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Bioavailability of zinc sources and their interaction with phytates in broilers and piglets

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Zinc (Zn) is essential for swine and poultry and native Zn concentrations in feedstuffs are too low to meet their Zn requirement. Dietary Zn bioavailability is affected by phytate, phytase and Zn supplemented in organic form is considered as more bioavailable than inorganic sources. A meta-analysis using GLM procedures was processed using broiler and piglet databases to investigate, within the physiological response of Zn, (1) the bioavailability of inorganic and organic Zn sources (Analysis I); (2) the bioavailability of native and inorganic Zn dependent from dietary phytates, vegetal and supplemental phytase activity (Analysis II). Analysis I: the bioavailability of organic Zn relative to inorganic Zn sources ranged, depending on the variable, from 85 to 117 never different from 100 ($P > 0.05$). The coefficients of determination of the regressions were 0.91 in broilers and above 0.89 in piglets. Analysis II: in broilers, bone Zn was explained by supplemental Zn (linear and quadratic, $P < 0.001$) and by supplemental phytase (linear, $P < 0.001$). In piglets, the interaction between dietary Zn and phytates/phytases was investigated by means of a new variable combining dietary phytic phosphorus (PP) and phytase activity. This new variable represents the remaining dietary PP after its hydrolysis in the digestive tract, mainly due to phytase and is called non-hydrolyzed phytic phosphorus (PP_{NH}). Bone Zn was increased with native Zn ($P < 0.001$), but to a lower extent in high PP or low phytase diets ($ZN_N \times PP_{NH}$, $P < 0.001$). In contrast, the increase in bone zinc in response to supplemental Zn ($P < 0.001$) was not modulated by PP_{NH} ($P > 0.05$). The coefficients of determination of the regressions were 0.92 in broilers and above 0.92 in piglets. The results from the two meta-analyses suggest that (1) broilers and piglets use supplemented Zn, independent from Zn source; (2) broiler use native Zn and the use is slightly enhanced with supplemental phytase; (3) however, piglets are limited in the use of native Zn because of the antagonism of non-hydrolyzed dietary phytate. This explains the higher efficacy of phytase in improving Zn availability in this specie.

Keywords: zinc, broiler, piglet, phytate, phytase

Implications

It is essential to provide dietary zinc efficiently to optimize animal's Zn status, limit environmental Zn load and to the sustainable use of resources. The provided data indicate that broilers have the capacity to use some native Zn, even bound to phytates, which limits the beneficial effect of phytase in improving Zn bioavailability. In contrast, piglets seem not able to efficiently use Zn bound to phytates. Therefore, low presence of the antagonist phytate or high phytase activity presents an appropriate way to maximize Zn bioavailability. As phytates did not interact with supplemental zinc in broilers and piglets, any protection of supplemental Zn from reacting with phytates seems not necessary. This also resulted in similar bioavailability of organic and inorganic Zn sources in broilers and piglets.

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Introduction

As Zn is an essential element for the metabolism, a pollutant for the environment and a non-renewable resource, its use in animal nutrition needs to be efficient and sustainable.

Phytates are identified as the major dietary factor limiting Zn bioavailability in monogastrics, from the formation of insoluble phytate–zinc complexes. Their presence cannot be avoided in diets as phytate is the main storage form of phosphorus (P) in grains. Phosphorus in phytic form (PP) represents between 55% and 75% of total P in grains. Phytase hydrolyzes phytates and releases P to a similar extent in broilers and in piglets (Selle and Ravindran 2007 and 2008; Létourneau-Montminy *et al.*, 2010 and 2012). Phytase also releases Zn, but to a higher extent in piglets (Pallauf *et al.*, 1992 and 1994; Lei *et al.*, 1993; Adeola, 1995; Jondreville *et al.*, 2005) than in broilers (Biehl *et al.*, 1995; Mohanna and Nys, 1999b; Jondreville *et al.*, 2007). The dietary inclusion of 500 FTU of microbial

phytase (*Aspergillus niger*) into a maize and soybean meal-based diet allows to replace the inclusion of about 30 (Jondreville *et al.*, 2005) and 5 mg (Jondreville *et al.*, 2007) Zn from $ZnSO_4$ in pigs and broilers, respectively. The vegetal phytase may also contribute to release Zn.

Native Zn concentrations in feedstuffs are generally too low to meet the Zn requirement. Inorganic (oxides, sulfates, etc.) and organic Zn sources (non-ionic chemical bond between the Zn atom and the ligand, mostly an amino acid or a peptide) are supplemented by the feed industry where the second one, supposed to protect Zn from any reaction with phytates, is associated with a higher bioavailability. Zinc bioavailability is defined as the maximal Zn utilization for the biological functions in the metabolism, based on the amount of ingested Zn (Windisch, 2001). First, Wedekind *et al.* (1992) reported that Zn methionine was more available (+30%) than Zn sulfate to broilers. Later, two further broiler experiments reported an improved bioavailability for zinc with protein as ligand (Cao *et al.*, 2002; Ao *et al.*, 2006), but a reduced bioavailability for zinc methionine (Cao *et al.*, 2002). However, reviews on Zn availability for poultry and pigs estimated organic and inorganic Zn sources as equivalent (Ammerman *et al.*, 1995; Jongbloed *et al.*, 2002).

The aim of this meta-analysis on broiler and piglet experiments was to investigate (1) the bioavailability of inorganic and organic Zn sources; (2) the bioavailability of Zn in response to dietary phytate content and phytase activity in diets supplemented or not with $ZnSO_4$.

Material and methods

Databases

Experiments on Zn availability in broilers and piglets published between 1986 and 2010 were selected. The experiments were selected separately for two purposes: the comparison of supplemented Zn sources (Analysis I); the investigation of Zn bioavailability in interaction with dietary phytate content and phytase activity (Analysis II). One broiler and one piglet database that included general information (e.g. author name, institute), qualitative data (e.g. diet type) and quantitative data (e.g. diet composition, dietary Zn concentration, Zn contents in animal tissues) were then created. To select relevant observations for the subsequent analyses, each selected publication, experiment and treatment was encoded (Sauvant *et al.*, 2008). The data represented the treatment mean value within an experiment.

Experimental treatments were included into the database for Analysis I, if (1) the dietary Zn content was maximum 90 mg Zn/kg diet for broilers and 155 mg Zn/kg diet for piglets meant to limit homeostatic Zn regulation, (2) inorganic and organic Zn sources were not fed in the same dietary treatment, (3) inorganic Zn and organic Zn treatments were iso-dosed, (4) the dietary phytase activity was <500 and 0 FTU/kg diet for broilers and piglets, respectively, (5) no other feed additive (e.g. amino acid, organic acid, etc.) than trace minerals were studied within an experiment. Regarding the second condition, the supplementation level for inorganic and organic Zn sources of the selected treatments were equal within experiments, otherwise factor disconnectedness may appear, which is not appropriate for a meta-analysis (Sauvant *et al.*, 2008). Two unpublished broiler studies (in 2002 and 2003) comparing the bioavailability of Zn sources were kindly provided by the company Pancosma (Geneva, Switzerland) and included into the broiler database. For Analysis II, experiments published by INRA between 1999 and 2010 were included into the database of each specie. All these studies dealt with the effect of phytase on Zn availability. To provide data having studied the effects of phytates and vegetal phytase on Zn bioavailability, two broiler experiments (Linares *et al.*, 2007) conducted with a similar method than the ones conducted by INRA were also included.

Eleven broiler experiments involving 72 treatments and 10 broiler experiments involving 62 treatments met the inclusion criteria for Analyses I and II, respectively. Thirteen piglet experiments involving 54 treatments and five piglet experiments involving 31 treatments met the inclusion criteria for Analyses I and II, respectively. Each experiment from the broiler and piglet database is summarized in Tables 1 and 2, respectively.

Calculations and choice of the dependent and independent variables

The selected dependent variables were plasma Zn (expressed in mg/l) and bone Zn (expressed in mg/kg dry matter (DM)) in broilers and plasma Zn, plasma alkaline phosphatase activity (expressed in ALP, U/l), liver Zn (expressed in mg/kg DM), bone Zn and absorbed Zn (expressed in mg/kg diet ingested) in piglets. These dependent variables responded to increasing dietary Zn following graphical examination of the data using Minitab (2007). A bone ash content of 450 g/kg bone DM was defined when bone Zn content was expressed on ash basis.

Dietary independent variables were related to Zn, phytates and phytase activity. Zinc content (expressed in mg/kg diet) was identified as total Zn (ZN_{TOT}) that was split into native Zn (ZN_N), supplemented inorganic Zn (ZN_I) and supplemented organic Zn (ZN_O). In Analysis I, inorganic Zn was either zinc oxide or zinc sulfate with the exception of three broiler observations using zinc acetate. Organic Zn had either Zn with glycine, lysine, methionine, hydrolyzed soy protein (HSProt), hydrolyzed protein (HProt) or yeast protein (YProt) as ligand. In Analysis II, Zn was exclusively supplemented as $ZnSO_4$. In case of missing information on ZN_N, a value was estimated using the published feed ingredient formulation and the standard Zn contents of each ingredient from INRA-AFZ (Sauvant *et al.*, 2004). In case of missing information on supplemented Zn level, it was calculated as the difference between ZN_{TOT} and ZN_N. When dietary Zn was expressed in DM, a standard DM value of 890 g/kg diet was defined to calculate the value into fresh matter basis. Related to dietary phytates for Analysis II, PP content (expressed in g/kg diet), vegetal phytase activity ($Phytase_V$, expressed in U/kg diet), supplemented (microbial *A. niger*) phytase activity ($Phytase_S$, expressed in FTU/kg diet) and a new variable named

'non-hydrolyzed phytic P' content (PP_{NH}, expressed in g/kg diet) were identified. The variable PP_{NH} was introduced into the piglet model to take into account the phytate hydrolysis, mainly from dietary phytase. This approach was based on the hypothesis that the quantities of P and of Zn released are proportional when phytates are hydrolyzed. This proportionality was suggested by Jondreville *et al.* (2005) who have estimated that 1 additional g of digestible P equals 50 mg of Zn as sulfate in pigs. The new variable PP_{NH} was calculated from the difference between dietary PP and the quantity of released P by phytase. The released P was estimated from an equation that predicts the amount of digestible P in the pig (Létourneau-Montminy *et al.*, 2012). The terms related to phytate hydrolysis (variables PP, $Phytase_V$ and $Phytase_S$) were extracted from this equation to estimate the absorbed P from phytate hydrolysis, which was divided by 0.75 (Létourneau-Montminy *et al.*, 2011), to represent the released P. PP_{NH} is the difference between PP and this value: $PP_{NH} = PP - ((0.208 \times PP + 0.156 \times Phytase_S - 0.0132 \times Phytase_S^2 + 0.00298 \times Phytase_S^2 \times PP + 0.052 \times Phytase_V)/0.75)$, with PP_{NH} and PP expressed as g/kg diet and $Phytase_S$ and $Phytase_V$ as 100 FTU/kg diet.

Mathematical model and statistical analysis

For Analysis I, the selected independent variables were ZN_N, ZN_I, ZN_O and the dependent variables were plasma Zn, plasma ALP, liver Zn, bone Zn, absorbed Zn. For Analysis II, the selected independent variables were ZN_N, ZN_I, PP_{NH} in pigs and ZN_N, ZN_I, $Phytase_V$ and $Phytase_S$ in broilers. The dependent variable was bone Zn. A graphical examination of the within- and between-experiment responses of each dependent variable to the main independent variables (ZN_{TOT} and PP_{NH} in pigs and ZN_{TOT} in broilers) was also performed, as previously described by Sauvant *et al.* (2008). Through this examination, the data from Linares *et al.* (2007) were excluded from the dataset, as the low PP treatments (0.03 g PP/kg diet) resulted in a maximized bone Zn content (plateau). This step made it possible to verify whether the relationship was the same within and between experiments and to choose the type of model to use. All statistical procedures were carried out using the GLM procedure of SYSTAT (2007). Descriptive statistics (mean and range of values) were generated for each variable. Pearson correlation matrices were calculated between ZN_N and ZN_I and between ZN_N and ZN_O (Analysis I), between ZN_I and $Phytase_V$ and ZN_I and $Phytase_S$ (broilers, Analysis II) and between ZN_N and PP_{NH} and ZN_I and PP_{NH} (piglets, Analysis II).

The following model was used to study the effect of supplemental inorganic or organic Zn sources on Zn status and on absorbed Zn in broilers and in piglets (Analysis I, equation (1)):

$$Y_{uxyz} = a + a_u + b \times ZN_{N_{ux}} + c \times ZN_{I_{uy}} + d \times ZN_{O_{uz}} + c' \times ZN_{I_{uy}}^2 + d' \times ZN_{O_{uz}}^2 + bc \times ZN_{N_{ux}} \times ZN_{I_{uy}} + bd \times ZN_{N_{ux}} \times ZN_{O_{uz}} + \varepsilon_{uxyz}$$

The model used to study the effect of Zn, phytates and phytases on Bone Zn content (Analysis II) was differentiated between animal species. As the new defined variable PP_{NH} is based on pig data (Létourneau-Montminy *et al.*, 2012) and as the graphical examination of the broiler data did not indicate any clear sign that dietary PP content would affect the response of bone Zn, PP_{NH} was only used in piglets. In addition, there was not enough intra-experimental variability for PP, ZN_N and $Phytase_V$ in the broiler database.

The following model was used to study the effect of dietary Zn and phytase on bone Zn content in broilers (Analysis II, equation (2)):

$$Y_{uvy} = a + a_u + c \times ZN_{I_{uy}} + c' \times ZN_{I_{uy}}^2 + f \times Phytase_{S_{uv}} + f' \times Phytase_{S_{uv}}^2 + cf \times ZN_{I_{uy}} \times Phytase_{S_{uv}} + \varepsilon_{uvy}$$

The following model was used to study the effect of dietary Zn, phytate and phytases on bone Zn content in piglets (Analysis II, equation (3)):

$$Y_{uwxy} = a + a_u + b \times ZN_{N_{ux}} + c \times ZN_{I_{uy}} + c' \times ZN_{I_{uy}}^2 + g \times PP_{NH_{uw}} + bg \times ZN_{N_{ux}} \times PP_{NH_{uw}} + cg \times ZN_{I_{uy}} \times PP_{NH_{uw}} + \varepsilon_{uwxy}$$

In all three equations, Y_{uxyz}, Y_{uvy} and Y_{uwxy} are the expected outcome for the dependent variable Y observed in experiment u with levels v, w, x, y and z of the independent variable $Phytase_S$, PP_{NH}, ZN_N, ZN_I and ZN_O, respectively. a is the intercept, a_u is the effect of the experiment u on the intercept a with the condition that the sum of each a_u is equal to 0. b, c, d, f, g and c', d', f' are the linear/quadratic coefficients of ZN_N, ZN_I, ZN_O, $Phytase_S$, PP_{NH} and ZN_I^2, ZN_O^2, $Phytase_S^2$, respectively. Combined coefficients of variables are their interactions. ε_{uxyz}, ε_{uwy} and ε_{uwxy} are the residual errors.

In Analysis I, three tests were run on each dependent variable to evaluate the difference between ZN_I and ZN_O by comparing the estimated coefficients for ZN_I *v.* ZN_O; ZN_I^2 *v.* ZN_O^2 and $ZN_N \times ZN_I$ *v.* $ZN_N \times ZN_O$. The relative bioavailability (RBV) from ZN_O to ZN_I was calculated from the ratio of the ZN_O response slope to the ZN_I response slope times 100. When $ZN_N \times ZN_I$ and $ZN_N \times ZN_O$ were significant, the RBV was calculated for several levels of ZN_N.

In all three equations, the experiment was introduced in the model as fixed effect in order to ensure a proper prediction of coefficients of the model and an accurate description of the error of prediction (Sauvant *et al.*, 2008). Non-significant variables were sequentially removed from the model in order to simplify the final equation. The coefficient of determination (R^2) and the root mean square error (r.m.s.e.) of each generated equation were calculated between the predicted and observed value from each treatment. Differences between variables were considered significant, when $P < 0.05$ and as tendencial when $P < 0.10$.

Graphical examinations were carried out at each stage of the meta-analysis process.

Results

Description of the databases

The broiler dataset (Table 1) included experiments based on synthetic, semi-synthetic, cereal/soybean meal- and maize/soybean meal-based diets with Zn contents ranging from 1 to 85 mg/kg and 20 to 110 mg/kg for Analysis I and II, respectively. The ZN_O sources had synthetic amino acids as ligands in 72% of the observations in Analysis I. Broiler bone Zn responded quadratically to dietary Zn in the dataset for Analysis I (bone Zn (mg/kg DM) $= -2.5 + 4.6 \times Zn - 0.028 \times Zn^2$, $R^2 = 0.95$, r.m.s.e. $= 12.4$) and in the dataset for Analysis II (bone Zn (mg/kg DM) $= -14.5 + 4.7 \times Zn - 0.026 \times Zn^2$, $R^2 = 0.92$, r.m.s.e. $= 13.7$) indicating that the homeostatic counter regulation of Zn has started with the upper dietary Zn levels. The piglet dataset (Table 2) included experiments based on semi-synthetic, cereal/soybean meal and maize/soybean meal diets with Zn contents ranging from 17 to 155 mg/kg and 28 to 128 mg/kg for Analysis I and II, respectively. The ZN_O sources had synthetic amino acid as ligands in 54% of the observations in Analysis I. Piglet bone Zn responded linearly to dietary Zn in the dataset for Analysis I (bone Zn (mg/kg DM) $= 44.0 + 0.84 \times Zn$, $R^2 = 0.97$, r.m.s.e. $= 9.7$) and in the dataset for Analysis II (bone Zn (mg/kg DM) $= 48.8 + 0.38 \times Zn$, $R^2 = 0.29$, r.m.s.e. $= 19.3$) indicating that the homeostatic counter regulation of Zn was negligeable. The descriptive statistics of the broiler and piglet data are presented in Tables 3 and 4, respectively. Some experiments did not report all dependent variables of interest; therefore, the number of observations across dependent variables was not constant. In Analysis I, Pearson correlations between ZN_N and each of the supplemented Zn source were low and not significant ($P > 0.10$). In Analysis II, Pearson correlations between ZN_I and $Phytase_S$ in broilers and between PP_{NH}, ZN_N and ZN_I in piglets were low and not significant ($P > 0.10$). Therefore, the effect of the dependent variables and their interactions could be adequately assessed from the different datasets to evaluate dietary Zn availability on broilers and piglets.

Bioavailability of zinc sources in broilers (Analysis I, equation (1))

The estimated ZN_N-, ZN_I- and ZN_O-dependent regressions for plasma Zn and bone Zn are presented in Table 5 and illustrated in Figure 1. Regression equations were calculated with an R^2 value of 0.91 for plasma Zn and bone Zn. The dependent variables increased linearly with increasing ZN_N ($P < 0.01$). They also increased linearly with increasing ZN_I and ZN_O ($P < 0.001$), but in an extent that decreased as ZN_N increased (interaction $ZN_N \times ZN_I$ and $ZN_N \times ZN_O$, $P < 0.01$). In addition, bone Zn responded quadratically to ZN_I and ZN_O ($P < 0.001$). There was no difference ($P > 0.10$) between the coefficients for ZN_I and ZN_O in any of the dependent variables. As a consequence, the calculated bioavailability of ZN_O relative to ZN_I was very close to 100%, ranging between 93% and 113% depending on the used variable.

Bioavailability of zinc sources in piglets (Analysis I, equation (1))

The estimated ZN_N-, ZN_I-, and ZN_O-dependent regressions for plasma Zn, plasma ALP, liver Zn, bone Zn and absorbed Zn were calculated with R^2 values above 0.89 (Table 6 and Figure 2). An increase in ZN_N did not improve the value of the dependent variables. It even reduced the response for absorbed Zn ($P = 0.08$), liver Zn ($P < 0.001$) and bone Zn ($P < 0.05$). The dependent variables responded linearly (absorbed Zn, plasma Zn, plasma ALP and bone Zn, $P < 0.001$ and liver Zn, $P < 0.01$) and quadratically (plasma Zn, $P < 0.05$ and plasma ALP, $P < 0.10$) with increasing supplemented Zn. No difference was calculated between coefficients for ZN_I and ZN_O ($P > 0.05$), except the coefficient for ZN_O^2, which was slightly inferior to the one for ZN_I^2 in plasma Zn ($P < 0.10$). As a consequence, the calculated bioavailability of ZN_O relative to ZN_I was very close to 100%, ranging between 85% and 117% for plasma Zn, plasma ALP, liver Zn, bone Zn and absorbed Zn.

Interaction between dietary phytase and zinc in broilers (Analysis II, equation (2))

The graphical analysis of the broiler bone Zn response to the dietary Zn contents revealed a concordant curvilinear response between experiments (data not shown). As the data from Linares *et al.* (2007) were discarded, there was no intra-experimental PP variability in any remaining experiment, which consequently excluded this variable from the model. The model included ZN_I and $Phytase_S$ as dependent variables to estimate bone Zn and revealed an R^2 value of 0.92 (Table 7). The improved bone Zn content originated from ZN_I (linear and quadratic, $P < 0.001$) and from $Phytase_S$ (linear, $P < 0.001$). In addition, the positive effect of ZN_I on bone Zn was reduced as $Phytase_S$ increased (interaction $ZN_I \times Phytase_S$, $P < 0.05$).

Interaction between dietary phytates, phytase and zinc in piglets (Analysis II, equation (3))

The graphical analysis of bone Zn response to dietary Zn revealed two distinct populations: one fed with high PP diets, without phytase supplementation and one fed with low PP diets or high PP diets, but including supplemented phytase (data not shown). The remaining PP after phytates hydrolysis from vegetal and supplemental phytase in the gut, represented by PP_{NH}, made it possible to implement the inter-dependent variables PP, $Phytase_V$ and $Phytase_S$ into a single variable. The estimated ZN_N, PP_{NH} and ZN_I dependent regression for bone Zn was calculated with an R^2 value of 0.92 (Table 8). The improved bone Zn content from ZN_N ($P < 0.001$) was clearly reduced by the interaction with PP_{NH} ($ZN_N \times PP_{NH}$, $P < 0.001$). Bone Zn increased linearly ($P < 0.001$) and quadratically ($P < 0.001$) with dietary Zn

Table 1 *Summary of the broiler experiments*

Exp. no.	Reference	Number of treatments	Diet type[a]	PP (g/kg)	$Phytase_V$ (U/kg)	$Phytase_S$ (FTU/kg)	ZN_N (mg/kg)	ZN_{TOT} (mg/kg)	ZN_I sources	ZN_O ligands	Plasma Zn	Bone Zn
For Analysis I												
1	Bao *et al.* (2007)	4	Cereal/soy	nd	nd	0	20	20, 40, 60, 70	Sulfate	YProt		X
2	Cao *et al.* (2002)	7	Maize/soy	nd	nd	0	21	21, 51, 81	Acetate	HProt, methionine		X
3	Gebert *et al.* (2002)	3	Cereal/soy	nd	nd	0	21	31	Sulfate	HSProt, glycine	X	X
4	Mohanna and Nys (1999a)	10	Cereal/soy	1.9	nd	0	20	20, 30, 45, 60	Sulfate	Methionine	X	X
5	Pancosma (2003)	6	Cereal/soy	nd	nd	0	27	42, 57	Sulfate	HSProt, glycine	X	
6	Pancosma (2002)	9	Maize/soy	nd	nd	0	44	44, 54, 64, 74, 84	Oxide	Methionine	X	X
7	Schlegel *et al.* (2010)	3	Cereal/soy	2.3	201	0	38	38, 53	Sulfate	Glycine	X	X
8	Swiatkiewicz *et al.* (2001)	7	Cereal/soy	nd	nd	0	44	44, 54, 64, 84	Sulfate	HSProt		X
9	Wedekind *et al.* (1992)	5	Soy isolate	nd	nd	0	13	13, 21, 28	Sulfate	Methionine	X	X
10	Wedekind *et al.* (1992)	7	Synthetic	nd	nd	0	1	1, 4, 7, 10	Sulfate	Methionine		X
11	Wedekind *et al.* (1992)	11	Maize/soy	nd	nd	0	45	45, 50, 55, 65, 75, 85	Sulfate	Methionine		X
For Analysis II												
101	Jondreville *et al.* (2007)	11	Maize/soy	2.4	40	0, 280, 390, 660, 850	33	33, 39, 45, 50, 55, 93, 94	Sulfate	–		X
102	Linares *et al.* (2007)	3	Cereal/casein	0.03, 1.4	110	0	24	24, 34, 44	Sulfate	–		X
103	Linares *et al.* (2007)	6	Cereal/casein	0.03, 1.4	0, 110	0	27	27, 37, 47	Sulfate	–		X
104	Mohanna and Nys (1999a)	4	Cereal/soy	1.9	nd	0	20	20, 30, 45, 60	Sulfate	–		X
105	Mohanna and Nys (1999a)	4	Maize/soy	1.5	nd	0	25	65, 75, 90, 110	Sulfate	–		X
106	Mohanna and Nys (1999b)	4	Maize/soy	3.1	70	0, 830	31	45, 66	Sulfate	–		X
107	Mohanna and Nys (1999b)	4	Maize/soy	2.0	110	0, 480	22	32, 52	Sulfate	–		X
108	Mohanna *et al.* (1999)	6	Maize/soy	2.4	40	0, 800	37	37, 51, 72	Sulfate	–		X
109	Mohanna *et al.* (1999)	6	Maize/soy	1.9	60	0, 1250	34	34, 44, 64	Sulfate	–		X
110	Schlegel *et al.* (2010)	4	Cereal/soy	2.3	201	0, 487	38	38, 53	Sulfate	–		X

PP = phytic phosphorus; $Phytase_V$ = vegetal phytase; $Phytase_S$ = supplemented phytase; ZN_N = native zinc; ZN_{TOT} = total zinc; ZN_I = inorganic zinc; ZN_O = organic zinc; nd = not described; YProt = yeast protein; HProt = hydrolyzed protein; HSProt = hydrolyzed soybean meal protein.
[a]Soy = soybean meal; cereal = other cereals than maize.

Table 2 *Summary of the piglet experiments*

Exp. No.	Reference	Number of treatments	Diet type[a]	PP (g/kg)	$Phytase_V$ (U/kg)	$Phytase_S$ (FTU/kg)	ZN_N (mg/kg)	ZN_{TOT} (mg/kg)	ZN_I sources	ZN_O ligands	Plasma Zn	ALP	Liver Zn	Bone Zn	Absorbed Zn
For Analysis I															
1	Cheng *et al.* (1998)	3	Maize/soy	2.5	nd	0	30	30, 130	Sulfate	Lysine	X		X	X	X
2	Cheng *et al.* (1998)	3	Maize/soy	2.5	nd	0	27	27, 127	Sulfate	Lysine	X		X	X	X
3	Lee *et al.* (2001a)	3	Maize/soy	nd	nd	0	35	155	Sulfate	Methionine, Hprot	X				
4	Lee *et al.* (2001b)	3	Maize/soy	nd	nd	0	35	155	Sulfate	Methionine, Hprot	X				
5	Männer *et al.* (2006)	4	Cereal/whey	nd	nd	0	25	25, 44	Sulfate	HSProt, glycine	X				X
6	Revy *et al.* (2002)	7	Maize/soy/whey	0.8	nd	0	28	28, 40, 46, 56	Sulfate	Methionine	X	X	X	X	X
7	Revy *et al.* (2004)	3	Maize/soy/whey	2.5	116	0	32	32, 50	Sulfate	Methionine	X	X	X	X	X
8	Schlegel *et al.* (2010)	6	Maize/casein, maize/soy	1.3, 2.3	27, 201	0	25, 38	25, 38, 40, 53	Sulfate	Glycine	X	X		X	
9	Susaki *et al.* (1999)	3	Cereal/soy/whey	1.5	nd	0	47	47, 147	Sulfate	Hprot	X		X	X	
10	Swinkels *et al.* (1996)	3	Soy isolate	nd	nd	0	17	17, 62	Sulfate	Hprot	X	X	X		
11	Swinkels *et al.* (1996)	4	Soy isolate	nd	nd	0	17	62	Sulfate	Hprot	X	X	X		
12	Wedekind *et al.* (1994)	4	Maize/soy	nd	nd	0	32	32, 40, 47	Sulfate, oxide	Methionine, lysine	X			X	
13	Zacharias *et al.* (2004)	8	Cereal/soy	nd	nd	0	35	65, 105	Sulfate	nd					X
For Analysis II															
101	Jondreville *et al.* (2005)	8	Maize/soy/whey	2.1	60	0, 150, 260, 510, 870	30	30, 40, 50, 67, 128	Sulfate	–				X	
102	Revy *et al.* (2002)	4	Cereal/whey	0.8	nd	0	28	28, 40, 46, 56	Sulfate	–				X	
103	Revy *et al.* (2004)	4	Maize/soy/whey	2.5	116	0, 1219	32	32, 50	Sulfate	–				X	
104	Revy *et al.* (2006)	9	Maize/soy/whey	2.9	150	0, 700	34	34, 44, 60,70, 90, 100	Sulfate	–				X	
105	Schlegel *et al.* (2010)	6	Maize/casein, maize/soy	1.3, 2.3	27, 201	0, 487	25, 38	25, 38, 40, 53	Sulfate	–				X	

PP = phytic phosphorus; $Phytase_V$ = vegetal phytase; $Phytase_S$ = supplemented phytase; ZN_N = native zinc; ZN_{TOT} = total zinc; ZN_I = inorganic zinc; ZN_O = organic zinc; ALP = alkaline phosphatase; nd = not described; HProt = hydrolyzed protein; HSProt = hydrolyzed soybean meal protein.
[a]Soy = soybean meal; cereal = other cereals than maize; Whey = whey powder.

Table 3 *Descriptive statistics of the broiler variables*[a]

Data		Analysis I		Analysis II
		Plasma Zn (mg/l)	Bone Zn (mg/kg DM)	Bone Zn (mg/kg DM)
No of observations		36	66	43
Dependent variable				
	Min	0.68	45	45
	Max	1.99	214	214
	Mean	1.48	138	150
	s.e.m.	0.063	6.5	6.7
Independent variables				
ZN_N (mg/kg diet)	Min	13	1	20
	Max	44	45	38
	Mean	28	28	31
ZN_I (mg/kg diet)	Min	0	0	0
	Max	40	60	85
	Mean	7	8	20
ZN_O (mg/kg diet)	Min	0	0	0
	Max	40	60	0
	Mean	11	11	0
PP (g/kg diet)	Min	–	–	1.50
	Max	–	–	3.10
	Mean	–	–	2.28
$Phytase_S$	Min	–	–	0
(U/kg diet)	Max	–	–	1250
	Mean	–	–	277
Pearson correlations				
$ZN_N - ZN_I$		0.16 ns	0.13 ns	–
$ZN_N - ZN_O$		0.02 ns	0.03 ns	–
$ZN_I - phytase_S$		–	–	−0.23 ns

DM = dry matter; Min = minimum value; Max = maximum value; Mean = mean value; s.e.m. = standard error of the mean; ZN_N = native zinc; ZN_I = inorganic zinc; ZN_O = organic zinc; PP = phytic phosphorus; $Phytase_S$ = supplemented phytase.
ns: $P > 0.10$.
[a]Experiments 1 to 11 for Analysis I and experiments 101, 104 to 110 for Analysis II, described in Table 1.

supplementation. PP_{NH} did not interact with supplemented Zn ($ZN_I \times PP_{NH}$, $P > 0.10$). As PP_{NH} is dependent from dietary PP level and from vegetal and supplemented phytase activity, the evolution of bone Zn content with increasing levels of supplemental Zn was calculated using the equation from Létourneau-Montminy *et al.* (2012) and the regression from Table 8 in diets with varying PP (2.5 g PP/kg representing maize–soybean meal diets and 1.5 g PP/kg representing cereal-based diets enriched with milk by-products), varying levels of phytase addition (0, 500 and 1000 FTU/kg) and of endogenous phytase activity (0, 200 U/kg) in the diet with lower PP level, simulating its inactivation or not through pelleting process for example. This simulation is illustrated in Figure 3.

Discussion

Bioavailability of supplemented zinc sources

The two supplemented Zn sources (ZN_I and ZN_O) were available to broilers and to piglets as the dependent variables responded positively (Analysis I). The positive response for plasma Zn and bone Zn in broilers and for plasma Zn and ALP in piglets decreased progressively with increasing dietary Zn content probably because of the approach of a physiological maximum (plateau). It was expressed with the negative quadratic effect of supplemented Zn ($ZN_I \times ZN_I$ and $ZN_O \times ZN_O$) and with the interaction between ZN_N and supplemented Zn ($ZN_N \times ZN_I$ and $ZN_N \times ZN_O$) in broilers and with the quadratic effect of supplemented Zn ($ZN_I \times ZN_I$ and $ZN_O \times ZN_O$) in piglets. The broiler bone Zn responded slightly better to ZN_O than ZN_I with increasing ZN_N, but far away from any significant value. The piglet plasma Zn responded to a higher extent with the quadratic effect of ZN_O compared with the one of ZN_I, however, the response was counteracted by the numerically lower linear coefficient of ZN_O (0.0125 *v.* 0.0147). This eliminated any visible difference between the sources (Table 6; Figure 2). Taking into account the linear and quadratic effects on supplemented Zn and their interactions with ZN_N, ZN_O and ZN_I were finally equally bioavailable in broilers and in piglets. With the used dataset for broilers, it is however debatable to which extent the quadratic response of bone Zn had a softening effect on the ZN_I and ZN_O slopes and to which extent this may have attenuated potential differences.

Table 4 *Descriptive statistics of the piglet variables*[a]

Data		Analysis I					Analysis II
		Plasma Zn (mg/l)	Plasma ALP (U/l)	Liver Zn (mg/kg DM)	Bone Zn (mg/kg DM)	Absorbed Zn (mg/kg diet ingested)	Bone Zn (mg/kg DM)
No. of observations		46	23	23	28	28	31
Dependent variable							
Min		0.15	25	92	34	5.5	33
Max		1.83	315	311	174	39.4	103
Mean		0.73	152	177	85	17.2	66
s.e.m.		0.064	14.1	13.6	8.1	1.60	3.8
Independent variables							
ZN_N (mg/kg diet)	Min	17	17	17	25	25	25
	Max	47	28	47	47	35	38
	Mean	29	26	27	32	30	31
ZN_I (mg/kg diet)	Min	0	0	0	0	0	0
	Max	120	45	100	100	100	102
	Mean	18	11	22	14	18	19
ZN_O (mg/kg diet)	Min	0	0	0	0	0	0
	Max	120	45	100	100	100	0
	Mean	23	11	22	15	19	0
PP_{NH} (g/kg diet)	Min	–	–	–	–	–	0.33
	Max	–	–	–	–	–	2.00
	Mean	–	–	–	–	–	1.12
Pearson correlations							
$ZN_N - ZN_I$		0.11 ns	−0.33 ns	0.12 ns	0.12 ns	0.16 ns	–
$ZN_N - ZN_O$		0.19 ns	−0.33 ns	0.12 ns	0.12 ns	0.13 ns	–
$PP_{NH} - ZN_N$		–	–	–	–	–	0.42 ns
$PP_{NH} - ZN_I$		–	–	–	–	–	−0.17 ns

ALP = alkaline phosphatase; DM = dry matter; Min = minimum value; Max = maximum value; Mean = mean value; s.e.m. = standard error of the mean; ZN_N = native zinc; ZN_I = inorganic zinc; ZN_O = organic zinc; PP_{NH} = non-hydrolyzed phytic phosphorus.
ns = $P > 0.10$.
[a]Data from experiments described in Table 2.

Nevertheless, The results suggest a similar bioavailability of ZN_I and ZN_O, in line with previous qualitative reviews on the subject (Ammerman *et al.*, 1995; Jongbloed *et al.*, 2002).

Zinc bioavailability in response to dietary phytates content and phytase activity

Only bone Zn was selected as independent variable for Analysis II. Bone Zn content is a reliable indicator for Zn bioavailability as it is highly correlated with dietary Zn content (Hill *et al.*, 1986; Wedekind *et al.*, 1994; Mohanna and Nys, 1998; Revy *et al.*, 2003) and as it's maxima (plateau) is reached when dietary Zn content is higher than needed for other parameters. When dietary zinc content is increased, the approach of a physiological plateau for bone Zn, most probably explains the negative quadratic effect of supplemented Zn observed in broilers ($ZN_I \times ZN_I$, $P < 0.001$ in Analysis II) and in piglets ($ZN_I \times ZN_I$, $P < 0.05$ in Analysis II) and the negative interaction between supplemented Zn and supplemented phytases observed in broilers ($ZN_I \times Phytase_S$, $P < 0.05$ in Analysis II).

In broilers, as PP, ZN_N and $Phytase_V$ could not be taken into account for bone Zn content (Analysis II), only ZN_I and $Phytase_S$ remained in the model. The equation presented in Table 7 shows, as expected, that dietary Zn and phytase supplementations improve bone Zn concentration. The calculated ZN_I equivalency for $Phytase_S$ is 1.0 mg ZN_I/100 FTU in a non-Zn-supplemented diet. This value for non-supplemented Zn diets is compatible with the equivalency published by Jondreville *et al.* (2007).

In piglets, the accuracy of the new variable PP_{NH} was verified using non-supplemented Zn data. Although bone Zn content was poorly correlated to PP and ZN_N content ($R^2 = 0.003$), bone Zn content was linearly dependent from PP_{NH} and ZN_N in unsupplemented Zn diets (Bone Zn = 18.07 ($P = 0.11$) + 2.4082 ($P < 0.001$) × ZN_N − 1.2033 ($P < 0.001$) × PP_{NH}, $R^2 = 0.93$, r.m.s.e. = 4.60). PP_{NH} is therefore a reliable variable and the release of P and Zn from phytates are proportional. In equation (3) (Table 8), the positive coefficients for ZN_N and ZN_I and the negative effect of PP_{NH} on ZN_N, but not on ZN_I coefficients for bone Zn content suggests that phytates reduced Zn bioavailability from native Zn only in pigs. The antagonism of vegetal phytates on native zinc bioavailability, was observed earlier in human nutrition (Sandström *et al.*, 1987). More recently, Rodrigues-Filho *et al.* (2005) found that phytates and Zn are, at least partially, bound in wheat grains and Revy *et al.* (2003) observed a positive linear relation between these two components in vegetal feed ingredients (about 10 mg Zn for 1 g PP), which also suggests that they are

Table 5 *Adjusted dependent variable response to dietary zinc sources (mg/kg diet) in broilers (Analysis I)*[a]

	Plasma Zn (mg/l)		Bone Zn (mg/kg DM)	
Model	Coefficient	*P*-value	Coefficient	*P*-value
Intercept	0.692	***	6.44	ns
ZN_N	0.0155	**	3.35	***
ZN_I	0.0493	***	4.78	***
ZN_O	0.0446	***	5.00	***
ZN_I^2		ns	−0.0333	***
ZN_O^2		ns	−0.0401	***
$ZN_N \times ZN_I$	−0.000945	***	−0.0544	***
$ZN_N \times ZN_O$	−0.000773	**	−0.0481	***
R^2	0.91		0.91	
r.m.s.e.	0.161		12.3	
ZN_I *v.* ZN_O	ns		ns	
ZN_I^2 *v.* ZN_O^2	–		ns	
$ZN_N \times ZN_I$ *v.* $ZN_N \times ZN_O$	ns		ns	
RBV average[b]	93		113	
RBV with ZN_N low[b]	91		108	
RBV with ZN_N medium[b]	92		113	
RBV with ZN_N high[b]	95		118	

DM = dry matter; ZN_N = native zinc; ZN_I = inorganic zinc; ZN_O = organic zinc; R^2 = coefficient of determination; r.m.s.e. = root mean square error; RBV = relative bioavailability.
***$P < 0.001$; **$P < 0.01$; ns: $P > 0.10$.
[a]The model was based on equation (1). Data from experiment nos 1 to 11 are described in Table 1.
[b]Calculated RBV from ZN_O to ZN_I. The three defined ZN_N levels for low, medium and high were 15, 30 and 40 mg/kg diet, respectively.

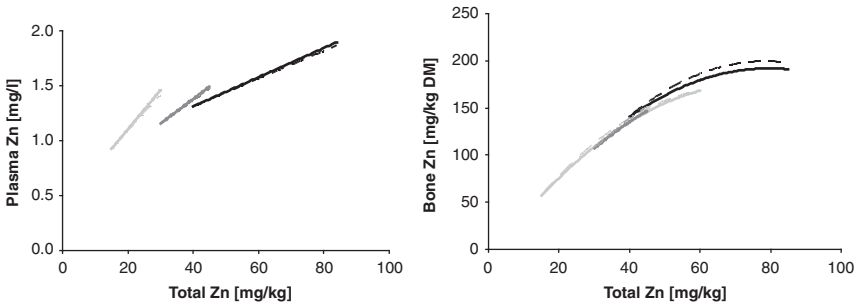

Figure 1 Response of plasma zinc (mg/l) and bone zinc (mg/kg dry matter) to total dietary zinc (mg/kg diet) in diets supplemented with inorganic (continuous curve) or with organic (dashed curve) sources in broilers (Analysis I)[a,b]. [a]Data from experiment nos 1–11 described in Table 1. [b]ZN_I and ZN_O were supplemented within their range of validity to a low (light gray), medium (gray) and high (black) level of ZN_N. The three defined ZN_N levels were 15, 30, 40 mg/kg for plasma Zn and bone Zn.

bound. The facts that native Zn would be bound to phytates and that native Zn bioavailability in pigs was consequently reduced (Analysis II) explain the findings in Analysis I, where piglet's Zn absorption and Zn status was not improved or even reduced with increasing ZN_N. In contrary to ZN_N, PP_{NH} was not an antagonist for ZN_I bioavailability in piglets (Analysis II). This finding is in contradiction with the reduced Zn absorbability, Zn status or growth from experiments having studied the effect of supplemental phytate (mostly as sodium phytate, $C_6H_6Na_{12}O_{24}P_6$) in semi-synthetic diets containing or not containing supplemental Zn (O'Dell and Savage, 1960; Oberleas *et al.*, 1962; Rimbach and Pallauf, 1992; Rimbach *et al.*, 1995; Windisch and Kirchgessner, 1999). As phytate from sodium phytate is easily ionizable under a wide pH range, ionized Zn from supplemental sources may rapidly bind to phytic acid (Davies and Nightingale, 1975). Under such experimental conditions, organic Zn sources were also better absorbed than Zn as $ZnSO_4$, probably from its reduced reaction with phytic acid issued from added sodium phytate (Schlegel and Windisch, 2006). However, as pointed out by Fordyce *et al.* (1987), interactions between sodium phytate and supplemental Zn may be enhanced compared with the interactions between plant phytates and supplemental Zn. This hypothesis was already made by Erdman (1979) who did not notice any effect of the presence of soy in rat diets on the bioavailability of Zn added as $ZnCO_3$. Thus, the present data suggest that any protection of supplemental Zn sources from PP appears not necessary in diets containing plant phytates. This is consolidated by the present

Table 6 *Adjusted dependent variable response to dietary zinc sources (mg/kg diet) in piglets (Analysis I)*[a]

	Plasma Zn (mg/l)		ALP (U/l)		Liver Zn (mg/kg DM)		Bone Zn (mg/kg DM)		Absorbed Zn (mg/kg diet ingested)	
Model	Coefficient	P-value	Coefficient	P-value	Coefficient	*P*-value	Coefficient	P-value	coefficient	P-value
Intercept	0.508	***	61.3	***	251	***	92.7	***	44.4	*
ZN_N		ns		ns	−4.757	***	−1.051	*	−1.211	+
ZN_I	0.0147	***	6.751	***	0.757	***	0.871	***	0.214	***
ZN_O	0.0125	***	6.601	***	0.736	**	0.874	***	0.250	***
ZN_I^2	−0.000113	***	−0.0786	+						
ZN_O^2	−0.000075	*	−0.0835	*						
R^2	0.93		0.91		0.92		0.96		0.90	
r.m.s.e.	0.0943		21.0		23.8		7.42		2.98	
ZN_I *v.* ZN_O	ns		ns		ns		ns		ns	
ZN_I^2 *v.* ZN_O^2	+		ns		–		–		–	
RBV[b]	85		98		97		100		117	

ALP = alkaline phosphatase; DM = dry matter; ZN_N = native zinc; ZN_I = inorganic zinc; ZN_O = organic zinc; R^2 = coefficient of determination; r.m.s.e. = root mean square error; RBV = relative bioavailability.
$^{***}P < 0.001$; $^{**}P < 0.01$; $^{*}P < 0.05$; $^{+}P < 0.10$; ns: $P > 0.10$.
[a]The model was based on equation (1). Data from experiment nos 1 to 13 are described in Table 2.
[b]Calculated RBV from ZN_O to ZN_I.

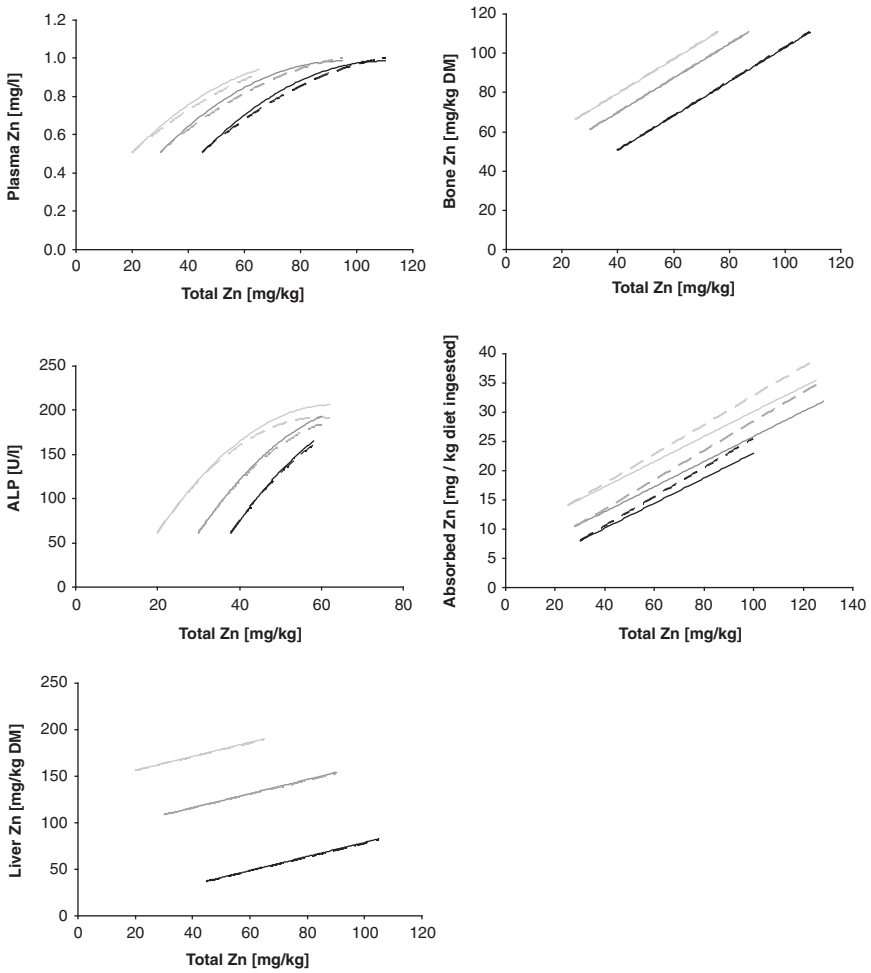

Figure 2 Response of plasma zinc (mg/l), plasma alkaline phosphatase (ALP) (U/l), liver zinc (mg/kg dry matter (DM)), bone zinc (mg/kg DM) and absorbed zinc (mg/kg ingested Zn) to total dietary zinc (mg/kg diet) in diets supplemented with inorganic (continuous curve) or with organic (dashed curve) sources in piglets (Analysis I)[a,b]. [a]Data from experiment nos 1 to 13 described in Table 2. [b]ZN_I and ZN_O were supplemented within their range of validity to either a low (light gray), medium (gray) and high (black) level of ZN_N. The three defined ZN_N levels were 25, 28, 30 mg/kg for absorbed Zn; 20, 30, 45 mg/kg for plasma Zn and liver Zn; 20, 30, 38 mg/kg for plasma ALP and 25, 30, 45 mg/kg for bone Zn.

Table 7 *Bone zinc content (mg/kg DM) from broilers dependent from the dietary content of supplemented Zn (mg/kg diet) and supplemented phytases (100 FTU/kg diet; Analysis II)*[a]

	Bone Zn	
Model	Coefficient	*P*-value
Intercept	95	***
$Phytase_S$	3.25	***
$Phytase_S \times Phytase_S$		ns
ZN_I	3.323	***
$ZN_I \times ZN_I$	−0.02550	***
$ZN_I \times Phytase_S$	−0.0935	*
R^2	0.92	
r.m.s.e.	12.5	

DM = dry matter; $Phytase_S$ = supplemented phytase; ZN_I = inorganic zinc; R^2 = coefficient of determination; r.m.s.e. = root mean square error.
***$P < 0.001$; *$P < 0.05$; ns: $P > 0.10$.
[a]The model was based on equation (2). Data from experiment no. 101, 104 to 110 described in table 1.

Table 8 *Bone zinc content (mg/kg DM) from weaned piglets dependent from the dietary content of non-hydrolyzed phytic phosphorus (g/kg diet) and from native and supplemented zinc (mg/kg diet; Analysis II)*[a]

	Bone Zn	
Model	Coefficient	*P*-value
Intercept	30.7	*
ZN_N	1.97	***
PP_{NH}		ns
$ZN_N \times PP_{NH}$	−1.15	***
ZN_I	1.01	***
$ZN_I \times ZN_I$	−0.00422	*
$ZN_I \times PP_{NH}$		ns
R^2	0.92	
r.m.s.e.	5.86	

DM = dry matter; PP_{NH} = non-hydrolyzed phytic phosphorus; ZN_N = native zinc; ZN_I = inorganic zinc; R^2 = coefficient of determination; r.m.s.e. = root mean square error.
***$P < 0.001$; *$P < 0.05$; ns. $P > 0.10$.
[a]The model was based on equation (3). Data from experiment nos 101 to 105 are described in Table 2.

meta-analysis indicating that organic Zn sources were not more bioavailable than inorganic Zn sources in broilers nor in piglets (Analysis I).

As the form of supplemental Zn was not a limiting factor for dietary Zn bioavailability in broilers and piglets, and as these two species differed in the efficiency of dietary Zn use, ZN_N bioavailability needs to be discussed between species. The data from Analysis I suggests that broilers are more efficient in using ZN_N than piglets and the data from Analysis II show that ZN_N was negatively affected by PP_{NH} in piglets and that $Phytase_S$ was more efficient in piglets to improve ZN_N bioavailability than in broilers. Zinc bioavailability results from dietary Zn solubility in the digestive tract before absorption (Susaki *et al.*, 1999), which is dependent from pH conditions (Cao *et al.*, 2000; Jongbloed *et al.*, 2002). Early in

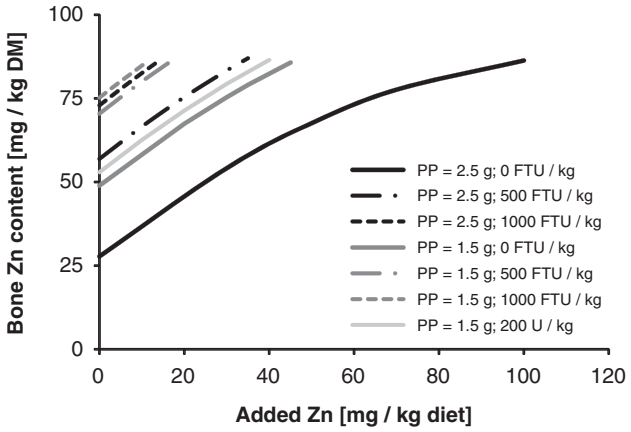

Figure 3 Model of piglet bone zinc (mg/kg dry matter) response to supplemental zinc (mg/kg diet) in various diets (Analysis II)[a,b]. [a]Data from experiment nos 101 to 105 described in Table 2. [b]PP_{NH} (g/kg) equivalencies for each diet: PP = 2.5 g/kg, 0 FTU/kg: 1.81; PP = 2.5 g/kg, 500 FTU/kg: 1.33; PP = 2.5 g/kg, 1000 FTU/kg: 0.49; PP = 1.5 g/kg, 0 FTU/kg: 1.08; PP = 1.5 g/kg, 500 FTU/kg: 0.34; PP = 1.5 g/kg, 1000 FTU/kg: 0.17; PP = 1.5 g/kg, 200 U/ kg: 0.95

1963, Lease measured that 66% of Zn from soybean meal was soluble when the raw material was previously digested with pepsin at pH 3, followed with an alcalinization to pH 6.8. *In vitro*, phytic acid bound with Ca^{2+}, Cd^{2+}, Zn^{2+} and Cu^{2+} becomes soluble from a pH lower than 4 to 5 (Kumar *et al.*, 2010). The present data suggests that the gizzard pH would be sufficiently low to release, at least partially, native Zn from phytates (even not hydrolyzed), which is then rapidly absorbed in the beginning of the duodenum before pH of the digestive tract rises. The piglet stomacal pH is generally higher than in the gizzard (Létourneau-Montminy, 2009; Schlegel *et al.*, 2010), and piglets seem not capable to release a significant amount of native Zn from phytates. The capacity of broilers to release native Zn from phytates would also explain the 8 times lower Zn equivalence of supplemental phytase (500 FTU/kg diet) in broilers compared with the equivalence in piglets (Jondreville *et al.*, 2005 and 2007) also when the capacity of supplemented phytase to hydrolyze PP is similar between the two species (Selle and Ravindran 2007 and 2008; Létourneau-Montminy *et al.*, 2010 and 2012). It is also in accordance with the lower Zn requirements in this species compared with piglets (National Research Council 1994 and 1998).

Conclusions

The results from the four meta-analyses suggest that (1) broilers and piglets use supplemented Zn, independent from Zn source; (2) broilers are able to use native Zn and the use is slightly enhanced with supplemental phytase; (3) however, piglets are limited in the use of native Zn due to the antagonism of non-hydrolyzed dietary phytate. These results imply that the consideration of dietary native Zn and PP content and phytase activity are key solutions for an

adapted Zn supplementation and an efficient Zn use in broilers and piglets.

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