N or P. J Cereal Sci 61:26–32. https://doi.org/10.1016/j.jcs.2014.09.009

Lu S, Miller MH (1989) The role of VA mycorrhizae in the absorption of P and Zn by maize in field and growth chamber experiments. Can J Soil Sci 69:97–109. https://doi.org/10.4141/cjss89-009

Lu X, Tian X, Cui J, Zhao A, Yang X, Mai W (2011) Effects of combined phosphorus-zinc fertilization on grain zinc nutritional quality of wheat grown on potentially zinc-deficient calcareous soil. Soil Sci 176:684–690. https://doi.org/10.1097/SS.0b013e3182331635

Maftoun M, Moshiri F (2010) Growth, mineral nutrition and selected soil properties of lowland rice, as affected by soil application of organic wastes and phosphorus. J Agr Sci Tech-Iran 10:481–492

Mai W, Tian X, Lu X (2011a) A study on zinc-phosphorus interaction of wheat plants at different growth stages. Acta Agric Boreali Sin 26: 205–213 (In Chinese with English abstract)

Mai WX, Tian XH, Lu XC, Yang XW (2011b) Effect of Zn and P supply on grain Zn bioavailability in wheat. Chin J Eco-Agric 19:1243–1249 (In Chinese with English abstract)

Moraghan JT (1984) Differential responses of five species to phosphorus and zinc fertilizers. Commun Soil Sci Plan 15:437–447. https://doi.org/10.1080/00103628409367486

Orabi AA, El-Kobbia T, Fathi AI (1985) Zinc-phosphorus relationship in the nutrition of corn plants (*Zea mays* L.) as affected by the total carbonate content of the soil. Plant Soil 83:317–321. https://xs.scihub.ltd/. https://doi.org/10.1007/BF02184302

Racz GJ, Haluschak PW (1974) Effects of phosphorus concentration on Cu, Zn, Fe and Mn utilization by wheat. Can J Soil Sci 54:357–367. https://doi.org/10.4141/cjss74-049

Ragab SM (1980) Phosphorus effects on zinc translocation in maize. Commun Soil Sci Plan 11:1105–1127. https://doi.org/10.1080/00103628009367108

Singh JP, Karamanos RE, Stewart JWB (1986) Phosphorus-induced zinc deficiency in wheat on residual phosphorus plots. Agron J 78:668–675. https://doi.org/10.2134/agronj1986.00021962007800040023x

Smith EG, Janzen H, Ellert B (2017) Effect of fertilizer and cropping system on grain nutrient concentrations in spring wheat. Can J Soil Sci 98:125–131. https://doi.org/10.1139/cjps-2017-0079

Totawat KL, Saeed M (1990) Zinc-phosphorus interaction on growth and nutrient uptake by maize (*Zea mays* L.). Ann Arid Zone 29:19–23

Vafaei G, Sarraf A (2014) Effect of phosphorus and zinc fertilizer application to increasing the quality of nourishment in winter wheat. Int J Biosci 5:82–87

Zan YL (2012) Effect of nitrogen and phosphorus fertilizer rate on yield, nutrient utilization and grain mineral nutrient quality of wheat in dryland. Yangling, Shaanxi: PhD Dissertations of Northwest A&F University. (In Chinese with English abstract)

Zhang W, Liu D, Li C, Chen X, Zou C (2017c) Accumulation, partitioning, and bioavailability of micronutrients in summer maize as affected by phosphorus supply. Eur J Agron 86:48–59. https://doi.org/10.1016/j.eja.2017.03.005

Zhao RF, Zou CQ, Zhang FS (2007) Effects of long-term P fertilization on P and Zn availability in winter wheat rhizosphere and their nutrition. Plant Nutr Fertil Sci 13:368–372 (In Chinese with English abstract)