Effect of dietary phytic acid on performance and nutrient uptake in the small intestine of piglets

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ABSTRACT: An experiment was conducted with piglets to determine the effect of dietary phytic acid supplementation on performance, electrophysiological properties of jejunum mounted in Ussing chambers, sodium-dependent glucose transporter 1 (SGLT1) protein expression in jejunum, and plasma glucose and Na concentrations. Sixteen piglets with an average initial BW of 7.40 ± 0.36 kg were randomly assigned to 2 experimental diets with 8 piglets per diet. The diets were casein-cornstarch-based and were either unsupplemented or supplemented with 2% phytic acid (as Na phytate). The basal diet was formulated to meet the recommendation of NRC (1998) for energy, AA, minerals, and vitamins for piglets. The experiment lasted for 21 d, and at the end, BW gain and feed consumption were determined, and blood samples were collected for determination of plasma glucose and Na concentrations. The piglets were then euthanized to determine jejunal electrophysiological properties (transmural potential difference and short-circuit current) and SGLT1 protein expression. Phytic acid supplementation reduced ADG (P = 0.002), ADFI (P = 0.017), and G:F (P = 0.001) from 316.1 to 198.2 g, 437.4 to 360.3 g, and 0.721 to 0.539 g/g, respectively. Phytic acid supplementation also tended to reduce (P = 0.088) potential difference (−3.80 vs. −2.23 mV) and reduced (P = 0.023) short-circuit current from 8.07 to 0.1 µA/cm². However, phytic acid supplementation did not affect SGLT1 protein, and blood plasma glucose and Na concentrations. In conclusion, dietary phytic acid reduced growth performance and transmural short-circuit current in the jejunum of piglets. The reduced transmural short-circuit current in the jejunum by phytic acid implies reduced active Na transport in the jejunum by the phytic acid. Therefore, it seems that dietary phytic acid reduces growth performance of pigs partly through reduced capacity of the small intestine to absorb Na.

Key words: growth performance, phytic acid, pig, protein expression, sodium-dependent glucose transporter 1, transmural electrophysiological property

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INTRODUCTION

Phytic acid (PA) was shown to increase endogenous Na loss in broilers (Cowieson et al., 2004) and reduce the apparent ileal Na digestibility in piglets to a negative value (Woyengo et al., 2009), indicating increased ileal endogenous Na flow in pigs because of PA. However, there is a lack of information on the mechanisms by which PA increases the ileal endogenous Na flow.

The amount of the endogenous secreted nutrient that appears at the terminal ileum represents a proportion of the nutrient, which is not reabsorbed in the small intestine. Sodium is additionally absorbed from the small intestine by co-transportation with other nutrients including glucose and galactose (Fordtran et al., 1968), and its absorption has been shown to increase with an increase in glucose absorption (Fordtran, 1975; Schiller et al., 1997). Also, the active transport of nutrients such as glucose into enterocytes generates an osmotic flow of water into the enterocytes, which, in turn, results in an increase in absorption of Na by solvent drag (Fordtran et al., 1968). Phytic acid has been shown to reduce ileal digestibility of energy (Liao et al., 2005), of which a major source in practical swine diets is starch that yields glucose after hydrolysis. Phytic acid was also shown to reduce α-amylase and maltase activities.
in the duodenum of broilers (Liu et al., 2008), implying that PA reduces glucose absorption because of the reduced abundance of this monosaccharide. It was thus hypothesized that the increased ileal endogenous Na flow by PA is partly due to reduced availability of glucose for absorption. The objective of this study was to determine the effect of dietary PA on piglet performance, jejunal electrophysiological properties, sodium-dependent glucose transporter 1 (SGLT1) protein expression, and blood plasma indices.

MATERIALS AND METHODS

All experimental procedures were reviewed and approved by the University of Manitoba Animal Care Protocol Management and Review Committee, and pigs were handled in accordance with guidelines described by the Canadian Council on Animal Care (CCAC, 1993).

Experimental Animals and Housing

Sixteen piglets (Yorkshire-Landrace × Duroc; balanced for sex) with an initial BW of 7.40 ± 0.36 kg were obtained immediately after weaning, and group-housed in pens (8 pigs/diet) and monitored for consumption of a commercial starter diet to ensure that they were healthy and able to eat. After 3 d, piglets were housed individually in pens (1.5 × 1.2 m) with smooth sides and plastic-covered expanded metal flooring in a temperature-controlled room (30 ± 2°C) and fed the experimental diets.

Experimental Diets and Procedure

The 2 diets fed were a casein-cornstarch-based diet without PA (control) and the control plus 2.0% PA (as Na phytate; Sigma-Aldrich Corporation, St. Louis, MO). Phytic acid was supplemented at 2.0% because we had previously observed increased endogenous loss of Na and Mg because of supplementation with 2.0% PA (Woyengo et al., 2009). The basal diet was formulated to meet NRC (1998) energy, AA, minerals, and vitamin recommendations for piglets (Table 1). Both the control diet and the PA-supplemented diet were formulated to be the same in available P content (0.42%) by including in the diets the same amounts of casein, monocalcium phosphate, and limestone, which were the available P sources in the diets. The diets were fed ad libitum to the piglets for 21 d in a completely randomized design with 8 piglets per diet. At the end of the experiment, BW gain and feed consumption were determined. In addition, blood samples (10 mL) were collected from each pig via jugular vein puncture into Vacutainer tubes coated with lithium heparin (Becton Dickinson & Co., Franklin Lakes, NJ). The samples were immediately centrifuged at 2,000 × g for 10 min at 4°C to recover plasma, which was immediately stored at −20°C until used for glucose and Na analyses.

After the blood collection, the piglets were anesthetized by an intramuscular injection of ketamine:xylazine (20:2 mg/kg; Bimeda-MTC Animal Health Inc., Cambridge, Ontario, Canada), and euthanized by an intravenous injection of Na pentobarbital (50 mg/kg of BW, Bimeda-MTC Animal Health Inc.). The abdomen and the thorax were cut open by a midline incision. Two 10-cm pieces (samples) of the jejunum (160 cm below the pylorus) were obtained from piglets by cutting off the mesentery at the line of its attachment to the intestine for determination of SGLT1 protein abundance and electrophysiological properties. Samples to be used for SGLT1 protein expression were immediately frozen in liquid nitrogen and stored at −80°C until required for analysis. The samples for determination of electrophysiological properties were rinsed with ice-cold Ringer buffer with the following composition (mmol/L): NaCl, 115; NaHCO3, 25; K2HPO4, 2.4; CaCl2, 1.2; MgCl2, 1.2; KH2PO4, 0.4; and d-glucose, 10. The pH of the buffer was adjusted to 7.4 using 50% HCl. After rinsing, they

<table>
<thead>
<tr>
<th>Table 1. Composition and analysis of basal diets</th>
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<tr>
<td><strong>Item</strong></td>
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<td>Ingredient, % of diet</td>
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<td>Cornstarch</td>
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<td>Lactose</td>
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<td>Casein</td>
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<td>Cellulose</td>
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<td>Monocalcium phosphate</td>
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<td>Salt</td>
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<td>Calculated composition, %</td>
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<td>CP</td>
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<td>Ca</td>
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<td>Na</td>
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<td>P</td>
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1Phytic acid = control diet plus 2% phytic acid.
2Supplied per kilogram of finished diet: retinol, 2,479 µg; cholecalciferol, 25 µg; α-tocopherol, 13.4 mg; phylloquinone, 1.1 mg; thiamine, 4 mg; riboflavin, 5 mg; pantothenic acid, 15 mg; nicotinamide, 36.8 mg; cyanocobalamin, 25 mg; pyridoxine, 4.4 mg; biotin, 200 mg; Pteroyl(mono)glutamic acid, 1 mg; choline, 781 mg; Cu, 6 mg as copper sulfate; I, 0.28 mg as calcium iodide; Fe, 100 mg as ferrous sulfate; Mn, 40 mg as manganese dioxide; Se, 0.30 mg as sodium selenite; and Zn, 100 mg as zinc oxide.
were transported in the ice-cold Ringer buffer to the laboratory, where they were opened along the mesenteric border and the mucosa inspected for digesta particles. If digesta particles were present, they were gently washed off with the Ringer buffer at 4°C. The samples of jejunum were kept in the ice-cold Ringer buffer (for approximately 4 min), which was continuously gassed with a mixture of 95% O2 and 5% CO2 until required for measurements.

**Determination of Electrophysiological Properties**

The electrophysiological properties (transmural potential difference and short-circuit current) were determined using a modified Ussing chambers (VCC-MC6, Physiologic Instruments Inc., San Diego, CA) containing pairs of current (Ag wire) and voltage (Ag/AgCl pellet) electrodes housed in 3% agar bridges and filled with 3 M KCl. The potential difference reflects the transmural potential difference that is generated by ion movement across the epithelium, whereas short-circuit current reflects the net transmural ion movement (Ussing, 1994; Wright and Loo, 2000).

Four milliliters of the Ringer buffer solution was added to mucosal chambers, and 4 mL of Ringer buffer solution enriched with 10 mmol/L of d-mannitol instead of d-glucose, was added to serosal chambers. Both the mucosal and serosal chambers were continuously gassed with a mixture of 95% O2 and 5% CO2. The temperature of the chambers was maintained at 37°C. The possible potential difference existing between the mucosal and serosal chambers was offset before tissue mounting. After gently stripping off serosal and longitudinal muscle layers using micro-forceps, the tissues were mounted in the Ussing chambers employing a tissue holder with a mixture of 95% O2 and 5% CO2 until required for measurements.

**Determination of SGLT1 Protein Abundance and Plasma Glucose and Na**

Sodium-dependent glucose transporter 1 protein abundance in the jejunum was determined by Western Immunoblotting Analysis. In brief, approximately 1 g of mucosa from pig jejunum was removed and transferred to cold lysis buffer containing 20 M Tris-HCl (pH 7.4), 150 mmol/L of NaCl, 1 mmol/L of EDTA, 1 mmol/L of EGTA, 2.5 mmol/L of Na pyrophosphate, 1 mmol/L of β-glycerophosphate, 1 mmol/L of Na orthovanadate, 1% Triton X-100, 2.1 µmol/L of leupeptin, and 1 mmol/L of phenylmethylsulfonyl fluoride. The mucosa was homogenized and sonicated before centrifugation for 5 min at 3,000 × g at 4°C. Supernatant was collected for determining protein concentration using the Bradford assay. Proteins (100 µg) were separated by electrophoresis on a 10% SDS polyacrylamide gel. Partitioned proteins were transferred to a nitrocellulose membrane. The membrane was blocked using BSA. The membrane was probed with rabbit anti-SGLT1 polyclonal antibody (Millipore, Billerica, MA) at 1:2,000 dilutions. Horseradish peroxidase-conjugated anti-rabbit IgG antibody (Cell Signaling Technology Inc., Danvers, MA) at 1:1,000 dilutions was used as the secondary antibody. The corresponding protein bands were visualized using enhanced chemiluminescence reagents and analyzed with a gel documentation system (Bio-Rad Gel Doc1000, Hercules, CA). Plasma was assayed for glucose and Na (Nova Stat Profile M Blood Gas and Electrolyte Analyzer, Nova Biomedical Corporation, Waltham, MA).

**Statistical Analysis**

The data were subjected to ANOVA as a completely randomized design (Steel et al., 1997) using the GLM procedure (SAS Inst. Inc., Cary, NC). Treatment means (control vs. control plus PA) were compared using the t-test procedure (Steel et al., 1997).

**RESULTS**

Analyzed chemical composition of the diets is presented in Table 1. The analyzed values of CP, Ca, Mg, K, Na, and P in the diets were fairly close to calculated values. Phytic acid-supplemented diet had greater P and Na contents than the control. Phytic acid supplementation reduced ADG (P = 0.002), ADFI (P = 0.017), and G:F (P = 0.001) of the pigs (Table 2). Data on the effect of dietary PA on electrophysiological properties of the jejunum of piglets mounted in Ussing chambers are presented in Table 3. Phytic acid supplementation tended to reduce (P = 0.088) total potential difference and reduced (P = 0.023) total short-circuit current. Phytic acid supplementation tended to reduce (P = 0.088) total potential difference and reduced (P = 0.023) total short-circuit current. However, PA sup-
plementation did not reduce SGLT1-sensitive potential difference and short-circuit current.

Phytic acid supplementation did not affect the SGLT1 protein expression (Figure 1). Also, PA supplementation did not affect the blood plasma glucose and Na concentrations (Table 4).

**DISCUSSION**

The total P content was greater in PA-supplemented diet than in the control, which was due to the increased content of P in PA. However, PA-bound P is poorly available for utilization by piglets. Therefore, it is highly unlikely that dietary P affected the response criteria that were measured in the current study. Both the calculated and the analyzed values of Na were slightly greater for the PA-supplemented diet than the control diet, which is attributed to the fact that the PA used in the current study was in form of Na phytate, which is rich in Na (13.8%). However, this slightly greater concentration of Na in a PA-supplemented diet could not have affected nutrient absorption and, hence, performance of piglets because of the following 3 reasons. First, diet is a very minor source of Na in the intestinal lumen required for uptake of nutrients by enterocytes; the major sources of the Na in the intestinal lumen are various types of gastrointestinal secretions (Fregly, 1981; Wapnir and Teichberg, 2002). Second, the concentration of Na in the small intestinal lumen of pigs has been shown not to increase with an increase in dietary intake of Na (Ehrlein et al., 1999). This is due to the fact that an increase in dietary intake of Na by pigs results in a decrease in gastrointestinal secretion of Na (Partridge, 1978) because the movement of Na from the blood into small intestinal lumen decreases when the hypertonic solution enters the intestinal lumen (Fregly, 1981). Third, pigs are tolerant to diets with increased Na content (up to 5.5% DM of diet) provided that water is offered to the pigs ad libitum (Mason and Scott, 1974). In the current study, water was offered to the piglets ad libitum. Thus, a small change in the Na content of a diet, which is a minor source of luminal Na, was not expected to affect nutrient absorption.

Dietary Na supply has indeed been shown to have no effect on absorption of other nutrients (Ehrlein et al., 1999). However, dietary sugars (glucose and fructose) have been shown to stimulate Na absorption in human intestine (Fordtran, 1975; Schiller et al., 1997). Glutamine has also been shown to stimulate Na absorption in human small intestine (Coëffier et al., 2005) and in rabbit small intestine (Nath et al., 1992). With regard to performance, an increase in dietary NaCl from 0.5 to 13.1% was shown not to affect the growth performance, blood hematocrits, or serum Na content of sheep, which had been offered water ad libitum (Meyer and Weir, 1954). Also, an increase in dietary NaCl from 0.4 to 0.8% did not affect the feed intake and growth rate of rats that had been offered water ad libitum (Schedl et al., 1988).

Phytic acid supplementation reduced pig performance, which was likely a result of reduced digestibility and increased endogenous losses of nutrients because of dietary PA. Phytic acid has been shown to reduce apparent digestibility of minerals (Kemme et al., 1999;
Bohlke et al., 2005; Woyengo et al., 2009) and energy (Liao et al., 2005) in pigs, implying that it reduces the availability of nutrients for utilization by the animals. Phytic acid has also been shown to reduce the apparent ileal Na and Mg digestibilities in piglets to negative values (Woyengo et al., 2009), indicating increased endogenous flow of these minerals at the terminal ileum of pigs. An increase in endogenous nutrient losses in the gut is associated with increased maintenance requirements for the lost nutrients and of the energy spent on secretion of nutrients (Nyachoti et al., 1997). Therefore, an increase in endogenous loss of nutrients because of PA implies that the presence of the PA in diets for the pigs results in increased maintenance requirements of energy and other nutrients, thereby reducing the availability of energy and nutrients for tissue deposition.

It is a well-established fact that dietary phytase supplementation improves P availability in pigs because of PA hydrolysis (Selle and Ravindran, 2008). Because of this improved availability of P because of phytase, the available P in phytase-supplemented swine diets has been reduced without any effect on performance (Harper et al., 1997; Matsui et al., 2000; Stahl et al., 2000). However, in the current study, the basal diet, to which PA was added, was formulated to be adequate in available P. Therefore, the reduced performance of piglets because of PA implies that dietary phytase supplementation can improve pig performance not only by improving P availability, but also by alleviating other antinutritional effects of PA.

The short-circuit current values observed in the current study for the control diet are within the range of values (−80 to 60 µA/cm²) reported by Lessard et al. (2009) and Smith et al. (2010) for jejunum of piglets. The potential difference and short-circuit current were less in the jejunum of piglets that had been fed a PA-supplemented diet when compared with piglets fed the control diet. In Ussing chambers, the potential difference reflects the transmural potential difference that is generated by ion movement across the epithelium, whereas short-circuit current reflects the net transmural ion movement (Ussing, 1994; Wright and Loo, 2000). In the current study, the Ringer buffer solution that was used to bath the mucosal side was the same as the one used on the serosal side except that glucose was added in the mucosal solution, whereas mannitol was added at the same molarity to the serosal solution to maintain osmotic balance across the tissue. Therefore, potential difference and short-circuit current reflected active transport of ions from the mucosal side to the serosal side, and hence PA reduced the active absorption of ions in the jejunum.

The magnitude by which the total short-circuit current was reduced by PA (8.07 vs. 0.10 µA/cm²) was great. Other studies have also shown considerable changes in short-circuit current in the intestine because of the presence of fiber or other antinutritive factors in diets for pigs and poultry. For instance, Awad et al. (2008) reported a decrease in short-circuit current in the jejunum of broilers from 32 to 7 µA/cm² because of the presence of inulin in diets, whereas Lessard et al. (2009) reported an increase in short-circuit current in jejunum of pig from 44 to approximately 160 µA/cm² because of dietary inclusion of fumonisin, which is a mycotoxin that interferes with intestinal barrier function. Therefore, the presence of antinutritive factors such as PA in diets for pigs could result in a substantial change in short-circuit current as observed in the current study.

Sodium absorption is the major generator of the potential difference and short-circuit current across the epithelium (Ussing and Zerahn, 1951; Ussing, 1994; Wright and Loo, 2000).

**Table 4.** Effect of dietary phytic acid on plasma sodium and glucose concentrations of piglets

<table>
<thead>
<tr>
<th>Item</th>
<th>Control</th>
<th>Phytic acid</th>
<th>SEM</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glucose, mg/dL</td>
<td>132</td>
<td>131</td>
<td>14</td>
<td>0.968</td>
</tr>
<tr>
<td>Na⁺, mmol/L</td>
<td>131</td>
<td>132</td>
<td>2</td>
<td>0.606</td>
</tr>
</tbody>
</table>

1Data are means of 8 pigs; sodium and glucose concentrations were determined in blood plasma collected in pigs that were in fed state.
2Control = a casein-cornstarch-based diet without phytic acid, and phytic acid = control diet plus 2% phytic acid.
ever, PA binds to Ca and Mg and thereby reduces the ions in the Ringer buffer (Grubb, 1991). The Na-K-ATPase, which is located on the basolateral membrane of the enterocytes actively pumps Na from the same enterocytes to interstitial fluid, creating an electrochemical gradient that serves as the driving force for movement of Na from the lumen to enterocytes. Because of this movement of Na from the intestinal lumen into the enterocytes and then to interstitial fluid, transepithelial potential difference and short-circuit current are created. Sodium is absorbed partly by co-transportation with other nutrients such as glucose (Fordtran, 1975). Therefore, an increase in absorption of nutrients co-transported with Na results in an increase in the absorption of the latter, leading to changes in transepithelial potential difference and short-circuit current (Wright and Loo, 2000). Also, the transport of nutrients (solutes) such as glucose and minerals into enterocytes generates an osmotic flow of water into the enterocytes, which, in turn, can result in an increase in absorption of Na by solvent drag (Fordtran et al., 1968), leading to further changes in transepithelial potential difference and short-circuit current when the Na ions are actively pumped from the enterocytes.

Phytic acid has been reported to reduce in vitro starch digestibility and carbohydrate absorption (estimated by breath hydrogen) and glycemic index in humans (Thompson et al., 1987) and to reduce ileal digestibility of energy of the piglets (Liao et al., 2005). The major source of energy in practical swine diets is starch. Phytic acid has also been reported to decrease the activity of α-amylase in vitro (Deshpande and Cheryan, 1984) and to reduce activities of α-amylase, sucrase, and maltase in the duodenum of broilers (Liu et al., 2008), implying that PA reduces carbohydrate digestibility and hence availability of glucose for absorption.

Glucose and galactose are absorbed in the small intestine by SGLT1 protein, whose expression is reduced with a decrease in the availability of glucose for absorption (Dyer et al., 1997). Therefore, the reduction of glucose absorption by PA is expected to result in a reduced expression of the SGLT1 protein, and hence the capacity of the small intestine to absorb glucose and Na. However, in the current study, PA did not reduce the SGLT1 sensitive potential difference and short-circuit current. Also, PA supplementation did not reduce SGLT1 protein expression in the jejunum of piglets. Therefore, it seems that the reduced ion uptake in the jejunum of piglets fed the PA-supplemented diet was also due to other processes.

In addition to Na, other ions in the Ringer buffer solutions, such as Ca and Mg, are actively transported from the mucosal to serosal side of the jejunum, also generating a positive short-circuit current. These ions are actively transported in the small intestine by proteins, of which activity increases with a decrease in their availability in diets in an effort to maintain adequate levels of Ca and Mg in the body (Hoenderop and Bindels, 2005; Khanal and Nemere, 2008). However, PA binds to Ca and Mg and thereby reduces the availability of these minerals, meaning that the expression of proteins that are involved in the active transport of these minerals may be enhanced in animals fed a PA-containing diet. Therefore, it is difficult to explain other mechanisms (apart from reduced SGLT1 protein expression) by which active ion uptake in the jejunum (mounted in Ussing chambers) of piglets fed the PA-supplemented diet could be reduced. However, as previously discussed, Na is absorbed not only by co-transportation with other nutrients, but by solvent drag as well (Fordtran et al., 1968). The reduced ion absorption in jejunum from piglets fed the PA-supplemented diet implies that the concentration of solutes in the cytoplasm of enterocytes was less for jejunum from piglets fed the PA-supplemented diet, meaning that the absorption of Na by solvent drag in the jejunum from piglets fed the PA-supplemented diet was also decreased. Therefore, the Na absorption may have been reduced in the jejunum from piglets fed the PA-supplemented diet regardless of whether the reduction was due to a decrease in SGLT1 protein expression or not. The ileal endogenous flow of a nutrient is dependent on its secretion and reabsorption. Therefore, the PA-induced increase in the ileal endogenous Na flow at the terminal ileum that we have previously observed (Woyengo et al., 2009) could partly be due to reduced absorption of Na.

Because PA was shown to increase the endogenous flow of Na at the terminal ileum of piglets (Woyengo et al., 2009), piglets fed the PA-supplemented diet in the current study were expected to have decreased blood plasma Na concentration. However, this was not the case because there was no effect of PA on the plasma Na concentrations. This lack of effect of PA on the plasma Na concentration could be attributed to an increase in (re)absorption of Na in the large intestine. It should, however, be noted that the basal-lateral membrane of enterocytes is impermeable to Na ions, and therefore, the enterocytes rely on Na ions coming from the intestinal lumen for their functioning (Ussing, 1994). Hence, the increased ileal endogenous flow of Na because of dietary PA that we have previously observed can still result in reduced availability of Na to enterocytes, thereby leading to Na deficiency in the same cells.

In conclusion, dietary PA can reduce growth performance and active ion transport in jejunum of piglets. The reduced active ion transport by PA implies that the latter reduces the capacity of the small intestine to absorb nutrients. Sodium is absorbed partly by co-transportation with other nutrients and by solvent drag and PA has been reported to increase the endogenous flow of Na at terminal ileum of pigs. Thus, the reduced capacity of the small intestine (by PA) to absorb nutrients implies that PA increases the ileal endogenous Na flow partly by reducing the reabsorption of endogenously secreted Na. The results also show that dietary PA reduces growth performance of pigs partly through reduced capacity of the small intestine to absorb Na.
LITERATURE CITED


