

Bioavailability of Phosphorus in Feeds of Plant Origin for Pigs* – Review –

D. Weremko, H. Fandrejewski and T. Zebrowska
Polish Academy of Sciences, The Kjelanowski Institute of
Animal Physiology and Nutrition, 05-110 Jablonna near Warsaw, Poland
and

In K. Han¹, J. H. Kim and W. T. Cho
Department of Animal Science and Technology, College of Agriculture and
Life Sciences, Seoul National University, Suweon 441-744, Korea

ABSTRACT: Phosphorus has been known as an essential component of animal body. However, the requirement has not been determined precisely because of the variable bioavailabilities of feedstuffs from plant origin. The bioavailability of P in various feedstuffs of plant origin varies from 10 to 60%. Digestibility and availability of the P differed considerably depending on the feed. The lowest values were found for maize (under 20%), the highest for wheat and triticale (over 50%). This is due to the proportion of phytate and the presence of intrinsic phytase. And the digestive tract of monogastric animals does not contain sufficient amounts of phytase, an enzyme that hydrolyses the unavailable phytate

complexes to available, inorganic orthophosphates. Microbial phytase supplementation improves the P availability, and both intrinsic plant and microbial phytase improves the availability of P in feedstuffs of plant origin. In a mixture of feeds with low and high activity of intrinsic phytase and/or supplemented by commercial phytase, the P availability is additive. However, in the light of current results it seems that exceeding the P availability equal to 60-70% is unrealizable even at large microbial phytase doses.

(Key Words: Pigs, Phosphorus, Bioavailability, Intrinsic Phytase, Commercial Phytase)

INTRODUCTION

Availability of phosphorus in feedstuffs and feed additives used in pig nutrition ranges from 20 to 100%. The differences among phosphorus sources should be taken into account in formulation of diets providing an optimal phosphorus supply and utilization. Excessive amounts of dietary phosphorus are excreted by the animals and discharged into the environment leading to pollution and eutrophication of surface waters.

The main objectives of current nutritional studies on phosphorus are as follows:

- to determine animal requirements of phosphorus precisely,

- to identify the main factors influencing of phosphorus bioavailability,

- to develop better methods of determining phosphorus bioavailability,

- to use the enzyme phytase to enhance phosphorus utilization from feeds of plant origin.

Phosphorus is an essential component of animal body, which plays an important role in the development and maturation of the skeletal system, as well as in numerous other metabolic pathways. It is found chiefly (about 80%) in the bones (Oslage, 1964). Phosphorus is a component of many compounds in the soft tissues - as phospholipids, nucleic acids and ATP. Phosphorus also participates in the mineralization of bone tissue, metabolism of carbohydrate, fat and nitrogen compound, and is essential in transmembrane transport of metabolites. It is indispensable, particularly in processes related to energy metabolism.

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¹ Address reprint requests to In K. Han.

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The requirement for phosphorus in pigs are still not recognized sufficiently. Two basic methods are used to determine phosphorus requirements: the empirical method and the factorial method. In the first method the requirement of P is determined on the basis of one or a few easily measured and important production traits, e.g. daily body gains, feed utilization. The factorial method is more reliable since it is based on biological basis and it requires measuring the retention of the element in the body (or fetus and milk), its obligatory losses, and its availability.

Recent studies on the chemical composition of pigs body have provided new data on net P requirements (Jongbloed et al., 1991a; Hendriks and Moughan, 1993; Ketaren et al., 1993; Kwon et al., 1995ab). It was found that in the body weight range from 20 to 100 kg, over 5 g of P is deposited per kilogram weight gain (Rymarz et al., 1982; Jongbloed, 1987), and depends on the proportion of lean body mass in the daily gain. Phosphorus deposition declines markedly from the age of 7 months (Rymarz, 1982; Fandreyewski and Weremko, 1994). The rate of P deposition in the body of meat pigs is somewhat slower than that of Ca (Rymarz, 1986). Phosphorus deposition, expressed in more modern terms, e.g. in relation to protein deposition, is about 3.4 g per 0.1 kg protein deposited in the body (Rymarz et al., 1982), and it can differ depending on sex (Fandreyewski and Rymarz, 1986), but not on breed (Rymarz et al., 1982). Recent studies carried out at the Kielanowski Institute of Animal Physiology and Nutrition point to the possibility of reducing the net P requirement to a certain degree, which is characteristic of modern pigs, especially in fast growing animals.

The values reported in the literature on the availability in most of single and many feed mixtures are variable. In feedstuffs of plant origin P occurs in association with phytates, and the variation in P availability may be partly ascribed to the presence of native enzyme phytase which cleaves phytates and affected P availability (Jongbloed and Kemme, 1990a; Dügelhoef et al., 1994).

The objective of this paper is to review the current state of knowledge about the bioavailability of phosphorus from feeds of plant origin.

MATERIALS AND METHODS

Intestinal absorption of phosphorus

Phosphorus digestion starts in the stomach (Lantzsch et al., 1988; Moore and Tyler, 1995). Inorganic phosphates are liberated by alkaline phosphatase by hydrolysis of such compounds as phosphosugars, phos-

phorylated amino acids and phosphonucleotides, or by phytase from phytin complexes.

Most phosphorus is absorbed from the digestive tract as inorganic phosphate present in the diet or liberated from organic components before absorption. Phosphorus is absorbed mainly in the small intestine (Jorgensen and Fernandez, 1984; Partridge et al., 1986; Breves and Scherer, 1991; Harrison and Harrison, 1961; Wasserman and Taylor, 1976; Radde et al., 1980; Jungbluth and Binswanger, 1989). Some experiments carried out on pigs with re-entrant cannulas (Drochner, 1984) or simple T-cannulas (Gueguen et al., 1981) in the ileum and caecum showed that some amount of P was absorbed in the large intestine. It seems, however, that the proportion of P absorbed in the large intestine is little in comparison with the small intestine. At a high dietary calcium level part of the phosphate binds with Ca, forming insoluble polycalcium salts that are excreted with the faeces.

Studies on the mechanism of phosphorus absorption in pigs are not numerous. Some authors (e.g., Wasserman, 1981; Quamme, 1985) tend to agree the concept that the transport of phosphates by the intestinal wall is an active process (Gueguen et al., 1968; Partridge et al., 1986), although it can also occur through a passive mechanism, independent of Na⁺ (Borowitz and Ghishan, 1985; Cross et al., 1990), or through both mechanisms (Bartlett et al., 1995). The absorbed phosphates enter the circulation, by way of which P is delivered to the bones, soft tissues and kidneys. Phosphorus metabolism is regulated by the parathyroid gland hormone, parathormone as well as by calcitonin and vitamin D (Harrison and Harrison, 1961; Wasserman and Taylor, 1976; Radde et al., 1980; Jungbluth and Binswanger, 1989).

Endogenous phosphorus from pancreatic juice, bile, intestinal juice and epithelium cells is mostly reabsorbed. It seems, however, that about 10% of phosphorus in faeces is of endogenous origin. According to Jongbloed (1987), it is about 8-10 mg (together with a small amount of metabolic P) per kilogram of body weight. However, this value is variable, since the dietary level of P varies considerably, as do feeding intensity, fibre concentration and interactions among mineral components, particularly P and Ca. Some mineral components are P antagonists (and vice versa: table 1), which is already evident in the digestive and absorption processes. This makes the objective evaluation of P availability from particular feedstuffs or feed mixtures more difficult and complicated, since not all antagonisms between minerals are foreseeable and possible to prevent.

Table 1. Interrelationships of phosphorus with other elements common to pigs diets

Interrelationships			
Antagonistic	P	→	Se
Antagonistic	P	←	Cu
Mutually antagonistic	P	↔	Ca, Fe, Al, Mn, Mg, Zn

Source: Peo Jr (1991).

Methods of determining phosphorus digestibility and availability

The definition of phosphorus availability is generally accepted as the part of the P content in the feed that can be absorbed and fully utilized by an animal. Currently three terms describing the availability of phosphorus are used: the traditional term - apparent digestibility, and the newer terms - intestinal digestibility and availability. As can be expected, these terms are not fully equivalent. Moreover, there is controversy about the qualitative interpretation of differences and similarities between them. These difficulties result primarily from the specificity of determining the nutritional value of phosphorus, which in contrast to major organic elements, is not easy to do. Although phosphorus plays a very important role in the body, it should be emphasized that it is not a major nutrient, since major mineral elements are of secondary importance, following energy and amino acids, in the feeding of pigs. Moreover, phosphorus is an example of an element that is subject to mechanisms ensuring homeostasis.

The apparent digestibility of phosphorus is measured as the difference between intake with feed and excretion in faeces. This is the relatively easy measurement to make, but the results may be burdened with some errors, e.g. not strictly adhering to methodological rigors, especially if the depressive effects of large doses of calcium are ignored (Jongbloed, 1987; Lantzsich, 1989). The result of measuring phytate hydrolysis may also depend on the selection of the indicator used in the indirect method (Lantzsich et al., 1988).

True digestibility of phosphorus is estimated from difference between the P intake with feed and voided in faeces with the correction for the endogenous P excretion. Apparent digestibility is lower than true digestibility because the endogenous excretion of P into faeces is not accounted for. In some pig feeding systems (e.g. German, DLG; Die Deutsche Landwirtschafts-Gesellschaft, 1992) the P availability is expressed as intestinal digestibility. According to DLG system, when calculating P availability in the small intestine, the coefficients 0.9, 0.6 or 0.4 are

used when P is from a mineral source, a non-phytate component or phytate component, respectively. When the digestibility of phosphorus from an unknown source is measured by the difference method, basic feedstuffs devoid of native phytin should be used, e.g. maize (Jongbloed, 1987; Jongbloed and Kemme, 1990b).

The availability of P can be measured by the slope ratio method. In this method, the pigs receive a semisynthetic diet with a gradually increasing P content coming from the studied feed, or from a source that provides complete (or nearly so) assimilation of phosphorus in the body. Monosodium phosphate is usually used as the reference since 100% of it is digested, absorbed and deposited in the body. The procedure requires using diets with phosphorus contents in amounts smaller than the total P requirement of the animals, so that linear reaction to increasing the mineral component content in the diet occurs. Evaluation is conducted on young animals, which are sacrificed after about 5-6 weeks test period. Specific bones are then taken from the carcass (e.g. the femur, radius, metacarpals, metatarsals, tail vertebrae) and subjected to chemical and physical analysis, which usually include breaking point and ash content (Cromwell, 1980). Other criteria for measuring available P value such as level of P in serum, serum alkaline phosphatase, growth and feed utilization are, according to the opinion of many authors (Cromwell, 1989; Dellaert et al., 1990), less sensitive indicators. After determining partial regression coefficients, the phosphorus availability coefficient is computed, which is the quotient of the regression of two equations calculated for the experimental and control diets.

Organic and inorganic phosphorus in feedstuffs

In feeds of plant origin phosphorus occurs in two forms: in phytate-less available and nonphytate-more available form. Phytates are organic compounds of phosphoric acid and inositol. Each molecule of phytic acid contains six atoms of phosphorus and is a typical chelating agent that makes difficult to digest complexes when it binds divalent cations of metals or protein. Breaking up these complexes liberates the elements, particularly the P.

Phytates occur in the generative parts of plants; they are almost never found in the vegetative parts. High amounts of phytates occur in the aleurone layer of wheat, barley and oat grain, as well as in maize and pea germ. The role of phytates in both seeds and grain is to store phosphorus and calcium, magnesium, zinc, iron and manganese cations.

A review of published studies on P availability in

Table 2. Phosphorus content in feeds of plant origin

Feedstuff	Number of trials	Non-phytate P (%)	Phytate (%)	Phytate P % of total P	Author(s)
Cereals:					
Maize	11	0.08	0.22	73	Eeckhout and Paepe (1994)
	10	0.09	0.17	65	Nelson et al. (1968)
	—	0.05	0.23	82	Dügelhoef et al. (1994)
	—	0.09	0.21	70	Pointillart (1988)
	—	0.03	0.28	90	Oksbjerg (1988)
	7	0.11	0.21	66	Jongbloed and Kemme (1990b)
	31	0.09	0.29	76	Lantzsich (1990)
	mean	0.08	0.23	75	
Barley	5	0.15	0.19	56	Nelson et al. (1968a)
	9	0.15	0.22	59	Eeckhout and Paepe (1994)
	—	0.11	0.26	70	Oksbjerg (1988)
	20	0.14	0.26	65	Lantzsich (1990)
	—	0.14	0.26	65	Pointillart (1988)
	—	0.15	0.26	63	Berk and Schulz (1993)
	6	0.16	0.28	64	Jongbloed and Kemme (1990b)
mean	0.14	0.25	63		
Wheat	2	0.10	0.20	67	Nelson et al. (1968a)
	13	0.12	0.23	66	Eeckhout and Paepe (1994)
	56	0.14	0.22	61	Barrier et al. (1996)
	—	0.10	0.28	74	Berk and Schulz (1993)
	—	0.12	0.28	70	Pointillart (1988)
	27	0.11	0.30	73	Lantzsich (1990)
	5	0.12	0.29	71	Jongbloed and Kemme (1990b)
	—	0.11	0.31	74	Dügelhoef et al. (1994)
	mean	0.11	0.26	70	
Triticale	—	0.08	0.27	77	Oksbjerg (1988)
	6	0.12	0.25	68	Eeckhout and Paepe (1994)
	—	0.12	0.28	70	Pointillart (1988)
	—	0.10	0.32	76	Dügelhoef et al. (1994)
	—	0.17	0.37	69	Berk and Schulz (1993)
	mean	0.12	0.30	72	
Rye	2	0.14	0.21	60	Eeckhout and Paepe (1994)
Oats	6	0.14	0.22	61	Eeckhout and Paepe (1994)
	9	0.15	0.19	56	Lantzsich (1990)
	4	0.16	0.25	61	Nelson et al. (1968)
	mean	0.15	0.22	59	
Sorghum	5	0.08	0.19	70	Eeckhout and Paepe (1994)
By products:					
Maize feed gluten	6	0.23	0.35	60	Nelson et al. (1968a)
	9	0.41	0.45	52	Eeckhout and Paepe (1994)
	10	0.35	0.63	64	Jongbloed and Kemme (1990b)
	mean	0.33	0.48	59	

Table 2. CONTINUED

Feedstuff	Number of trials	Non-phytate P (%)	Phytate (%)	Phytate P % of total P	Author(s)
Wheat bran	—	0.22	0.68	75	Pointillart (1988)
	5	0.18	1.02	85	Eeckhout and Paepe (1994)
	4	0.43	0.96	69	Nelson et al. (1968a)
	mean	0.27	0.87	76	
Wheat middlings	1	0.12	0.35	74	Nelson et al. (1968a)
	5	0.37	0.50	57	Eeckhout and Paepe (1994)
	6	0.24	0.96	80	Jongbloed and Kemme (1990b)
	mean	0.24	0.60	70	
Rice bran	2	0.46	1.10	71	Eeckhout and Paepe (1994)
	3	0.23	1.44	86	Nelson et al. (1968a)
	4	0.32	1.38	81	Jongbloed and Kemme (1996b)
	mean	0.34	1.31	79	
Protein Sources :					
Peas	11	0.21	0.17	45	Eeckhout and Paepe (1994)
	4	0.24	0.24	50	Jongbloed and Kemme (1990b)
	4	0.23	0.31	57	Lantzsch (1990)
	mean	0.23	0.24	51	
Lupins	1	0.20	0.05	20	Eeckhout and Paepe (1994)
	4	0.32	0.42	57	Lantzsch (1990)
	mean	0.26	0.24	39	
Field beans	1	0.27	0.23	46	Eeckhout and Paepe (1994)
	9	0.20	0.44	68	Lantzsch (1990)
	—	0.21	0.47	69	Berk and Schulz (1993)
	mean	0.23	0.38	61	
Soybean meal	—	0.30	0.30	50	Pointillart (1988)
	15	0.31	0.35	53	Eeckhout and Paepe (1994)
	3	0.28	0.38	58	Nelson et al. (1968a)
	3	0.26	0.40	61	Jongbloed and Kemme (1990b)
	—	0.21	0.47	69	Berk and Schulz (1993)
	5	0.31	0.39	56	Lantzsch (1990)
mean	0.28	0.38t	58		
Rapeseed meal	5	0.71	0.41	37	Eeckhout and Paepe (1994)
	—	0.33	0.77	70	Pointillart (1988)
	1.5	0.49	1.01	67	Lantzsch (1990)
	mean	0.51	0.73	58	
Cottonseed meal	4	0.27	0.65	71	Nelson et al. (1968a)
Peanut meal	—	0.18	0.42	70	Pointillart (1988)
	3	0.36	0.32	47	Eeckhout and Paepe (1994)
	mean	0.27	0.37	59	
Sunflower seed meal	11	0.65	0.42	39	Eeckhout and Paepe (1994)
	4	0.27	0.83	75	Lantzsch (1990)
	4	0.27	0.89	77	Jongbloed and Kemme (1996b)
	—	0.24	0.96	80	Pointillart (1988)
mean	0.36	0.77	68		

Table 3. Phytase activity in feeds of plant origin

Feedstuff	Number of trials	Phytase activity (U/kg)	Author(s)
Cereals:			
Maize	—	trace	Pointillart (1988)
	11	0–46	Eeckhout and Paepe (1994)
	2	56	Own study
	—	≤ 100	Dügelhoef et al. (1994)
Barley	—	200	Pointillart (1988)
	—	310	Berk and Schulz (1993)
	9	408–882	Eeckhout and Paepe (1994)
	2	750	Own study
Wheat	—	300–2,000	Pointillart (1988)
	56	508	Barrier-Guillot et al. (1996)
	—	750	Dügelhoef et al. (1994)
	—	815	Berk and Schulz (1993)
	13	915–1,581	Eeckhout and Paepe (1994)
	2	936	Own study
Triticale	—	840	Dügelhoef et al. (1994)
	—	1,200	Pointillart (1988)
	2	1,395	Own study
	—	1,475	Berk and Schulz (1993)
	6	1,475–2,039	Eeckhout and Paepe (1994)
Rye	2	1,782	Own study
	2	5,130	Eeckhout and Paepe (1994)
Oats	6	0–108	Eeckhout and Paepe (1994)
Sorghum	5	0–76	Eeckhout and Paepe (1994)
By products:			
Maize feed gluten	9	0–177	Eeckhout and Paepe (1994)
Wheat bran	—	600–17,000	Pointillart (1988)
	5	1,180–5,208	Eeckhout and Paepe (1994)
	1	2,800	Helander et al. (1994)
Wheat middlings	5	2,825–5,042	Eeckhout and Paepe (1994)
Protein sources:			
Peas	11	36–183	Eeckhout and Paepe (1994)
Soybean meal	—	trace	Pointillart (1988)
	—	trace	Berk and Schulz (1993)
	15	0–120	Eeckhout and Paepe (1994)
Rapeseed meal	—	trace	Pointillart (1988)
	5	0–36	Eeckhout and Paepe (1994)
	4	11–23	Own study
Sunflower meal	—	trace	Pointillart (1988)
	11	0–185	Eeckhout and Paepe (1994)
Peanut meal	—	trace	Pointillart (1988)
	3	0–8	Eeckhout and Paepe (1994)

feeds of plant origin for pigs (table 2) shows that phytate P accounts for at least one half of total P. Among cereals, its highest content is found in maize, wheat and triticale (70-73%), while the lowest in rye and oat grain (60%). In the remaining feeds, the phytate P contents are usually more variable and lower in the seeds of legumes than in oil-plants. The nonphytate P content in cereal grain is about half that in other feeds. Therefore, when composing a diet for pigs based exclusively on feeds of plant origin, it is possible to fully cover their requirements for amino acids and metabolic energy, but it will always have an available phosphorus deficit, even assuming that nonphytate P utilization is complete. An exception is rapeseed meal, in which the total and nonphytin P contents is high (1.16 and 0.51%, respectively).

Phytase

For many years it has been accepted that only the nonphytate form of phosphorus in plant feedstuffs is fully available to pigs, while phytate P is not utilized at all (NAS-NRC, 1960). Studies carried out in the last two decades, however, show that the availability of P from feeds of plant origin to monogastric animals is not directly proportional to the ratio of phytate to nonphytate P, and that there are considerable differences among feeds (Cromwell, 1980, Reddy et al., 1982). It thus became evident that total P digestibility in feedstuffs of plant origin depends to a considerable extent on the activity of phytase, which, among others, was shown by Pointillart et al. (1984, 1987).

The digestive tract of monogastric animals does not contain sufficient amounts of phytase, an enzyme that hydrolyses the unavailable phytate complexes to available, inorganic orthophosphates (Davis and Motzok, 1972; Peeler, 1972; Taylor, 1965; Nelson, 1967; Cromwell, 1979). Although phytases can be isolated from the mucosal layer of pig intestine, these are only trace amounts (Cooper, 1983). Phytase is, in fact, a plant enzyme. Its activity depends on the temperature and pH (Scheuermann et al., 1988; Headon, 1992; Irving, 1980; Simons et al., 1990). Most phytases occurring naturally have an optimum pH between 5 and 5.6 (Reddy et al., 1982; Irving, 1980; Simons et al., 1990).

Phytase occurs naturally in many feeds, but in various amounts (table 3). Among cereals, the highest phytase contents are found in rye grain (over 5,000 U/kg), triticale (up to 2,030 U/kg) and wheat (up to 1,500 U/kg). Maize kernels, oats and sorghum contain little phytase (no more than 100 U/kg). More phytase than in cereal grains is found in wheat bran (even in excess of 5,000 U/kg). High protein feeds, even those that are not subjected to

such technological processing as peas, contain no more than 200 units of phytase per kilogram. It should be stressed here that the native phytase level depends not only on the kind of feedstuff, but also on the conditions under which the feed was produced and processed. Phytases are inactivated during thermal processing, such as drying, granulating or extracting at temperatures exceeding 80°C (Nair et al., 1991). A good example of this are the results of Jongbloed and Kemme's experiments (1990c), in which the high temperatures used considerably reduced P digestibility in the studied feeds, e.g. in wheat from 50 to 27% (table 4). Conversely, the addition of microbial phytase at doses of 750-1,000 U/kg of feed devoid of native phytase (or with only trace amounts) restored phosphorus digestibility.

Table 4. Effect of intrinsic and microbial phytase on the digestibility of phosphorus (%) in some feeds

Feed	Without intrinsic phytase	With intrinsic phytase	With supplemented by microbial phytase
Wheat mildings	19	33	—
Wheat	27	50	—
Wheat	—	62	74 (750)
Maize	18 (< 100)	—	56 (750)
Maize+SBM	13 (< 50)	—	43 (750)
	29	—	64 (1,000)

In brackets is shown phytase activity (U/kg).

Source: Jongbloed and Kemme (1990c), Pallauf et al. (1992), Simons et al. (1990).

The advantageous effect of phytase on phosphorus digestibility in feeds of plant origin was recognized some time ago. This gave rise to the idea of adding exogenous phytase to feeds for monogastric animals, especially to feeds that do not have a naturally occurring enzyme.

Nelson et al. (1968b and 1971) were the first to use microbial phytase obtained from *Aspergillus ficuum*. From this time it has been intensively studied, especially in recent years. Phytase is currently readily available commercially; the best known preparations are made by BASF, Degusa, Alltech, Novo-Nordisk and Alko Ltd., Rajamäki. It is used in various doses depending on the feed.

The effectiveness of phytase rises along a dose-dependent curve, as can be seen from the data presented in table 5. A distinct improvement in P digestibility (from 10 to 20%) is already visible at dose of up to 500 U/kg. Increasing the dose further (to 1,000 U/kg) increases P

digestibility, but less distinctly. In our own studies (Weremko and Fandrejewski, 1996), exceeding the 1,000 U/kg in a mixture composed of rapeseed meal and cereals did not further improve digestibility. In light of the current results it can be said that even at large phytase doses, exceeding P availability equal to 60-70% is highly unlikely. It should be added that digesting phytate by phytase, as any other enzymatic process, requires certain conditions, mainly time. Thus soaking the feed in warm water before feeding is a way to increase P availability by 5-10%, and has been demonstrated experimentally (Orda et al., 1994; Näsi et al., 1995). It is difficult to assume, however, that this way of preparing feeds will become prevalent in practice.

Table 5. Effect of microbial phytase addition to feeds on the apparent digestibility of phosphorus (%)

Feedstuff	Phytase activity U/kg	Apparent digestibility of P	Author (s)
Tapioca + maize + barley + SBM + sunflower meal	0	33	Mroz et al. (1993)
	300	47	
	600	54	
Field beans + wheat + peas + barley	0	48	Pallauf et al. (1993)
	350	67	
	700	71	
Wheat + barley + SBM + wheat bran	0	54	Pallauf et al. (1994)
	350	66	
	700	71	
Maize + dehulled SBM	0	15	Cromwell et al. (1993) ¹
	250	20	
	500	27	
	1,000	40	
Maize + SBM	0	29	Pallauf et al. (1992)
	500	55	
	1,000	64	
Maize + SBM	0 ²	39	Kwon et al. (1995a)
	500	51	
	0 ³	47	
	500	52	
Maize + Wheat + SBM	0 ³	54	Kwon et al. (1995b)
	500	55	
	1,000	59	
	0 ⁴	58	
	500	61	
Cereals + RSM	1,000	63	Own study
	0	33	
	1,000	47	
	1,250	46	
	1,500	48	

¹ availability ² weaned piglets ³ growing pigs ⁴ finishing pigs.

Table 6. Apparent digestibility and availability of phosphorus in feeds of plant origin

Feedstuffs	Number of trials	Availability (%)	Apparent digestibility (%)	Author (s)
Cereals:				
Maize	5	9		Stober et al. (1979)
	4	10		Ross et al. (1983)
	—	12		Cromwell and Stahly (1980)
	4	12		Burnell et al. (1989)
	5		12	Calvert et al. (1978)
	8	14		Cromwell (1992)
	—		17	Oksbjerg (1988)
	7		17	Jongbloed and Kemme (1990b)
	9		17	Jongbloed (1987)
	4	18		Ross et al. (1983)
	6	18		Coffey et al. (1992)
	3		18	Dügelhoef et al. (1994)
	—	19		Kuznetsov et al. (1987)
4		23	Wecke et al. (1994)	
Wheat	16		40	Barrier et al. (1996)
	5		44	Jongbloed (1987)
	6		45	Berk and Schulz (1993)
	5		47	Jongbloed and Kemme (1990b)
	5	49		Cromwell (1992)
	4	50		Burnell et al. (1989)
	—	51		Cromwell and Stahly (1980)
	4		62	Dügelhoef et al. (1994)
	16		68	Rodehutscord et al. (1996)
	—	69		Kuznetsov et al. (1987)
Barley	6	28		Coffey et al. (1992)
	4		29	Calvert et al. (1978)
	2	30		Cromwell (1992)
	5	31		Stober et al. (1979)
	—	31		Cromwell and Stahly (1980)
	6		32	Jongbloed (1987)
	6		38	Berk and Schulz (1993)
	5		39	Jongbloed and Kemme (1990b)
	—	43		Kuznetsov et al. (1987)
	4		45	Rodehutscord et al. (1996)
—		51	Oksbjerg (1988)	
Triticale	4	46		Burnell et al. (1989)
	1	46		Cromwell (1992)
	—		49	Oksbjerg (1988)
	4		52	Dügelhoef et al. (1994)
	6		55	Berk and Schulz (1993)
Oats	5	21		Coffey and Cromwell (1993)
	2	22		Cromwell (1992)
	6	23		Stober et al. (1980b)
	—	49		Kuznetsov et al. (1987)
Sorghum	6	28		Coffey et al. (1992)

Table 6. CONTINUED

Feedstuffs	Number of trials	Availability (%)	Apparent digestibility (%)	Author (s)
By products:				
Maize feed gluten	10		20	Jongbloed and Kemme (1990b)
	5	57		Coffey and Cromwell (1993)
	4	59		Burnell et al. (1989)
Wheat bran	2	29		Cromwell (1992)
	5	33		Coffey and Cromwell (1993)
	6	35		Stober et al. (1980b)
	6		41	Jongbloed (1987)
	8	55		Hew et al. (1982)
Wheat middlings	6		28	Jongbloed and Kemme (1990b)
	6	34		Stober et al. (1980b)
	5	34		Coffey and Cromwell (1993)
	6		41	Jongbloed (1987)
	3	41		Cromwell (1992)
Rice bran	4		12	Jongbloed and Kemme (1990b)
	8	25		Hew et al. (1982)
	1	25		Cromwell (1992)
Hominy feed	4	14		Burnell et al. (1989)
	1	14		Cromwell (1992)
	7		19	Jongbloed and Kemme (1990b)
Protein sources:				
Soybean meal	—	18		Cromwell and Stahly (1980)
	6	18		Coffey et al. (1992)
	—	21		Kuznetsov et al. (1987)
	6		24	Jongbloed (1987)
	6		26	Berk and Schulz (1993)
	4	31		Cromwell (1992)
	6		31	Rodehutschord et al. (1996)
	4		32	Wecke et al. (1994)
	6	38		Ross et al. (1982)
	—		38	Gomes et al. (1990)
Soybean meal dehulled	6	22		Ross et al. (1982)
	5	23		Cromwell (1992)
	3		38	Jongbloed and Kemme (1996b)
Rapeseed meal	2	16		Cromwell and Coffey (1993)
	1	21		Cromwell (1992)
	4		32	Larsen and Sandström (1993)
	4		23	Yong-Gang Liu et al. (1995)
Sunflower meal	1	3		Cromwell (1992)
	4		16	Jongbloed and Kemme (1990b)
	—		30	Gomes et al. (1990)
	—	45		Kuznetsov et al. (1992)
Cottonseed meal	—	0		Cromwell and Stahly (1980)
	6	0		Stober et al. (1980a)
	2	1		Cromwell (1992)
Peanut meal	8	12		Hew et al. (1982)
	1	12		Cromwell (1992)
Peanut hulls	3		20	Lindemann et al. (1984)
Peas	4		45	Jongbloed and Kemme (1990b)
Field beans	6		21	Berk and Schulz (1993)

Digestibility and availability of phosphorus in feedstuffs

Table 6 presents the results of studies on P availability measured by the slope ratio technique and apparent P digestibility in various feedstuffs. Table 7 provides the average values for both of these determinations and compares them with each other. A relatively high degree of agreement between the results ($r = 0.95$) was found, but average digestibility value was nearly 6% higher than availability. This is not in accordance with the opinion of Dellaert et al. (1990) who believe that in order to calculate digestibility on the basis of availability, it is necessary to use a coefficient of 0.9. This discrepancy may be explained by the fact that the data used for the comparison were taken from various laboratories and, therefore, were

Table 7. Availability and apparent digestibility of phosphorus (%) in some feeds of plant origin (Summarized data from table 6).

Feedstuff	Availability	Apparent digestibility
Maize	14	17
Rapeseed meal	19	27
Sunflower meal	24	23
Soyabean meal	25	31
Barley	33	39
Wheat middlings	36	35
Wheat bran	38	41
Triticale	48	52
Wheat	56	51
Mean	33 (14-56)	35 (17-52)

Table 8. Apparent digestibility of phosphorus in relation to the phytate and phytase activity

Feedstuff	Phosphorus		Phytase activity (U/kg)		Digestibility (%)	Author(s)
	Total	Phytate	Intrinsic	Added		
Maize	2.80	2.32	< 100	—	18	Dügelhof et al. (1994)
				750	56	
	3.30	2.20	20	—	29	Pointillart (1984)
	3.50	2.50	56	—	16	Own study
Wheat	4.22	3.12	440	—	62	Dügelhof et al. (1994)
				750	74	
	3.2	1.56	664	—	40	Barrier et al. (1996)
	3.0	1.88	438	—	40	
	1.9	0.90	520	—	42	
	2.7	2.01	470	—	39	
	3.60	2.40	160	—	46	Pointillart (1984)
3.60	2.30	936	—	38	Own study	
Barley	4.40	2.82	550	—	45	Rodehutschord et al. (1996)
				750	66	
	4.11	2.59	310	—	38	Berk and Schulz (1993)
	4.20	2.60	750	—	37	Own study
Triticale	4.23	3.22	540	—	52	Dügelhof et al. (1994)
				750	67	
	5.40	3.66	1,475	—	55	Berk and Schulz (1993)
	3.60	2.50	1,395	—	40	Own study
SBM	7.17	4.66	0	—	31	Rodehutschord et al. (1996)
				750	73	
	6.81	4.69	0	—	26	Berk and Schulz (1993)
Maize + SBM	3.3	2.6	< 50	—	13	Jongbloed et al. (1992)
				1,500	43	
	3.3	2.7	0	—	20	Simons et al. (1990)
				1,000	46	
	4.4	3.5	0	—	16	Näsi (1990)
			500	40		

unavoidably burdened with error.

Digestibility and availability of the P differed considerably depending on the feed. The lowest values were found for maize (under 20%), the highest for wheat and triticale (over 50%). Such large differences in the bioavailability of P among feedstuffs must be caused by the lack or presence of native phytase, and not only differences in the proportion of phytate P in total P, which in this case was similar (table 2).

The presented review of the literature shows that there are several ways in which the digestibility of plant P can be improved. The most important are (1) mixing appropriate combinations of feedstuffs, in which one or more of the components is characterized by high native phytase activity (Pointillart, 1991; Helander et al., 1994; Jongbloed, 1991b, 1992; BASF, 1992; Kwon et al., 1995b), (2) supplement feeds with a microbial phytase additive (Simons et al., 1990; Jongbloed et al., 1992; Pallauf et al., 1994; Nelson et al., 1968b; Schoner, 1992; Leunissen and Young, 1992; Näsi, 1990; Lei et al., 1993; Cromwell et al., 1993; Kwon et al., 1995ab) or (3), use both of these methods simultaneously. The availability of P in feeds of plant origin also depends on the composition of P compounds. In effect, it depends on at least several factors, and the importance of each of them individually is not known well enough.

An attempt to rank them by importance was undertaken in this review. Table 8 presents a compilation of the results of 9 experiments in which both forms of P (phytate and nonphytate), as well as native phytase activity were evaluated in plant feeds. Exogenous phytase at doses of 500-1,500 U/kg was added to some feeds.

The average count of total P was 4.1 g/kg feed, of which 71% was phytate P. Apparent digestibility was $44.7 \pm 19\%$. A preliminary analysis of the data in table 8 already shows that P digestibility is influenced by several factors. This was confirmed by multiple regression analysis, which had the following form:

$$Y = 0.10 \times X_1 + 0.90 \times X_2 + 0.76 \times X_3 + 1.08 \times X_4,$$

$$R = 0$$

where:

- Y - digestible P, g/kg
- X_1 - phytate P content, g/kg
- X_2 - nonphytate P content, g/kg
- X_3 - native phytase activity (in thousands of units)
- X_4 - added microbial phytase (in thousands of units)

This equation shows that the digestibility of phytate P

is about 10%, which is in agreement with the studies by Cromwell (1990) on the availability of isolated phytate P, while the coefficient 0.89 for the nonphytate P indicates its high digestibility (89%), which remains in agreement with other authors (Vipermann et al., 1974). These calculations are also corroborated by the advantageous effect of phytase on P digestibility: it is slightly higher in the case of microbial phytase than the native form of the enzyme. In the analyzed material, it was possible to attribute 30% of the digested nutrient in the diet to the microbial phytase (at an average level of 620 U/kg). Windisch et al. (1994) reported that when phytase was added to the diet in amounts of 1,000 U/kg, the amount of added mineral phosphorus can be reduced by 1 g/kg of feed.

CONCLUSIONS

Two main methods, the apparent digestibility and slope ratio technique have been commonly used for assessing the bioavailability of P in feedstuffs of plant origin. The results obtained by these methods provide complementary information.

The bioavailability of P in various feedstuffs of plant origin varies from 10 to 60%. This is due to the proportion of phytate P and the presence of intrinsic phytase. Proportion of phytate P in total P is variable in wide range (40-90%) in cereals, by-products and high-protein feeds. Also activity of intrinsic phytase varies in wide range (0-5,000 U/kg). Microbial phytase supplementation improve the P availability. It is already visible at dose of up to 500 U/kg. The higher dose increase P availability, but less distinctly.

Both intrinsic plant and microbial phytase improve the availability of P in feedstuffs of plant origin. In a mixture of feeds with low and high activity of intrinsic phytase and/or supplemented by commercial phytase, the P availability is additives. However, in the light of current results it seems that exceeding the P availability equal to 60-70% is unrealizable even at large microbial phytase doses.

REFERENCES

- BASF. 1992. Phytase: Interesting facts about Natuphos. BASF, Edition 29
- Barlet, J. P., M. J. Davicco and V. Coxam. 1995. Physiologie de l'absorption intestinale du phosphore chez l'animal. *Reprod. Nutr. Dev.* 35, 475-489.
- Barrier-Guillot, B., P. Casado, P. Maupetit, C. Jondreville and F. Gatel. 1996. Wheat phosphorus availability: 1-*In vitro* study; factors affecting endogenous phytase activity and

- phytic phosphorus content. *J. Sci. Food Agric.* 70, 62-68.
- Berk, A. and E. Schulz. 1993. Die Verdaulichkeit des Phosphorus aus unterschiedlichen Futtermitteln beim Schwein während der Mast. In Kongressband 1993 Hamburg. Vorträge zum Generalthema des 105. VDLUFA-Kongresses vom 20-25.09.1993 in Hamburg: Qualität und Hygiene von Lebensmitteln in Produktion und Verarbeitung, 309-312.
- Borowitz, S. M. and F. K. Ghishan. 1985. Maturation of jejunal phosphate transport by rat brush border membrane vesicles. *Pediat. Res.* 19, 1308-1312.
- Breves, G. and B. Schröder. 1991. Comparative aspects of gastrointestinal phosphorus metabolism. *Nutr. Res. Rev.* 4, 125-140.
- Burnell, T. W., G. L. Cromwell and T. S. Stahly. 1989. Bioavailability of phosphorus in triticale, hominy feed and corn gluten feed for pigs. *J. Anim. Sci.* 67, suppl. 2, 126 (abstr.)
- Calvert, C. C., R. J. Besecker, M. P. Plumlee, T. R. Cline and D. M. Forsyth. 1978. Apparent digestibility of phosphorus in barley and corn for growing swine. *J. Anim. Sci.* 47, 420-426.
- Coffey, R. D., G. L. Cromwell and T. S. Stahly. 1992. Bioavailability of phosphorus in monocalcium phosphate, corn, dehulled soybean meal, barley, sorghum and wheat for growing pigs. *J. Anim. Sci.* 70, suppl. 1, 228 (abstr.)
- Coffey, R. D. and G. L. Cromwell. 1993. Determination of the phosphorus availability in several feed ingredients for growing pigs. *J. Anim. Sci.* 71, suppl. 1, 158 (abstr.)
- Cooper, J. R. and H. S. Gowing. 1983. Mammalian small intestinal phytase (EC 3.1.3.8.). *Br. J. Nutr.* 50, 673-678.
- Cross, H. S., H. Debiec and M. Peterlik. 1990. Mechanism and regulation of intestinal phosphate absorption. *Miner. Electrolyte Metab.* 16, 115-124.
- Cromwell, G. L. 1979. Availability of phosphorus in feedstuffs for swine. *Proc. Distillers Fed Research Conf.* pp. 40-52.
- Cromwell, G. L. 1980. Biological availability of phosphorus for pigs. *Feedstuffs* 52, 38-42.
- Cromwell, G. L. 1989. Requirements, biological availability of calcium, phosphorus for swine evaluated. *Feedstuffs* 60, 23, 16-20.
- Cromwell, G. L. 1990. Application of phosphorus availability data to practical diet formulation. *Proc. Carolina Nutr. Conf.* pp 55-75. Raleigh, NC.
- Cromwell, G. L. 1992. The biological availability of phosphorus in feedstuffs for pigs. *PigNews Inform.* 13, 75N-78N.
- Cromwell, G. L. and T. S. Stahly. 1980. Effects of phosphorus source and level on bone development and growth in pigs. *Proceedings International Pig Veterinary Society.* 1980, 336.
- Cromwell, G. L. and R. D. Coffey. 1993. An assessment of the bioavailability of phosphorus in feed ingredients for nonruminants. *Proc. Maryland Nutr. Conf.* Baltimore, Maryland, March 19, 1993.
- Cromwell, G. L., R. D. Coffey and H. J. Monegue. 1993. Phytase (Natuphos) improves phytate phosphorus utilization in corn-soybean meal for pigs. *J. Anim. Sci.* 71, suppl. 1, 165 (abstr.)
- Davies, M. I. and I. Motzok. 1972. Properties of chick intestinal phytase. *Poul. Sci.* 51, 494.
- Dellaert, B. M., G. F. V. Van der Peet, A. W. Jongbloed and S. Beers. 1990. A comparison of different techniques to assess biological availability of feed phosphates in pig feeding. *Neth. J. Agric. Sci.* 38, 555-566.
- Die Deutsche Landwirtschafts-Gesellschaft. 1992. Futterwerttabellen, Hanover.
- Drochner, W. 1984. Einfluss wechselnder Rohfaser- und Pektin-gehalte im Futter auf einige präcaecale und postileale Verdauungsvorgänge beim wachsenden Schwein. *Fortschr. Tierphysiol. Tierernährng.* 14, 125.
- Dügelhof, M., M. Rodehutschord, H. Spiekers and E. Pfeffer. 1994. Effects of supplemental microbial phytase on availability of phosphorus contained in maize, wheat and triticale to pigs. *Anim. Feed Sci. Technol.* 49, 1-10.
- Eeckhout, W. and M. De Paepe. 1994. Total phosphorus, phytate-phosphorus and phytase activity in plant feedstuffs. *Anim. Feed Sci. Technol.* 47, 19-29.
- Fandrejewski, H. and A. Rymarz. 1986. Effect of feeding level on Ca, P, K and Na content in the bodies of growing boars and gilts. *Livest. Prod. Sci.* 14, 211-215.
- Fandrejewski, H., D. Weremko and A. Rymarz. 1994. Mineral body composition of female pigs at 7-9 month of age. In *Proceedings of the Symposium on Minerals in Animal Nutrition. Poznań 8-9 IX 1994*, 257-260.
- Gomes, C. P., G. J. M. M. De Lima, M. M. F. Gomes and T. E. Filho. 1990. Availability of phosphorus in soyabean meal, defatted rice bran and sunflower meal for pigs. *Revista da Sociedade Brasileira de Zootecnia.* 19, 6, 498-502; 14 ref.
- Gueguen, L., P. Besancon and A. Rerat. 1968. Digestive utilization of absorption and efficiency of retention of phytic phosphorus in pigs. *Annales de Biologie Animale, Biochimie, Biophysique.* 8: 273-280.
- Gueguen, L., S. M. Bagheri and A. Rerat. 1981. Influence of wheat bran on the intestinal absorption of minerals in the pig. Role of the hind gut. In *Proceedings XIIth Int. Congr. Nutr. San Diego USA* (abstr. 268).
- Harrison, H. E. and H. C. Harrison. 1961. Intestinal transport of phosphate: action of vitamin D, calcium and potassium. *Am. J. Physio.* 201:1007-1012.
- Headon, D. R., 1992. Biotechnology: A case study in identifying glycocomponents and enzymes to assist in reducing pollution. *Improving Nutrient Utilization While Reducing Pollution: New Dimensions Through Biotechnology Proc.* Alltech, 6th Annual European Lecture Tour, 15-35.
- Helander, E., M. Näsä and K. Partanen. 1994. Inclusion of wheat bran in barley-soybean meal diets with different phosphorus levels for growing-finishing pigs I. Effects on nutrient digestibility and mineral balances in finishing pigs. *J. Agric. Sci. in Finland* 3, 27-39.
- Hendriks, W. H. and P. J. Moughan. 1993. Whole-body mineral composition of entire male and female pigs depositing protein at maximal rates. *Livest. Prod. Sci.* 33, 161-170.
- Hew, V. F., G. L. Cromwell and T. S. Stahly. 1982. The bioavailability of phosphorus in some tropical feedstuffs for pigs. *J. Anim. Sci.* 55, suppl. 1, 277 (abstr.)
- Irving, G. C. J. 1980. Phytase. In: *Inositol phosphorus*. Ed.: Cosgrove, D. J., Amsterdam: Elsevier. pp. 85-127.
- Jongbloed, A. W. 1987. Phosphorus in the feeding of pigs; effect of diet on the absorption and retention of phosphorus by growing pigs. *Doctoral Thesis, Wageningen Agricultural University*, pp. 343.
- Jongbloed, A. W. and P. A. Kemme. 1990a. Effect of pelleting

- mixed feeds on phytase activity and the apparent absorbability of phosphorus and calcium in pigs. *Anim. Feed Sci. Technol.* 28, 233-242.
- Jongbloed, A. W. and P. A. Kemme. 1990b. Apparent digestible phosphorus in the feeding of pigs in relation to availability, requirement and environment. 1. Digestible phosphorus in feedstuffs from plant and animal origin. *Neth. J. Agric. Sci.* 38, 567-575.
- Jongbloed, A. W. and P. A. Kemme. 1990c. In: *Mestproblematiek: aanpak via de voeding van varkens en pluimvee. Verslag van de themadag Veevoeding en Milieu, Lelystad, 19 April 1990, Lelystad: IVVO pp. 33-42.*
- Jongbloed, A. W., H. Everts and P. A. Kemme. 1991a. Phosphorus availability and requirements in pigs. *Rec. Adv. Anim. Nutr.* 65-80.
- Jongbloed, A. W., P. A. Kemme and Z. Mroz. 1991b. Effect of supplementary microbial phytase in diets for pigs on digestibility of P and phytic acid in different sections of the alimentary tract. *J. Anim. Sci.* 69 (Suppl. 1): 374 (Abstr.)
- Jongbloed, A. W., Z. Mroz and P. A. Kemme. 1992. The effect of supplementary *Aspergillus niger* phytase in diets for pigs on concentration and apparent digestibility of dry matter, total phosphorus, and phytic acid in different sections of the alimentary tract. *J. Anim. Sci.* 70, 1159-1168.
- Jorgensen, H. and J. A. Fernandez. 1984. The influence of level of minerals and dietary fat on the apparent absorption of minerals at the terminal ileum and overall in growing pigs. Paper 35th EAAP, The Hague.
- Jungbluth, A. W. and U. Binswanger. 1989. Unidirectional duodenal and jejunal calcium and phosphorus transport in the rat. Effects of dietary phosphorus depletion, ethane-1-hydroxy-1, I-diphosphate and 1,25-dihydroxycholecalciferol. *Research in Experimental Medicine.* 189: 439-449.
- Ketaren, P. P., E. S. Batterham, E. White, D. J. Farrell and B. K. Milthorpe. 1993. Phosphorus studies in pigs 1. Available phosphorus requirements of grower/finisher pigs. *Br. J. Nutr.* 70, 249-268.
- Kuznetsov, S. G., A. P. Bataeva and B. D. Kalnitskii. 1987. Biological availability of phosphorus in feeds for pigs. *Byulleten Vsesoyuznogo Nauchno-issledovatel'skogo Instituta Fiziologii, Biokhimmii i Pitaniya Sel'skokhozyaistvennykh Zhivotnykh.* 2, 86, 44-48; 6 ref.
- Kwon, K., I. K. Han, K. S. Sohn and C. H. Kwon. 1995a. Effects of microbial phytase on performance, nutrient digestibility and phosphorus excretion in growing-finishing pigs fed corn-soy diets. *Kor. J. Anim. Sci.* 37(4):341-352.
- Kwon, K., I. K. Han, K. S. Sohn, C. H. Kwon and J. H. Kwack. 1995b. Effects of microbial phytase on performance, nutrient digestibility and phosphorus excretion in weaning-growing pigs fed corn-wheat-soy diets. *Kor. J. Anim. Sci.* 37(4):353-362.
- Lantzsich, H. J., 1989. Einführung und Stand der Diskussion zur intestinalen Verfügbarkeit des Phosphorus beim Schwein. In: *Industrieverband Agrar e. V., Fachausschuß steigender Ca-Gehalte in Futtee, 46, Tagung der GEH, Göttingen.*
- Lantzsich, H. J. 1990. Untersuchungen über ernährungsphysiologische effekte des phytats bei Monogastriern (Ratte, Schwein). *Übers. Tierern hrg.* 18, 197-212.
- Lantzsich, H. J., S. E. Scheuermann and K. H. Menke. 1988. Gastrointestinal hydrolysis of phytate from wheat, barley and corn in young pigs. *J. Anim. Physiol. a. Anim. Nutr.* 59, 273-284.
- Larsen, T. and B. Sandström. 1993. Effect of dietary calcium level on mineral and trace element utilization from a rapeseed (*Brassica napus* L.) diet fed to ileum-fistulated pigs. *Br. J. Nutr.* 69, 211-224.
- Lei, X., P. K. Ku, E. R. Miller, D. E. Ullrey and M. T. Yokoyama. 1992. Influence of wupplemental microbial phytase activity level on utilization of phytate phosphorus in a corn-soybean meal diet for weanling pigs. *J. Anim. Sci.* 70 (Suppl. 1): 71 (Abstr.)
- Leunissen, M. and L. G. Yong. 1992. Microbial phytase addition to diets of young pigs. *J. Anim. Sci.* 70 (Suppl. 1): 61 (Abstr.)
- Lindemann, M. D., R. J. Moore and E. T. Komegay. 1984. Charakterization of peanut hulls as a feedstuffs for swine. *J. Anim. Sci.* 59, suppl. 1, 54 (abstr.)
- Liu, Yong-Gang, B. Smits, A. Steg, R. Jongbloed, S. K. Jensen and B. O. Eggum. 1995. Crambe meal: digestibility in pigs and rats in comparison with rapeseed meal. *Anim. Feed Sci. Technol.* 52, 257-270.
- Moore, J. H. and C. Tyler. 1955. Studies on the intestinal absorption and excretion of calcium and phosphorus in the pig. *Br. J. Nutr.* 9, 63-80.
- Mroz, Z., A. W. Jongbloed, P. A. Kemme and K. Geerse. 1993. Digestibility and urinary losses of calcium and phosphorus in pigs fed a diet with suboptimal levels of both elements and graded doses of microbial phytase (Natuphos). In *Proceedings of the Symposium on Enzymes in Animal Nutrition*, p. 217-221.
- Nair, V. C. 1991. Production of Phytase by *Aspergillus ficuum* and reduction of phytic acid content in canola meal. *J. Sci. Food Agric.* 54, 355-365.
- NAS-NRC, National Academy of Sciences-National Research Council. 1960. Nutrient requirements for domestic animals. 2. Nutrient requirements for pigs.
- Näsi, M. 1990. Microbial phytase supplementation for improving availability of plant phosphorus in the diet of the growing pigs. *J. Agric. Sci. Finland* 62, 435-443.
- Näsi, J. M., E. H. Helander and K. H. Partanen. 1995. Availability for growing pigs of minerals and protein of a high phytate barley-rapeseed meal diet treated with *Aspergillus niger* phytase or soaked with whey. *Anim. Feed Sci. Technol.* 56, 83-98.
- Nelson, T. S. 1967. The utilization of phytate phosphorus by poultry-A review. *Poult. Sci.* 46:862.
- Nelson, T. S., L. W. Ferrara and N. L. Storer. 1968a. Phytate phosphorus content of feed ingredients derived from plants. *Poultry Sci.* 47, 1372-1374.
- Nelson, T. S., T. R. Shieh, R. J. Wodzinski and J. H. Ware. 1968b. The availability of phytate phosphorus in soybean meal before and after treatment with a mold phytase. *Poultry Sci.* 47, 1842-1848.
- Nelson, T. S., T. R. Shieh, R. J. Wodzinski and J. H. Ware. 1971. Effect of supplemental phytase on the utilization of phytate phosphorus by chicks. *J. Nutr.* 101, 1289-1294.
- Oksbjerg, N. 1988. Digestibility and utilization of total phosphorus and phytate phosphorus in cereals for growing pigs. *Proceedings of the 4th International Seminar on Digestive Physiology in pigs.* Polish Academy of Sciences, Jabonna.

- 352-356.
- Orda, J., A. Wiliczekiewicz, B. Fuchs and J. Pre. 1994. Influence of different plant phosphorus and hydrothermic treatment on mineralisation and physical features of swine bones. In Proceedings of the Symposium on Minerals in Animal Nutrition. Poznań 8-9 IX 1994, 261-268.
- Oslage, H. J. 1964. Body composition and accretion of matter by growing fattening pigs. V. Mineral content and accretion of minerals by growing fattening pigs. Z. Tierphysiol. Tierernähr. Futtermittelk. 19, 330-357.
- Pallauf, J., D. Hohler, G. Rimbach and H. Neusser. 1992. Effect of microbial phytase supplementation to a maize-soya-diet on the apparent absorption of phosphorus and calcium in piglets. J. Anim. Physiol. a. Anim. Nutr. 67, 30-40.
- Pallauf, J. and G. Rimbach. 1993. Phytase as an example for the use of enzymes as feed additives in animal nutrition. Proceedings of the 4th Symposium "Vitamine und weitere Zusatzstoffe bei Mensch und Tier" 30.9/1.10.1993 Jena/Thüringen, 354-363.
- Pallauf, J., G. Rimbach, S. Pippig, B. Schindler and E. Most. 1994. Effect of phytase supplementation to a phytate-rich diet based on wheat, barley and soya on the bioavailability of dietary phosphorus, calcium, magnesium, zinc and protein in piglets. Agricol. Res. 47, 1, 39-48.
- Partridge, I. G., D. Simons and H. Bergner. 1986. The effects of treated straw meal on ileal and faecal digestibility of nutrients in pigs. Arch. Tierernähr. 36, 351-359.
- Peeler, H. T. 1972. Biological availability of nutrients in feeds: Availability of major mineral ions. J. Anim. Sci. 35, 695-712.
- Peo, E. R. 1991. Calcium, phosphorus, and vitamin D in swine nutrition. Swine Nutrition. Edited by Miller R. E. et al., 1991. 165-182.
- Pointillart, A. 1988. Phytate phosphorus utilization in growing pigs. Proceedings of the 4th International Seminar on Digestive Physiology in pigs. Polish Academy of Sciences, Jabonna. 319-326.
- Pointillart, A. 1991. Enhancement of phosphorus utilization in growing pigs fed phytate-rich diets by using rye bran. J. Anim. Sci. 69, 1109-1115.
- Pointillart, A., N. Fontaine and M. Thomasset. 1984. Phytate phosphorus utilization and intestinal phosphatases in pigs fed low phosphorus: wheat or corn diets. Nutr. Rep. Int. 29, 473-483.
- Pointillart, A., A. Fourdin and N. Fontaine. 1987. Importance of cereal phytase activity for phytate phosphorus utilization by growing pigs fed diets containing triticale or corn. J. Nutr. 117, 907-913.
- Quamme, G. A. 1985. Phosphate transport in intestinal brush-border membrane vesicles: effect of pH and dietary phosphate. Am. J. Physiol. G, 168-176.
- Radde, I. D., D. Davis, J. Sheepers and H. G. McKercher. 1980. Bidirectional transmucosal ^{45}Ca and ^{32}P fluxes across the small intestine of the young piglet: Relationship to intestinal Ca^{2+} - Mg^{2+} -ATPase activity and postnatal age. In Pediatric Diseases Relate to Calcium, pp. 153-163. [H. F. DeLuca and C. S. Anast, editor]. Oxford: Blackwell Scientific Publications.
- Reddy, N. R., S. K. Sathe and D. K. Salunkhe. 1982. Phytates in legumes and cereals. Adv. Food Res. 28, 1-92.
- Rodehutsord, M., M. Faust and H. Lorenz. 1996. Digestibility of phosphorus contained in soybean meal, barley, and different varieties of wheat, without and with supplemental phytase fed to pigs and additivity of digestibility in a wheat-soybean-meal diet. J. Anim. Physiol. a. Anim. Nutr. 75, 40-48.
- Ross, R. D., G. L. Cromwell and T. S. Stahly. 1983. Biological availability of the phosphorus in high-moisture and pelleted corn. J. Anim. Sci. 57, suppl. 1, 96 (abstr.)
- Ross, R. D., G. L. Cromwell and T. S. Stahly. 1982. Biological availability of the phosphorus in regular and dehulled soybean meal for growing pigs. J. Anim. Sci. 55, suppl. 1, 93 (abstr.)
- Rymarz, A. 1986. Chemical body composition of growing pigs. Ca, P, K, Na and Mg contents in the body. Pig News and Information. 7, 2, 177-181.
- Rymarz, A., H. Fandziejewski and J. Kielanowski. 1982. Content and retention of calcium, phosphorus, potassium and sodium in the bodies of growing gilts. Livest. Prod. Sci. 9, 399-407.
- Scheuermann, S. E., H. J. Lantzsch and K. H. Menke. 1988. *In vitro* and *in vivo* experiments on the hydrolysis of phytate II. Activity of plant phytase. J. Anim. Physiol. a. Anim. Nutr. 60, 55-63.
- Schoner, F. J. 1992. Review of the biological effects and the ecological importance of phytase in broiler and layers. The 4th BASF animal nutrition forum. Edition 30. pp. 17-27.
- Simons, P. C. M., H. A. J. Versteegh, A. W. Jongbloed, P. A. Kemme, P. Slump, K. D. Bos, M. G. E. Wolters, R. F. Beudeker and G. J. Verschoor. 1990. Improvement of phosphorus availability by microbial phytase in broilers and pigs. Br. J. Nutr. 64, 525-540.
- Stober, C. R., G. L. Cromwell and T. S. Stahly. 1979. Availability of phosphorus in corn and barley for the pig. J. Anim. Sci. 49, suppl. 1, 97 (abstr.)
- Stober, C. R., G. L. Cromwell and T. S. Stahly. 1980a. Biological availability of the phosphorus in cottonseed meal for growing pigs. J. Anim. Sci. 51, suppl. 1, 49 (abstr.)
- Stober, C. R., G. L. Cromwell and T. S. Stahly. 1980b. Biological availability of the phosphorus in oats, wheat middlings and wheat bran for pigs. J. Anim. Sci. 51, suppl. 1, 80 (abstr.)
- Taylor, T. G. 1965. The availability of the calcium and phosphorus of plant materials for animals. Proc. Nutr. Soc. 24:105-112.
- Vipperman, P. E., E. R. Peo and P. J. Cunningham. 1974. Effect of dietary calcium and phosphorus level upon calcium, phosphorus and nitrogen balance in swine. J. Anim. Sci. 38, 758-765.
- Wasserman, R. H., 1981. Intestinal absorption of calcium and phosphorus. Fed. Proc. 40, 68-72 Wecke C., Reinisch F., Liebert F., and R. Kler. 1994. Absorption and utilization of phosphorus in maize and soybean meal by piglets with respect to phytase supplementation. VIth International Symposium on Digestive Physiology in Pigs. Bad Doberan, 4-6th October 1994. Proceedings-vol.II EAAP-Publ. No 80, 339-341.
- Wasserman, R. H. and A. N. Taylor. 1976. Gastrointestinal absorption of calcium and phosphorus. In Handbook of Physiology, Section 7, Wndoctionology, vol. 7, Parathyroid

- Gland. pp. 137-155. [G. D. Aurbach. outow] Washington, DC: American Physiology Society.
- Weremko, D. and H. Fandziejewski. 1996. Digestible phosphorus in feedstuffs from cereal grains and rapeseed meal. In Proceedings of the International Conference on Nutritional Value and Utilization of Feeds Results of Common Research. *Jab onna*, 23 January 1996, 30-32.
- Windisch, W., M. Kirchgessner and F. X. Roth. 1994. Effekt eines Zusatzes mikrobieller Phytase zu einer Weizen-Gerste-Soja-Diät auf zootechnische Leistungen und scheinbare Verdaulichkeiten von Phosphor, Calcium und Magnesium bei abgestufter P-Versorgung von Ferkeln. *Agribiol. Res.* 47, 90-99.