Development of Intestinal Immunoglobulin Absorption and Enzyme Activities in Neonatal Pigs Is Diet Dependent

Annette R. Jensen, Jan Elnif, Douglas G. Burrin* and Per T. Sangild

Department of Animal Science and Animal Health, Division of Animal Nutrition, Royal Veterinary and Agricultural University, DK-1870 Frederiksberg, Denmark and *U.S. Department of Agriculture/ARS Childrens Nutrition Research Center, Department of Pediatrics, Baylor College of Medicine, Houston, TX 77030

ABSTRACT Uptake of colostrum just after birth is essential to stimulate intestinal growth and function, and in many species, including pigs, colostrum also provides immunological protection via the absorption of immunoglobulin G (IgG). In this study, intestinal growth, IgG absorptive capacity and enzyme activities were investigated in newborn pigs in response to different diets. Newborn piglets were bottle-fed porcine colostrum (PC), bovine colostrum (BC), porcine plasma (PP), porcine milk (PM), bovine colostrum containing porcine plasma (BCP) or a milk replacer (MR) every 3 h (15 mL/kg) for up to 2 d. Bovine serum albumin (BSA) was added to the diets as a macromolecule marker. The percentage of absorbed BSA just after birth was highest for piglets fed the PC diet (30–50%), lower for those fed the BC and BCP diets (23–30%) and lowest for the PP, PM and MR diet-fed piglets (7–20%, P < 0.05 relative to those fed colostrum). Porcine IgG was absorbed more efficiently than bovine IgG. Intestinal closure occurred earlier in MR and BCP piglets (within 12 h after birth) than in PC pigs. At 2 d of age, intestinal mucosal weight (120% increase from birth) and villus morphology were similar in the PC, BCP and MR groups. All 3 groups also had increased aminopeptidase A activity compared with values at birth (100% increase). Compared with PC pigs, the BCP group had higher sucrase and maltase activities (+50% and +200%, respectively) and lower aminopeptidase N activity (−50%, P < 0.05). Similarly, MR pigs showed elevated sucrase activity (+40%) and lowered maltase, lactase and aminopeptidase N activities (−20% to −50%, P < 0.05) compared with PC pigs. We conclude that porcine and bovine colostrum contain factors that stimulate the intestinal endocytotic and enzymatic capacity in newborn pigs. A milk replacer can produce normal gut growth, but may be inefficient in mediating normal macromolecule transport and disaccharidase activity. Bovine colostrum mixed with porcine plasma proteins may be a useful substitute for porcine colostrum in artificial rearing of newborn pigs. J. Nutr. 131: 3259–3265, 2001.

KEY WORDS: • colostrum • immunoglobulin • disaccharidase • peptidase • intestinal closure • piglets

In all mammals, there is a fundamental transition in the nutritional conditions at the time of birth. The fetus receives a continuous supply of parenteral nutrients via the placenta, whereas the newborn must adapt to an independent uptake of colostrum and milk nutrients via the gastrointestinal tract. The first intake of colostrum provides not only nutrients for growth and development, but also passive immunity via the intestinal uptake of colostral immunoglobulins (Ig). The ability of the enterocytes to absorb large molecules by endocytosis is particularly important for neonatal farm animals (piglets, lambs, calves, foals) because the placenta in these species does not allow maternal Ig to be transferred across to the fetal circulation before birth (1).

The large neonatal mortality in farm animals (e.g., 10–20%) (2) indicates that the neonate often fails to adapt adequately, and in modern pig production, an increase in average litter size has further increased the risk for newborn piglets to die from starvation and lack of passive immunity. Rearing of piglets by surrogate mothers and the use of milk replacers (MR) have been employed to increase neonatal survival. It remains essential, however, that newborn piglets receive porcine Ig to achieve a sufficient degree of passive immunization. The use of bovine colostrum or MR for newborn pigs, without porcine Ig, is associated with reduced survival (3–5). Even when purified porcine Ig or plasma protein (including Ig) is added, passive immunization might be low because intestinal macromolecule absorption is greatly influenced by the composition of the fluid in which they are dissolved (6,7). There is no information on the efficiency of Ig absorption from plasma fed to newborn pigs, although plasma products have been widely used to improve digestibility and growth in weanling pigs (8,9).

In addition to its immunological role, colostrum has a marked stimulating effect on the growth and maturation of the neonatal gastrointestinal tract (10–13). Exposure to colostrum

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1 Supported by the Danish Agricultural and Veterinary Research Council.
2 To whom correspondence should be addressed. E-mail: psa@kvl.dk.
3 Abbreviations used: BC, bovine colostrum; BCP, bovine colostrum with porcine plasma; bigG, bovine immunoglobulin G; BSA, bovine serum albumin; HSA, human serum albumin; Ig, immunoglobulin; MR, milk-replacer; PC, porcine colostrum; plgG, porcine immunoglobulin G; PM, porcine milk; PP, porcine plasma.

has specific effects on the processing of some brush border enzymes in neonatal pigs, such as lactase-phloridzin hydratase, and this may affect the luminal hydrolytic activity (14, 15). Artificial diets seem less efficient than colostrum in stimulating intestinal growth and function in newborn pigs (15, 16). Diet-dependent effects could be most pronounced during the perinatal period when colostrum induces some fundamental changes in the enterocyte membrane in association with the endocytic uptake of protein macromolecules (17, 18). Few studies in neonatal pigs have followed the effects of different diets on intestinal function beyond the Ig absorption period (lasting ~ 24 h).

In the present experiments, we investigated the extent to which porcine colostrum (PC) was superior to bovine colostrum (BC), porcine plasma (PP) and a MR in stimulating intestinal uptake of protein macromolecules and enzyme activity in neonatal pigs. The objective of Experiment 1 was to compare the effect of feeding PC, BC, PP or porcine milk (PM) from the mother (ML) to piglets (3260–3300 g) at 3 and 6 h postpartum. Bovine colostrum (PC) was superior to bovine colostrum (BC) within 6 h of birth. Porcine milk was collected from a newborn group (infant feeding tube 8F, PharmaPlast, Lynge, Denmark) to mimic the normal metabolic and endocrine effects on the processing of some brush border enzymes in neonatal pigs, such as lactase-phloridzin hydrolase, and this may affect the luminal hydrolytic activity (14, 15). The pigs were assigned to receive PC (n = 6), BC containing PP (BCP, n = 6) or MR (n = 6) for 2 ds after birth. All piglets from the three fed groups were fitted with an orogastric tube (infant feeding tube 6F, Pharmaplast) for enteral feeding. To prevent the pigs from chewing the feeding tube, it was passed through the cheek and secured to the skin with sutures. Each piglet was also fitted with a vascular catheter (infant feeding tube 4F, Portex, UK), inserted into the dorsal aorta via the umbilical cord. The catheter was sutured to the cord and skin at 3–4 places. To prevent continuous bleeding from the cord, it was ligated with a soft cotton thread. Finally, a tight cotton body suit was fitted onto each pig to protect the catheters. All piglets were kept individually in infant incubators (Air-Shields, Harbor, PA).

PC, BC and PP were collected as described for Experiment 1. BC was mixed with freeze-dried PP and raw bovine milk cream, in the proportion 45:40:15, respectively, such that it had concentrations of energy (67.68 kJ/L) and protein (144.8 g/L) that were similar to those measured in the BC pool (6800 kJ/L and 146.5 g/L, respectively). The BC mixture was stored in small lots at ~20°C until use. The MR was made of three commercial products used for feeding infants 0–2 y of age (per L water: 80 g Pedipette 0–2, 70 g Maxipro and 75 mL Liquigen-MCT, all products kindly donated by SHS International, Liverpool, UK). The contents of macronutrients were as follows (per L solution): energy, 4140 kJ; protein (mainly whey protein concentrate), 67 g; carbohydrate (mainly glucose), 45 g; sodium, 0.30 g; potassium, 0.64 g; calcium, 0.59 g; and phosphorus, 0.42 g. The energy and protein concentrations of the milk replacer were designed to match those of sow’s milk (21). Because we wanted to study the effect of a MR diet independent of the presence of luminal Ig, no plasma proteins were included in this diet. To provide the MR pigs with some immunological protection, doses of 5 and 9 mL of maternal plasma per pig were injected at 6 and 12 h after birth, respectively, via the arterial catheter. This plasma was produced aseptically from centrifuged maternal blood (3000 × g for 15 min at 4°C), collected from a maternal uterine vein at the time of the caesarean section. Each piglet was fed 15 mL/kg every 3 h via the orogastric tube until tissue collection 45–48 h after the first feeding. At feeding time 0 (4–5 h after birth), BSA was included in the feed as a macromolecule marker (20 g/L, A-4503, Sigma), and at time 12 h, human serum albumin (HSA) was included as a marker (20 g/L, A-1653, Sigma). Arterial blood samples were taken from the pigs via the vascular catheter at the following time points before feeding: 0, 1.5, 3, 6, 9, 12, 13.5, 15, 18 and 21 h. Finally, a blood sample was taken when the pigs were killed for tissue collection (anesthesia with sodium pentobarbital, 200 mg/kg, intravenously). Plasma was prepared and stored for later biochemical analyses as described for Experiment 1.

**Macromolecule measurements**

Concentrations of porcine IgG (plgG), bovine IgG (blgG), BSA and HSA were determined by rocket immunoelectrophoresis (7,17,22). Four different monospecific antisera, raised against BSA, HSA, plgG and blgG in rabbits, were used in the electrophoresis assays (BSA: Z-0229, DAKO, Copenhagen, Denmark; HSA: A-0001, DAKO; IgG: Z-0247, DAKO; plgG: A226/RH, Biogenesis, Poole, UK). The standards used for measuring BSA and HSA were the same as those used for the feed solutions. The standards used to measure plgG and blgG were obtained from DAKO (plgG: X-0906) and Sigma (blgG: I-5306).

**Tissue collection**

For all pigs in Experiment 2, the small intestine, from the pyloric sphincter to the ileocolic junction, was rapidly removed by cutting along the mesenteric border, weighed and its length recorded in a relaxed state. The intestine was removed to an ice-cold metal plate along the mesenteric border, weighed and its length recorded in a relaxed state. The intestine was removed to an ice-cold metal plate along the mesenteric border, weighed and its length recorded in a relaxed state. The intestine was removed to an ice-cold metal plate along the mesenteric border, weighed and its length recorded in a relaxed state. The intestine was removed to an ice-cold metal plate along the mesenteric border, weighed and its length recorded in a relaxed state.
mucosa was determined on a dry matter basis after drying both the mucosa and the muscularis layers at 50°C for 72 h. The stomach and pancreas and a series of other internal organs (heart, kidney, liver, lungs, adrenals, spleen) were also removed and their wet weights recorded.

**Intestinal morphology**

Samples of fixed intestine from the proximal and distal regions were embedded in paraffin, sectioned (5 μm) and stained with hematoxylin and eosin. The mean villous height, crypt depth and intestinal circumference were quantified by an observer who was unaware of the sample source using a Axioshot microscope (Carl Zeiss, Oberkochen, Germany) and NIH image software version 1.60 (U.S. NIH, Bethesda, MD) in at least 15 vertically well-oriented villus-crypt columns.

**Enzyme analyses**

Frozen tissue from each of the three intestinal regions was homogenized in 1.0% Triton X-100 and the homogenates assayed for disaccharidase and peptidase activities (23). Sucrose (0.01 mol/L; no. 194018, ICN, Aurora, OH) and lactose (0.12 mol/L; L-3625, Sigma) dissolved in sodium maleate buffer (50 mmol/L, pH 6.0) were used as substrates for sucrase-isomaltase (EC 3.2.1.48–10) and lactase-phloridzin hydrolase (EC 3.2.1.23–62), respectively. Maltose (0.0112 mol/L; L-5885, Sigma) was used to measure maltase activity, which represents the combined activity of maltase-glucosaminylase (EC 3.2.1.20) and sucrase-isomaltase. Aminopeptidase N (EC 3.4.11.2), dipeptidyl peptidase IV (EC 3.4.14.5) and aminopeptidase A (EC 3.4.11.7) activities were measured using three peptidase-specific substrate solutions, i.e., 10 mmol/L L-alanine-4-nitroanilide (Merck, Darmstadt, Germany) in 50 mmol/L Tris-HCl, pH 7.3, 15 mmol/L glycyl-L-proline-4-nitro-anilide (Bachem, Bubendorf, Switzerland) in 50 mmol/L Tris-HCl, pH 8.0 and 10 mmol/L α-L-glutamic acid 4-nitroanilide (synchronized at the Institute of Protein Chemistry, Horsholm, Denmark) in 50 mmol/L Tris-HCl, pH 8.0, respectively. Activity was expressed per gram of wet intestinal tissue, and one unit of activity (U) represented 1 μmol of substrate hydrolyzed/min at 37°C.

**Data analyses**

All values presented in text and figures are means ± (SEM), with n as the number of pigs. The absorptive efficiency (%) of the two macromolecule markers (BSA and HSA) was calculated as the total amount present in plasma at the time of maximal concentration divided by the total intake. A plasma volume of 68 mL/kg body was assumed in the calculations (24). The metabolic clearance of macromolecules was neglected in the calculations. For blood values (plasma IgG, BSA, HSA), the effects of treatment were evaluated using a linear model and the MIXED procedure of SAS (25) with sample time as the repeated measure. For the tissue values (enzyme activities), the effects of treatment, region (proximal, middle, distal) and treatment × region interaction were tested using the GLM procedure (25) with the pig (nested within treatment) as the experimental test unit. Significant differences among means (P < 0.05) were detected by the Duncan’s Multiple Range test (25).

**RESULTS**

**Experiment 1**

**Immunoglobulin absorption.** The concentrations of plgG (g/L) in the four diets were 77.3 (PC), 0.8 (BC), 0.8 (PM) and 29.7 (PP). Analyzed across the three sample times at 6–12 h after the first meal, the plasma plgG level was significantly elevated in PC vs. PM and PP pigs (Fig. 1A). The level of plgG measured in the two last-mentioned groups (1–3 g/L), however, remained significantly higher than the level in BC pigs (<0.3 g/L).

**BSA absorption.** Absorption of BSA relative to BSA intake was highest in PC pigs, and reached ~50% 9 h after BSA intake (Fig. 1B). Relative BSA absorption in BC pigs was...
30% and significantly lower than in PC pigs. In PM and PP pigs, the proportions of absorbed BSA were similar, and both were lower than in the PC and BC groups (18–20%, Fig. 1B).

Experiment 2

Immunoglobulin absorption. Concentrations of plgG in the PC and BCP diets were 52.2 and 13.2 g/L, respectively. The concentration of blgG in the BCP diet was 47.5 g/L. Analyzed across sample times, the plgG concentration in plasma was significantly different among the three treatments with the highest value in PC piglets and the lowest in MR pigs (Fig. 2A). The plgG in the MR group (maximum 3.0 ± 0.3 g/L at 13.5 h) originated from the injection of porcine serum (see Materials and Methods) rather than uptake of Ig from MR. In the BCP piglets, a significant increase was observed over time for both plasma plgG (Fig. 2A) and blgG (data not shown). Absorption of blgG increased until 13 h; at that time, the concentration (5.0 ± 0.6 g/L) was similar to that of plgG (5.4 ± 0.7 g/L, Fig. 2A). The percentage of absorbed porcine IgG 3 h after the first meal was 22.6 ± 2.3% in the PC piglets. Correspondingly, the percentage of absorbed porcine and bovine IgG in the BCP group was 7.0 ± 3.0 and 3.3 ± 1.2% at 3 h.

BSA and HSA absorption. There were significant effects of treatment on the absorption of BSA (Fig. 2B). At 0–9 h after BSA ingestion, plasma BSA increased significantly in both of the colostrum groups, but faster in the PC than in the BCP group. Plasma BSA also increased in the MR group, although the values remained much lower than in the other two groups. At the time of maximal plasma BSA levels, 29.2 ± 2.7, 23.4 ± 3.0 and 7.7 ± 1.3% of the administered BSA had been absorbed in the PC, BCP and MR groups, respectively. When HSA was included into the meal at 12 h, the relative absorption of HSA (measured at 18 h) in the PC group was similar (22.7 ± 4.7%, Fig. 2C) to that of BSA for this group (29.2 ± 2.7%, Fig. 2B). In contrast, the relative absorption of HSA in the BCP and MR groups was significantly lower (5.0 ± 0.6 and 1.7 ± 0.9%, respectively, Fig. 2C) than the corresponding values for BSA (Fig. 2B).

Organ weights and intestinal morphometry. At the end of the 2-d protocol, there were no differences in body weight among the three fed groups (mean 1.41 ± 0.08 kg), and the mean body weights were only slightly (and not significantly) greater than those at birth. In contrast, significant increases occurred in the weights of the stomach (+31%, P < 0.05), pancreas (+81%, P < 0.001) and small intestine (+75%, Fig. 3A, P < 0.0001), and in intestinal length (+30%, Fig. 3B, P < 0.01) in all three groups from birth to 2 d. Because the proportion of dry mucosa also increased (+28%, Fig. 3C, P < 0.001) there was a total increase in the mucosal mass of +123% from birth to 2 d of age. The mean values of these gut growth parameters did not differ among the groups of pigs fed PC, BCP or MR.

Villus height and intestinal circumference (Fig. 4A and C, average values across the proximal and distal intestine) in the three fed groups did not differ significantly from those in newborn pigs. There was no significant effect of intestinal region (proximal, distal) on the intestinal growth parameters. Figure 5 shows representative micrographs of the mucosal histology for the four treatment groups (proximal intestine). In the two colostrum groups (PC and BCP, Fig. 5B and C), the epithelium and its vacuolated cells showed diffuse protein staining as a result of the uptake of intact colostral proteins. In contrast, the epithelium from pigs fed MR (Fig. 5D) contained enterocytes with largely empty vacuoles. Crypt depth increased significantly from birth to 2 d in the BCP and MR groups, but not in the PC group (Figs. 4B and 5).

There were no treatment differences for the wet weights of a series of internal organs (lungs, liver, spleen, heart, kidneys, adrenals), except that kidney weight in the MR group (10.8 ± 1.3 g) was less (P < 0.05) than in the two colostrum groups (14.7 ± 1.1 g, combined for PC and BCP).
**Enzyme activities.** For each enzyme, the mean activity per gram of tissue for the proximal, middle and distal intestine was calculated, and the results are presented in Figures 6 and 7. Analyzed across the three fed groups, there were significant effects of treatment for all measured enzyme activities, except that of dipeptidyl peptidase IV. There was also a significant treatment × region interaction for all six enzyme activities, except lactase activity.

Sucrase activity in 2-d-old pigs was unaffected in the PC and BCP groups, and elevated in the MR group, compared with newborn pigs (Fig. 6A). In contrast, maltase activity was highly elevated in the BCP group compared with the other three treatment groups (Fig. 6B). The increase in maltase activity in the BCP pigs was most pronounced in the middle and distal part of the small intestine (9-fold increase relative to newborn pigs). A pronounced increase also occurred in the PC pigs compared with newborn pigs (1.5-fold, \( P < 0.001 \) as tested by Student’s \( t \) test). Due to a large variation in maltase activity within the BCP group, this increase did not show up in the total treatment group comparison shown in Figure 6B (Duncan’s Multiple Range test). Taken together with the increase in intestinal mass (Fig. 3A), the increases in total intestinal maltase activity from birth to 2 d were calculated to be 3.5- and 13-fold, for the PC and BCP groups, respectively. Lactase activity was highest in the proximal and middle intestine, and across all regions, it decreased significantly from birth to 2 d of age in the MR group (to 35% of values at birth, Fig. 6C).

The MR group did not differ from the newborn group in intestinal aminopeptidase N activity (Fig. 7A), whereas feeding PC resulted in a marked increase, and BC feeding resulted in a decrease in this activity. These treatment effects were most pronounced in the distal small intestine. Dipeptidyl peptidase IV activity was not affected by treatment (Fig. 7B), whereas aminopeptidase A activity (Fig. 7C) was increased in all three fed groups, relative to values at birth, with the highest values in BCP pigs.

**DISCUSSION**

Artificial rearing of newborn infants or animals requires the use of suitable alternatives to mother’s milk, and milk substitutes must have a composition that meets neonatal biological needs. Particularly in situations of inadequate adaptation to postnatal life (e.g., premature or growth-retarded neonates), it is important that artificial diets are optimized to stimulate normal organ function and maturation. In the large farm animal species (pigs, cows, horses, sheep), neonatal mortality is relatively high, and the newborns are dependent on mother’s colostrum, not only for nutrients and luminal growth factors, but also for passive immunization via colostral Ig uptake. In these species, colostrum also contains a high amount of bioactive components (e.g., insulin-like growth factor-1, epidermal growth factor, insulin) that may be important for the maturation of the gastrointestinal tract and other visceral organs (11,15,16,26–30).

The present study has shown that newborn pigs preferentially absorb IgG (relative to IgG and other protein macromolecules) and that PC (rather than PM, PP or MR) is required to secure maximal macromolecule absorption during the first 24 h after birth. Colostrum obtained from another species, the cow, also allowed considerable uptake of macromolecules during the first 12 h after birth. Feeding BC mixed with PP proteins (the BCP diet) may thus provide a sufficient level of passive immunization of newborn pigs deprived of sow’s colostrum. Species-specific factors present in colostrum...
appear to facilitate the endocytosis of large molecules in neonatal pigs.

When the MR (containing few bioactive factors) were fed for 48 h, the increases in intestinal mucosal mass (+120%), villous height and intestinal dimensions were almost identical to the values after colostrum feeding. Nevertheless, elevated intestinal growth has been observed after feeding PC rather than a MR within the first 24 h after birth (10,11,15,16). In the latter studies, the growth effects may have been only temporary and associated at least in part with the extensive uptake of endocytosed protein into the mucosa during the immediate postnatal period. This hypothesis is supported by the finding that intestinal growth and villous structure at 7 d of age do not depend on whether PC or a MR is fed during the first 24 h after birth (31). Rapid intestinal growth in newborn pigs is therefore not solely dependent on colostral nutrients or growth factors, although colostrum may have other important effects (immunological, biochemical) on the developing gut.

In the present study, the effects of feeding colostrum on intestinal function were indicated by both the enhanced ability to facilitate absorption of macromolecules and a different enzymatic profile of the intestinal mucosa, compared with MR feeding (less sucrase, more maltase and lactase). The lowered sucrase activity in PC-fed pigs may be related to the lower crypt height (and possibly lower enterocyte turnover) in these pigs, because the enzyme exhibiting this activity (sucrase-isomaltase) is expressed mainly on immature cells at the lower part of the crypt-villus axis (32). The observed differences in enzyme activities are unlikely to be explained by changes in villous morphology and may thus result from direct diet-dependent effects on the biochemical characteristics of developing enterocytes. A large increase in average maltase activity from birth to 2 d of age, particularly in the BCP group (9-fold increase), indicates that maltase-specific stimulatory components are present in colostrum (both porcine and bovine) and/or in porcine plasma. Either the origin of colostrum (sow or cow) or the presence of PC in the BCP diet may explain why piglets fed the BCP diet differed from those fed the PC diet in sucrase, maltase and aminopeptidase N activities.

The circulating level of IgG in suckling pigs shows a positive relationship with disease resistance in early life (1). Not only the total level of Ig, however, but also their antigen specificity determines the degree of immunological protection. Hence, the absorption of blgG from cow’s colostrum by newborn pigs cannot provide notable passive immunity against pig pathogens. Nevertheless, previous studies have shown that newborn pigs survive much better if fed BC rather than MR just after birth (5). In addition to species- and antigen-specific Ig, colostrum may therefore contain nutrients and bioactive components that have a stimulating effect on maturation, growth and disease resistance in a species-independent manner.

The amount of blgG fed to the BCP piglets was >3 times that of plgG, yet the resulting concentrations of the two Ig in plasma were similar. Hence, selectivity exists among the IgG from different species (33), and absorption does not appear to occur entirely by nonspecific endocytosis of macromolecules. A preference to transport plgG from the gut lumen to the circulation, independently of diet, could be due to the presence of specific IgG receptors on intestinal enterocytes, similar to the Fc-receptors that exist on the brush border membrane of enterocytes in young rodents (34,35). To date, an Fc-receptor has not been identified in the intestine of piglets or calves (36,37).

The presence of bioactive components in colostrum may be responsible for the enhanced uptake of macromolecules (plgG and BSA) from the PC and BCP diets shortly after birth, compared with the PM, PP and MR diets. When macromolecule absorption was tested at 12 h, however, the absorption (using HSA as the macromolecule marker) was much lower in both the BCP and the MR groups, compared with the PC group. Thus, the lack of PC may induce an earlier cessation of macromolecule transport, also known as “intestinal closure.” This must be taken into account when Ig are included in diets other than PC for artificially reared piglets. This observation, together with the finding that the diet containing BCP induced changes in brush border enzyme activities that differed from the effect with PC, shows that the intestinal mucosa is very sensitive to dietary stimuli at this critical time. Nevertheless, it appears that feeding BCP is an effective way to ensure that artificially reared newborn pigs receive both immunological protection and a stimulation of intestinal growth and function that are similar to those induced by PC.

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LITERATURE CITED


