Review Article

Phosphorus nutrition of growing pigs

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A B S T R A C T

Phosphorus (P) is an essential nutrient for diverse biological processes, which aggregate to the animal's requirement for P, and nutritionists strive to meet this requirement accurately. The P demand for a growing pig comprises requirements for maintenance and tissue deposition. The P in feed ingredients, however, must be digested and absorbed before its ultimate partition between the 2 aforementioned requirement components. Phosphorus from various sources could behave differently during digestion and absorption, which results in their disparate bioavailability for pigs. The system of standardized total tract digestibility reflects true total tract digestibility of P and feed ingredient effects on specific endogenous P loss with relative ease of implementation, and this system guarantees satisfactory additivity in digestible P among the ingredients in a diet—the foundation for diet formulation. The basal endogenous P loss, which is much easier to measure than the specific endogenous P loss, is considered as part of the pig's maintenance requirement. With this arrangement, a digestibility framework is established both for measuring the P-providing capacity of various feed ingredients and for describing the pig's P requirement. This framework entails basic understanding of the function, digestion, absorption, excretion, and homeostasis of P as support pillars. Understanding the workings of this framework enables potential integration of factors such as environmental conditions and disease status in future P requirement models. The current review discusses dietary sources, digestion, absorption, bioavailability and requirement of P for growing pigs to understand the status quo, revealing the points of consensus as well as those of debate, and to encourage further investigation to provide more clarity.

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1. Introduction

Elemental phosphorus (P) is highly reactive and complexes with oxygen to form the tetrahedral phosphate when exposed to air (Ehret, 1948). Thus, phosphate becomes the nutritional currency of P for plants and animals. This currency can be mined from rock phosphate in nature, an irreplaceable and nonrenewable resource, and its misuse for farm animals can result in poor productivity of farm operations attributable to P deficiency or oversupply. In the case of oversupply, P runoff through waterways could occur with serious ecological repercussions. The avoidance of these disastrous scenarios entails understanding of general principles of P nutrition in farm animals and the exceptions to these principles to achieve high accuracy in P nutrition (Liu et al., 2016).

In general, P pools within the body could be envisaged as comprising a small pool circulating in body fluids for short-term vital functions, and a large pool within the skeleton, which by continuous deposition and resorption provides finite buffering capacity for maintaining constant levels in the small pool (Fernández, 1995). This large pool harbors approximately 77% of the whole-body P in a pig, which contrasts with 99% for calcium (Just Nielsen, 1973). The mass percentage of P in bone varies according to the status of bone. Phosphorus accounts for 18% of the ashed bone, 10% of the dry fat-free bone, and 4.5% of the wet bone (Crenshaw, 2001). A chemical distribution of P in the whole body of a 90-kg pig is illustrated in Fig. 1. In this illustration, P is 0.54% of the
pig live weight. In reality, the percentage of P in the pig live weight decreased from 0.64% to 0.43% when the pig grew from 8.5 to 146 kg (Mahan, 1998).

Phosphorus is required for diverse biological processes (Berndt and Kumar, 2009). The skeletal system—built with constituents in the chemical formula of Ca_{10}(PO_{4})_{6}(OH)_{2}—maintains the shape of the body, provides protection to internal organs, and functions as levers for body movement. The cell membrane is made of phospholipids, molecules that are usually portrayed as spheres, each with 2 tails hanging down with phosphate as the sphere. The phospholipid-based bilayer structure provides cell structural integrity and controls the flow of molecules in and out of the cell. The importance of DNA is supreme because of its sole commitment to transferring genetic information from generation to generation, and the backbone of DNA is made of sugars and phosphate groups joined by ester bonds. Adenosine-5’-triphosphate is dubbed the molecular currency unit for intracellular energy transfer, which entails the enzyme-catalyzed transfer of phosphoryl group (Knowles, 1980). Many key regulatory proteins in cells exist as either phosphorylated or dephosphorylated in reflection of the action of protein kinases or phosphatases, which are essential for the transduction of biological messages (Cohen, 1988).

The microbes colonizing the pig gut present another dimension of the pig’s requirement for P despite its smaller amount in comparison to the need of host. The microbes in the small intestine of pigs mainly engage in the digestion and absorption of nutrients whereas the microbes in the large intestine, as the main force of gut microbiota, participate in the degradation of fiber (Liu et al., 2017; Wang et al., 2020). Dietary fiber provides food for bacteria, promoting fermentation and multiplication of bacteria in the gastrointestinal tract, which might increase the bacterial utilization of P in the large intestine (Metzler and Mosenthin, 2008). A reduction in P available for bacteria in the large intestine due to enhanced P absorption in the small intestine with supplemental phytase could be related to the lower cellulase activity in feces of pigs (Metzler, 2007). Additionally, the P supply could interact with the health status and immune system of pigs. It has been shown that a low P diet has an effect on immune features in jejunum (Just et al., 2018), and receptor-activator of NF-κB ligand (RANK) might contribute to linking P homeostasis and immunity in swine (Oster et al., 2016).

2. Dietary sources of phosphorus

Dietary P is primarily provided by plant and animal feedstuffs and inorganic P supplements (Waldroup, 1999). Each source comprises different chemical forms of P which could be organic or inorganic, depending on the presence or absence of carbon in the compound.

2.1. Phosphorus of plant source

Phosphorus in plant seed is stored primarily in the form of phytic acid, also known as phytate or phytin (Eeckhout and De Pape, 1994). The terms phytic acid, phytate and phytin refer to free acid, salt, and calcium/magnesium/potassium salt, respectively, and have been used interchangeably in the literature (Cowieson et al., 2016). Phytic acid loosely binds bi- and trivalent cations under the acidic conditions of the stomach or precipitates as phytate at the neutral pH of small intestine, inhibiting the intestinal absorption of trace elements, and has thus been regarded as an antinutrient for decades (Schlemmer et al., 2001). Phytate-bound P is only partially degradable in swine because of the minimal secretion of phytase along the gastro-intestinal tract and the unfavorable chemical environment of a complete diet. As a consequence, dietary phytate concentration becomes a bottleneck and governs the magnitude of the animal’s response to exogenous supplementation of phytase (Selle and Ravindran, 2008).

The accumulation site of phytin in seeds and the content of phytate P vary appreciably among feedstuffs. Accumulation of phytin in seeds occurs during the maturation phase of seed development, the period of rapid cell expansion (Lott et al., 1995). The accumulation sites of phytin in monocotyledonous and dicotyledonous seeds are the aleurone layer and globoids (one of the inclusions of the protein body), respectively (Reddy et al., 1982). Corn is an exception, with 88% of the phytate P in a kernel contained in the germ fraction (O’Dell et al., 1972). Soybean has phytin contained in protein bodies distributed throughout the seed, but phytin is concentrated only in crystallloid and globoïd substructures in peanuts, cotton seed and sunflower seeds (Baker and Stein, 2013). Moreover, phytate in individual

Fig. 1. An illustration of the chemical distribution of phosphorus in the body of a 90-kg pig (Just Nielsen, 1973; Crenshaw, 2001).
feedstuffs might have different chemical properties, such as stability and solubility, which could affect their susceptibility to phytase. The concentration of phytate in cereal grains is generally lower than that of oilseeds; however, phytate P concentration as a percentage of total P content is usually higher in cereal grains than in oilseeds. As measured and reported by Eckhout and de Paepe (1994), the phytate P concentration in oats, wheat, triticale, maize, barley, rye and sorghum ranged from 0.15% to 0.25%; whereas phytate P as a percentage of total P content varied from 59% to 70%. On the contrary, the meats of peanut, rapeseed, sunflower and soybean contain 0.32% to 0.44% phytate P, which accounted for 36% to 53% of the total P. Attempts to predict the phytate P content from total P for different categories of feedstuffs have met with limited success for cereal byproducts and oilseeds (Table 1).

Novel varieties of grain and oilseed species have been developed to decrease the phytate concentration and to increase bioavailability of P in feedstuffs. For example, the digestibility of P in low-phytate corn was approximately 26 percentage points higher than in normal corn (Bohike et al., 2005), and the bioavailability of P in low-phytate soybean meal (SBM) was 12 to 26 percentage points higher than in conventional SBM (Sands et al., 2003). It is noteworthy that substantial amounts of intrinsic phytase and acid phosphatase activities were found in rye, wheat, rye bran, and wheat bran (Viveros et al., 2000). The efficacy of cereal phytase, however, was determined to be only 40% of that of microbial phytase (Zimmermann et al., 2002). Fortunately, the effects of cereals and microbial phytases on apparent P absorption in pigs were found to be additive (Zimmermann et al., 2003).

2.2. Phosphorus of animal and mineral sources

Feedstuffs of animal origin are a great source of energy, amino acids and minerals for pigs (Olukosi and Adeola, 2009; Sulabo and Stein, 2013; Kerr et al., 2019). These feedstuffs are rich in P, and have relatively higher P digestibility ranging from 68% to 91% (Jongbloed and Kemme, 1990). Structural analysis of meat and bone meal ashes demonstrated that there was no correlation between the bioavailability of P and the gastric acid of pigs should be pivotal to its dissolution and absorption in animals because the P solubility of the inorganic phosphate might not be important because both forms of P are equally digestible, but the bioavailability of P in anhydrous dicalcium phosphate appeared to be 88% of that in the hydrated form, because the dissolution in stomach may be slower for anhydrous dicalcium phosphate (Grimbergen et al., 1985).

Table 1

| Type of feedstuffs | Regression equation (Y: phytate P; X: total P) | R² |
|--------------------|-----------------------------------------------|----|
| Cereals³           | Y = 0.42 × X + 0.08                           | 0.20 |
| Cereals³           | Y = 0.49 × X + 0.05                           | 0.52 |
| Cereals byproducts¹| Y = 0.85 × X + 0.04                           | 0.95 |
| Wheat × wheat by-products²| Y = 0.83 × X + 0.06                 | 0.95 |
| Maize × maize by-products²| Y = 0.50 × X + 0.04             | 0.93 |
| Legume seeds¹     | Y = 0.43 × X + 0.02                           | 0.62 |
| Legume seeds¹     | Y = 0.54 × X + 0.04                           | 0.79 |
| Oilseeds¹         | Y = 0.95 × X + 0.20                           | 0.95 |
| Oilseed meals²    | Y = 0.24 × X + 0.18                           | 0.42 |

¹ Viveros et al. (2000).
² Eckhout and de Paepe (1994).
³ Jongbloed and Kemme (1990).
et al., 2006). Phytate degradation through the whole gastrointestinal tract was nearly 100% for diets with or without intrinsic phytate due to hindgut microbial activities (Jongbloed et al., 1992; Schlemmer et al., 2001; Angel et al., 2005). The main site of phytate hydrolysis by supplemented phytase is the stomach because the pH conditions of the stomach more closely match the pH optima of most commercial phytases than the small intestinal pH. As shown in Table 2, the greatest difference in the degradation of phytic acid or IP₆ attributable to phytase presence or supplementation was observed in either the stomach or duodenum, and this difference seemed to maintain throughout the small intestine before further action by microbes in the large intestine. This pattern holds true for phytases of both plant and microbial origins. For a diet rich in intrinsically phytase, 58% of total inositol phosphates in the stomach were phytate hydrolysis products, whereas for the diet with inactivated phytase, the phytate hydrolysis products only accounted for 17% (Schlemmer et al., 2001). In a diet with inactivated intrinsically phytase, almost no phytate degradation occurred in the stomach, whereas in a diet with 150 FTU/kg Aspergillus niger phytase, 22% of the dietary phytate was hydrolyzed, and the phytate degradation increased further up to 52% with the supplemental phytase at 300 FTU/kg (Kemme et al., 2006). With the supplementation of 1,500 FTU/kg A. niger phytase to a corn-soybean meal diet, an increase of approximately 48 percentage units in gastroduodenal hydrolysis of phytic acid was found, which compares to an uplift of 50 percentage units at the end of ileum (Jongbloed et al., 1992).

### 3.2. Absorption of P

It is generally accepted that the small intestine is the major site for P absorption in pigs as well as other simple-stomach species (Moore and Tyler, 1955; Partridge, 1978; Breves and Schröder, 1991). The large intestine, however, might also contribute to P homeostasis in pigs because the expression of some sodium/phosphate transporters were detected in the colon (Wubuli et al., 2019). A significant absorption of P occurred in the large intestine of pigs (Liu et al., 2000, 2017). The large intestine may play an important role in whole-body P homeostasis by recycling endogenous P secreted in the upper gastrointestinal tract (Fan et al., 2001), but the endogenous P secretion is of minor importance to gastrointestinal P turnover in nonruminants relative to ruminants (Breves and Schröder, 1991). Depending on the source of carbohydrate, net absorption or secretion of P could occur; cellulose and pectin caused a net secretion, but starch induced a net absorption or secretion of P could occur; cellulose and pectin caused a net secretion, but starch induced a net absorption. Cellulose and pectin are dietary fibers that are not fully degraded by the digestive enzymes, and they are fermented by gut microbiota, leading to the production of volatile fatty acids and fermentation products. These products are then absorbed by the large intestine, contributing to the absorption of P. Cellulose and pectin are also known to have a prebiotic effect, promoting the growth of beneficial gut microbiota.

Table 2

| References                        | Analyte          | Phytase, U/kg | Stomach | Duodenum | Ileum | Total tract |
|----------------------------------|------------------|---------------|---------|----------|-------|-------------|
| Jongbloed et al. (1992, corn-soybean meal diet) | Phytic acid     | 0             | 21.5    | 9.6      |       |             |
|                                |                  | 1,500         | 69.2    | 59.7     |       |             |
| Jongbloed et al. (1992, Dutch diet)   | Phytic acid     | 0             | 1.2     | –1.4     |       |             |
|                                |                  | 1,500         | 93.2    | 74.0     |       |             |
| Kemme et al. (2006)             | IP₆              | 0             | 7       | 27       |       |             |
|                                |                  | 150           | 22      | 43       |       |             |
|                                |                  | 900           | 52      | 65       |       |             |
| Schlemmer et al. (2001)         | Phytic acid     | 0.2           | 16.8    | 58.1     | 97.4  |             |
|                                |                  | 43.1          |         |         | 97.7  |             |
| Rosenfelder-Kuon et al. (2020)  | IP₆              | 0             | 18.4    | 96.6     |       |             |
|                                |                  | 750           | 76.3    | 97.5     |       |             |
|                                |                  | 1,500         | 83.2    | 98.6     |       |             |
|                                |                  | 3,000         | 85.0    | 97.4     |       |             |
| Rosenfelder-Kuon et al. (2020)  | IP₆              | 0             | 30.1-31.2 | 98.5-98.9 |       |             |
|                                |                  | 1,500         | 92.1-92.3| 98.9     |       |             |

3.3. Phosphorus excretion

The reasons for the excretion of P are the low P digestibility and the excessive dietary content of digestible P (Poulsen et al., 1999; Knowlton et al., 2004). Fecal P consists of undigested portions of phytate-bound and non-phytate P from plant sources, undigested portions of P from animal byproducts and mineral supplements, and surplus amount of bioavailable P in excess of animal needs (Waldroup, 1999). There are 3 factors influencing the excretion of P via feces: 1) inevitable P losses, which depend on the body weight of pigs, 2) the availability of dietary P, which relates to the dietary origin of the P, and 3) the regulatory P excretion, which is due to the adaptation in absorption and/or endogenous secretion to the level of P supply (Rodehutscord et al., 1999b). Fecal P excretion amounted to about 52%, 46%, and 55% of P intake in sows, weaners, and growing pigs, respectively, and in general, the growing period contributed up to 75% of the total P excretion (Poulsen et al., 1999). The urinary excretion of P depends on the P status of the pig (Rodehutscord et al., 1999b). As a major means of manure disposal,
land application has endangered the quality of ground water due to the relative excess of P in manure than that required by crops and the subsequent buildup of P in soil, which potentiates the movement of P during soil erosion and in surface water runoff (Kornegay and Versteegen, 2001). This concern calls for minimizing P excretion from pig farming with more efficient utilization of P in feed and meeting pig’s requirement for P without unnecessary waste.

3.4. Phosphorus homeostasis

Systemic P homeostasis is achieved by orchestrating intestinal absorption, bone formation and resorption, and kidney excretion and reabsorption through a hormonal network (Razzaque; 2009; Sabbagh et al., 2011; Martin et al., 2012). The main hormones implicated in the regulation of P homeostasis are parathyroid hormone (PTH), vitamin D₃ (cholecalciferol), and fibroblast growth factor-23 (FGF23) with its cofactor klotho (Lederer, 2014). Parathyroid hormone is more associated with P regulation in kidney and bone, whereas P absorption in the small intestine is stimulated by vitamin D (Breves and Schröder, 1991). In contrast to PTH, FGF23 inhibits renal tubular P reabsorption and suppresses circulating calcitriol (the active form of vitamin D₃) concentrations (Martin et al., 2012). There are numerous reviews on the hormonal homeostasis of P in intestine, bone and kidney in the literature with an emphasis on human nutrition and health. In pigs, the onset of vitamin D-dependent mechanism for active P absorption does not occur until weaning (Schröder et al., 1998). With the Ussing chamber technique, Lee et al. (1986) proved there are also vitamin D-independent local mechanisms governing the intestinal active P transport. Hormonal regulation may play a role only in the long-term regulation of P homeostasis, and the short-term post-prandial responses that occur independently of hormones may play a larger role than previously appreciated (Berndt and Kumar, 2009). Vitamin D₃ can be synthesized in skin through the action of ultraviolet irradiation. Vitamin D₃ is hydroxylated in the liver to form 25-hydroxycholecalciferol, the major circulating metabolite, which is further hydroxylated in the renal tubule cells to the most active metabolite of vitamin D₃, 1, 25-dihydroxycholecalciferol or to a less-active metabolite, 24,25-dihydroxycholecalciferol (Sommerville et al., 1978). A confined housing environment with insufficient sunlight could precipitate vitamin D deficiency resulting in a disturbance in the absorption and metabolism of Ca and P (NRC, 1998). Supplementing vitamin D₃ to pig diets did not affect the growth performance (Li et al., 1998; O’Doherty et al., 2010; Lindemann et al., 2012), but the vitamin D₃ supplementation to a low-Ca, low-P diet produced similar growth performance as the diet with adequate Ca and P when fed to 20 kg pigs (Adeola et al., 1998). Serum 25-hydroxycholecalciferol concentration, which is the specific vitamin D metabolite to indicate animal’s vitamin D status, was increased by oral gavage or intramuscular injection of vitamin D (Lindemann et al., 2012). Dietary administration of vitamin D₃ to pregnant and lactating sows is necessary to ensure normal skeletal mineralization in young pigs (Witschi et al., 2011). Dietary supplementation of 25-hydroxy cholecalciferol tended to promote normal endochondral ossification and inhibit osteochondrosis progression in pigs (Sugiyama et al., 2013).

4. Phosphorus bioavailability

Bioavailability is an abstract concept to describe the extent to which a nutrient in a feedstuff is absorbed and metabolized by the animal (Stein et al., 2007) and has been used without due prudence. Bioavailability of P could be interpreted as the amount of P in a feedstuff that is released during digestion, absorbed from the gastrointestinal tract, and used for maintenance and growth of grower pigs. Bioavailability cannot be measured in absolute terms, but can be quantified in a comparative sense relative to a standard.

4.1. Relative bioavailability of P

Relative bioavailability of P is derived from slope-ratio assays providing information on the P-providing capacity of a feed ingredient in comparison to a standard P source. The slope derived from the linear response variable with the test ingredient (bₜ) is compared with the slope of the response variable in the basal diets supplemented with the standard ingredient (bₛ), and the percentage value (bₜ/bₛ × 100) is referred to as the availability of that particular source of P (Littell et al., 1997). This kind of assay is usually considered as the ultimate standard against which other methods are judged (Lewis and Bayley, 1995), but suffers from the drawbacks of being costly, time consuming, and inefficient. Moreover, it requires a strict test for fundamental validity to determine whether regression lines for the reference and test ingredients intersect at the point of the basal diet, and a test for statistical validity to verify whether responses to the reference and test ingredients are linear and without curvature (Adeola, 2009). For availability assays where linearity of response is imperative, the dietary concentration of available P should not exceed 2 g/kg of feed (Ketaren et al., 1993). There are occasions where linear regression may not be sufficient to explain the majority of the total variance; nonlinear (asymptotic or sigmoidal) regression could be tried for a better fitting to the data (Ravindran et al., 1995). Bioavailability is usually estimated using P in monosodium, monocalcium or dicalcium phosphate as the standard. The response variables could be parameters describing growth performance and bone characteristics. Bone parameters are supposed to be very accurate because about 80% of the retained P is deposited in bone. In pigs, there was a strong dependency of P digestibility and bone measurements on supplemental P, but the blood parameters (alkaline phosphatase and plasma inorganic P) and chemical property (solubility) were less correlated (Dellaert et al., 1990). Bone ash concentration appeared to be more responsive than growth performance and P retention to dietary P supply (Ketaren et al., 1993). It is noteworthy that bones are not equally optimal for determination of P supply and various bone segments also mineralize differently (Sørensen et al., 2019). Either non-defatted or defatted bone processing methods can be used to assess bone mineralization; however, the defatted bone processing is preferred for grower -finisher pigs to minimize variation in mature pigs (Wensley et al., 2020). Dual-energy X-ray absorptiometry (DEXA) has been used successfully to evaluate bone mineral content and density in live pigs and generated comparable results with chemical and physical analysis (Bernau et al., 2020; Schlegel and Gutzwiler, 2020).

4.2. Phosphorus digestibility

Bioavailability of P reflects the net effects of digestion, absorption and post-absorptive utilization of P by tissues and organs. Digestion and absorption are prerequisites for bioavailability whereas utilization of the absorbed is proof of bioavailability (Sibbald, 1987). The marginal efficiency of using digestible P for post-absorption net requirement is approximately 95% (NRC, 2012). Therefore, P digestibility can be considered as an estimate of P bioavailability to a large extent. In theory, the digestibility of P in an ingredient can be calculated by multiplying its relative bioavailability of P with the digestibility of P in the mineral phosphate (the standard to which the test ingredient is compared), but such conversion has been challenged by relevant studies comparing digestibility and bioavailability of P. Low-phytate corn was determined to contain at least 5 times as much available P in

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compared to 3 times as much digestible P as normal corn (Spencer et al., 2000). Baker et al. (2013) compared STTD and relative bioavailability of P in pigs: the STTD of P in dicalcium phosphate and DDGS were determined to be 93.1% and 63.1%; indicating a relative bioavailability of 67.8% of P in DDGS to that in dicalcium phosphate, but the relative bioavailability of P in DDGS was measured to be 86% to 88% of that in dicalcium phosphate. In broilers, P digestibility and absorption also disagrees with relative bioavailability; P digestibility and absorption values obtained for some ingredients using diets that are semisynthetic or semi-purified, particularly when they contain low Ca levels, may not represent diets used in commercial practices (Munoz et al., 2020). Despite the discrepancy, the system of STTD of P has predominated over the system of P bioavailability in pigs as signaled by its adoption in Nutrient Requirement Council (NRC, 2012).

To measure P digestibility, 2 operational decisions are required regarding the use of marker or the classical quantitative comparison between input and output, and the choice between ileal and fecal sampling. Firstly it has been shown that the large intestine does not seem to play an important role in the digestion of P and there is no difference in true P digestibility between ileal and total tract levels (Fan et al., 2001; Shen et al., 2002; Ajakaiye et al., 2003; Dilger and Adeola, 2006), which contrasts the modifying effects of hindgut microbes on amino acids and the consequent preference of measuring amino acids digestibility at the ileal level over the total tract level (Sauer and Ozimek, 1986). Therefore, the determination of P digestibility from mouth to anus is justified by accuracy as well as ease of operation. The P secretion or absorption in the large intestine cannot yet be easily integrated in the current digestibility system, and their influence on the precision of diet formulation under practical conditions may be negligible. Secondly, indigestible markers could be included in feed and measured in digesta/feces as conceptualized in the index method for measuring P digestibility. The index method is laudable due to its labor-saving advantage via measuring the concentrations of the indigestible indicator in both feed and feces in replacement of the exact collection and records of feed intake and fecal output with great care to detail (Adeola, 2001; Agudelo et al., 2010). The index method also enables grab fecal sampling from pigs housed in groups in reflection of commercial housing conditions considering that the pigs housed individually and in groups have different feed intake patterns which have different effect on digestibility (de Haer and de Vries, 1993). Additionally, the markers have little to no impact on microbial metabolism and growth performance of pigs (Kerr et al., 2015).

The index method, however, could underestimate digestibility of dry matter and energy, which relates to the low recovery of marker and the property of feed (Adeola, 2001; Jang et al., 2014; Li et al., 2016). In terms of fecal P digestibility, the apparent total tract digestibility (ATTD) of P (38.5%) using the indicator method was significantly higher than that (36.7%) of the total collection method in Kemme et al. (1997b), and the opposite was reported by Agudelo et al. (2010) and Jang et al. (2014). In terms of sensitivity to treatment difference in fecal P digestibility, discrepancy also appeared to exist between the 2 methods (Kemme et al., 1997b; Agudelo et al., 2010). It is becoming more accepted that the type of marker is an influencing factor for measuring nutrient digestibility (Wang and Adeola, 2018), but the most appropriate choice among the markers is still debatable considering the conflicting results in the literature (McCarthy et al., 1974; Jagger et al., 1992; Brestensky et al., 2017; Prawirodirdjo et al., 2021). Moreover, the comparison among markers was based more on the digestibility of dry matter, organic matter, gross energy or amino acids without due attention to minerals. It is well-known that pigs should be adapted to the diets over several days for the marker to stabilize in feces before sample collection, and the fecal samples should be grabbed daily for at least 2 to 5 consecutive days and then composited to make a representative sample (Moughan et al., 1991; Agudelo et al., 2010; Jang et al., 2014; Liu et al., 2018b; Choi and Kim, 2019). Different digestibility systems (apparent, standardized, or true) were explored, and their differences have been discussed extensively in previous review papers (Sibbald, 1987; Stein et al., 2007; Adeola et al., 2016; She et al., 2017; Zhang and Adeola, 2017). An important point of debate is the additivity of nutrient digestibility among feed ingredients, and the essence of additivity boils down to whether the nutrient digestibility can be affected or not by the varying inclusion levels of each nutrient-providing feed ingredient.

The modifier “apparent” before P digestibility reflects the calculation that both the undigested P from feed as well as the endogenous loss from the pig have been deducted from the dietary P supply, or in other words, the true P-providing ability of feed has been diminished by the endogenous loss from the pig. Poor additivity and large variability of apparent P digestibility have been reported in the literature. Rodehuts cord et al. (1996) and Fan and Sauer (2002) found that the ATTD values of P measured for feed ingredients are not always additive when used in diet formulation for pigs. In previous studies where graded levels of P were investigated using index method, the ATTD values for P in corn ranged from –41.4% to 39.1% with 25 kg pigs (Shen et al., 2002), and from 18.8% to 42.5% in soybean meal with 6.8 kg pigs (Fan et al., 2001) and from 3.7% to 48.1% with 40 kg pigs (Ajakaiye et al., 2003). On the contrary, the ATTD of P in monocalcium phosphate did not change with increasing inclusion rate of monocalcium phosphate using either the direct method (Petersen and Stein, 2006) or the difference method (Stein et al., 2008). The ATTD of P in SBM and canola meal were also not affected by the inclusion level of test ingredient (Akinmusire and Adeola, 2009). Paradoxically, Dilger and Adeola (2006) found significant linear and quadratic effects of inclusion level of low-phytate SBM on the ATTD of P, but not of conventional SBM. The endogenous loss of P from pigs accounts for different proportions of the P supply due to varying inclusion rates of the feed ingredients and thereby challenges the additivity of apparent P digestibility. This exasperation for nutritionists could be moderated with the standardized P digestibility system.

The modifier “standardized” reflects the calculation that the undigested P from feed as well as the endogenous P loss from the pig specific to the feed have been deducted from the feed P supply; whereas, the inevitable basal endogenous P loss is considered as a factor of the pig’s requirement. NRC (2012) derived STTD of P for feed ingredients using basal endogenous P losses of 190 mg/kg dry matter intake to correct the ATTD of P in the literature. Indirectly, Almeida and Stein (2010) showed that STTD values for P are additive because no significant difference was observed among 4 diets formulated using values for STTD of P. NRC (2012) also asserted that using values for the STTD of P in practical diet formulation, additivity among feed ingredients is achieved, and diets are more accurately formulated compared with using values for ATTD of P. She et al. (2018) demonstrated that the STTD of P in corn, SBM and canola meal are more additive than their ATTD counterparts in pigs.

The modifier “true” before P digestibility means the true P-providing ability of feed as reflected by the calculation that only the feed-derived undigested P has been deducted from the P supply in feed. Different methods have been used to measure the true P digestibility. Fan et al. (2001) determined the gastrointestinal endogenous P output and true P digestibility values in plant ingredients based on the regression technique and index method. Based on the total collection method, Dilger and Adeola (2006) reevaluated the regression method to determine endogenous P losses and true digestibility of P. Fang et al. (2007a) determined the TTTD of P using a substitution method, which was not different from the regression method. Liu et al. (2014) proved that the
measured TTD of P in soybean and canola meals with the regression method was not affected by the inclusion of cornstarch or corn in the diet. Petersen and Stein (2006) estimated endogenous P losses and true digestibility of P in inorganic P sources based on a P-free diet. Fang et al. (2007b) demonstrated the additivity of TTD values for P in some cereals and oilseeds using the substitu-

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5. Requirement for P

The requirement for P could be estimated by factorial and empirical approaches. The factorial approach needs to quantify the components of net P requirement, which consists of maintenance P requirement to offset the inevitable P losses and the requirement for sustaining the growth of skeleton and tissues. Scientifically, the factorial method is advantageous because it can be applied to various systems of production (Jongbloed and Everts, 1992). An empirical approach uses the results of feeding trials with diets of various nutrient contents (Jongbloed, 1987). The empirical esti-

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Empirical P requirement estimates also reflect the disease challenges and environmental conditions specific to each feeding trial, which have not been captured by the existing modeling approach yet, and thus empirical studies can be used to validate and adjust the model-generated requirements. Zhai and Adeola (2013a,b,c) determined the TTTD of P in corn, soybean meal, and monocalcium phosphate using regression method, and estimated the TTTD-based P requirement to be 3.2, 3.1, 2.7, and 2.3 g/kg feed for 10 to 20, 20 to 40, 40 to 60, and 60 to 80 kg pigs of mixed sex. These requirement estimates were converted to their STTD equivalents (3.9, 3.2, 2.8 and 2.4 g/kg feed), which were higher than NRC (2012) recommendations for pigs under 33 kg and lower for pigs greater than 33 kg (Zhai, 2013). Recently, it has been validated that NRC (2012) recommendations for STTD P are reasonably accurate for 6 kg to 13 kg pigs when body weight gain was used as the response (Wu et al., 2019). In a cooperative study involving 11 participating stations, Adeola et al. (2015) estimated the STTD P requirements of 20 to 40 kg pigs and the results were higher than the recommendations by NRC (2012), Vier et al. (2015a, b) provided empirical evidence that the NRC (2012) accurately estimated the TTLD P requirement on for 11 to 23 kg pigs on a per-day basis, but underestimate on a percentage of the diet for both 11 to 23 kg and 24 to 130 kg pigs. The divergent estimates of P requirement especially when expressed on a percentage basis of diet might be associated with the difference in feed intake related to environmental factors either suppressing or stimulating the pig’s appetite. Saraiva et al. (2012) found that pigs under heat stress have reduced feed intake and possibly reduced protein accretion, resulting in reduced P requirement when expressed as a percentage of diet. The difference in feed intake associated with dietary energy density and the discrepancy between research and commercial conditions could lead to different P requirement estimates (Hastad et al., 2004). Adeola et al. (2015) pointed out the central factor for the discrepancy in estimates of P requirement for growth performance being the total dietary Ca concentration for the Ca to P ratio at which there was a breakpoint (requirement estimate) for digestible P.

6. Conclusions

Admittedly, a plethora of research has accumulated over the years with regards to P as a nutrient for growing pigs. This collective work has enabled a robust understanding about the key components of P nutrition of growing pigs: sources, digestion, absorption, bioavailability, excretion, and homeostasis, which culminated in defining and meeting the P requirement of pigs. The STTD P was recommended over the nebulous bioavailable P to accurately describe P requirement (Adeola and Cowieson, 2011) and has gained predominance in pigs. NRC (2012) updated the mathematical model to estimate requirement for STTD P of growing-finishing pigs between 20 and 140 kg live body weight and integrated in the model the requirements of pigs below 20 kg BW based on empirical studies. These model-generated requirements take into account the physiological state and genetic potential for growth, but don’t reflect the environmental conditions as well as disease challenges (NRC, 2012). This calls for actual P requirements under practical production conditions, and the principles and algorithms for narrowing the gap between model-generated and actual requirements need to be ascertained. Collaborative initiatives at certain time intervals to update both the P digestibility in up-to-date feed ingredients as well as P requirements in pigs under continuous genetic selection pressure should be organized. Moreover, the study protocols among the participating stations should be aligned to minimize variance and to facilitate meta-analysis. Last but not the least, P nutrition could not be separated from Ca nutrition. The recent work on measuring STTD Ca as well as optimizing the Ca to P ratio on the standardized digestible basis have shown the direction for further effort.

Author contributions

Conceptualization: H. Zhai; Data curation: J. Liu; Formal analysis: J. Liu; Investigation: H. Zhai, J. Liu; Methodology: H. Zhai, O. Adeola; Resources: J. Liu; Writing - Original Draft: H. Zhai, O. Adeola; Writing - Review & Editing: J. Liu, O. Adeola; Supervision: J. Liu; Project administration: J. Liu; Funding acquisition: J. Liu.

Declaration of competing interest

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work, and there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the content of this paper.

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