JOURNAL OF ANIMAL SCIENCE
The Premier Journal and Leading Source of New Knowledge and Perspective in Animal Science

Developmental changes in morphometry of the small intestine and jejunal sucrase activity during the first nine weeks of postnatal growth in pigs

O. Adeola and D. E. King

J ANIM SCI 2006, 84:112-118.

The online version of this article, along with updated information and services, is located on the World Wide Web at:
http://www.journalofanimalscience.org/content/84/1/112

American Society of Animal Science
www.asas.org

Downloaded from www.journalofanimalscience.org at Coastal Plain 55293 on May 28, 2014

Developmental changes in morphometry of the small intestine and jejunal sucrase activity during the first nine weeks of postnatal growth in pigs[1]

O. Adeola[2] and D. E. King

Department of Animal Sciences, Purdue University, West Lafayette, IN 47907-2054

ABSTRACT: The objective of this study was to investigate the development of small intestinal size and digestive capacity of the jejunum in growing pigs. The weight, length, surface area, and mucosa weight of the small intestine were measured when pigs were 1, 3, 5, and 9 wk of age. Sucrase and alkaline phosphatase (ALP) activities of the jejunal brush-border membrane, prepared by differential centrifugation and Mg^{2+} precipitation, were determined at the respective postnatal stages. Body weights increased 7-fold from 2.7 kg at 1 wk to 23.32 kg at 9 wk postnatal. Body weight gains were greater ($P < 0.05$) from wk 3 to 5 than from wk 1 to 3. Weights of the small intestine and of the intestinal mucosa increased faster ($P < 0.05$) from 3 to 5 wk than from 1 to 3 wk; the slowest increase occurred from 5 to 9 wk. Weights of the duodenum, jejunum, and ileum, and mucosa from the respective sections increased ($P < 0.05$) as pigs grew from 3 to 9 wk. Mucosa weight relative to the weight of the section was greater ($P < 0.05$) for the duodenum and jejunum than for the ileum at 9 wk of age. Between the ages of 3 and 9 wk, the increase in mucosa weight was highest for the jejunum followed by the duodenum and the ileum. The increase was greatest for the duodenum followed by the jejunum and the ileum when mucosal weight was expressed per unit of appropriate intestinal section weight. There was a 55-fold increase in jejunal sucrase activity from 1 to 9 wk; the greatest rate of increase occurred between 5 and 9 wk. Total jejunal ALP activities in pigs at 9 wk was greater ($P < 0.05$) than at 5 wk, which in turn was greater than at 1 wk of age. In summary, increases in BW during the first 9 wk of postnatal growth in pigs are accompanied by significant developmental changes in digestive capacity including intestinal weights, length, and area as well as jejunal brush-border sucrase and ALP activities.

Key words: digestive capacity, hydrolase, intestine, pig, postnatal development

©2006 American Society of Animal Science. All rights reserved. J. Anim. Sci. 2006. 84:112–118

INTRODUCTION

The growth of an animal depends in part on its capacity to digest and assimilate ingested macromolecules, and any impairment of this is expected to constrain growth. Postnatal intestinal growth, the initial appearance and development of intestinal digestive hydrolases, and the capacity of the intestines to absorb nutrients are important factors when characterizing how animals are able to assimilate ingested macromolecules (King et al., 2000). Hydrolases and nutrient transporters anchored on the brush border of enterocytes play significant roles in the final stages of digestion and assimilation of nutrients, and the capacity of an animal in this regard dictates its ability to attain conditions of optimal growth when nutrients are provided in adequate amounts. Studies on the development of digestive functions including hydrolases (Matasushita, 1985; Ferraris et al., 1992; Biviano et al., 1993) and transport systems (Buddington and Diamond, 1990; Tolza and Diamond, 1992; Soriano and Planas, 1998) have reported age-related differences in small intestine hydrolase activities and AA transport rates. Investigations of postnatal development of small intestinal hydrolase are largely limited to the use of whole mucosal homogenates. We have used purified enterocyte brush-border preparations to investigate the ontogeny of intestinal digestive functions in ducks (King et al., 2000) and pigs (Fan et al., 2002) and have observed age-related distinctions. In the current study, the observations are extended for both morphometry and hydrolases to pigs between the ages of 1 and 9 wk, a period that includes the transition from nursing to weaning. Therefore, the objective of this study was to investigate developmental patterns of digestive capacity in growing pigs using weights, linear and area dimensions of each

[1]Journal Paper No. 2005-17574 of the Purdue Univ. Agric. Res. Programs. The authors are grateful to C. Thomas, D. Ragland, D. Hong, and the staff of Purdue Univ. Swine Research Unit for technical assistance.

[2]Corresponding author: ladeola@purdue.edu

Received February 25, 2005.
Accepted August 16, 2005.

Downloaded from www.journalofanimalscience.org at Coastal Plain 55293 on May 28, 2014

section of the small intestine, and jejunal brush-border sucrase and alkaline phosphatase (**ALP**) activities as response criteria.

MATERIALS AND METHODS

Pigs

The intestinal morphometric measurements and mucosa samples in these studies were collected from 20 healthy pigs (2 barrows and 2 gilts from each of 5 litters) obtained from Purdue University Swine Research Center. The experimental protocol was approved by the Purdue University Animal Care and Use Committee. Littermate pigs were assigned for collection of intestinal morphometric measurements and mucosa at ages 1, 3, 5, or 9 wk. Pigs stayed with dams for 3 wk after parturition, after which they were provided free access to feed and water. Diets were based on corn and soybean meal and were formulated with CP concentrations, trace minerals, and vitamins to meet or exceed NRC (1998) recommendations for the different growth phases. During the period from 3 to 5 wk, the corn-soybean meal diet offered to pigs contained 10% whey, 4% Menhaden fish meal, and 0.375% ZnO and was formulated to contain 21% CP, 1.35% lysine, 0.75% Ca, 0.65% total P, and 0.48% nonphytate P (as-fed basis). From 5 to 9 wk old, the corn-soybean meal diet was formulated to contain 19% CP, 1.1% lysine, 0.7% Ca, 0.6% total P, and 0.41% nonphytate P (as-fed basis).

Chemicals

Dye reagent for protein determination was purchased from BIO-RAD Laboratories (Richmond, CA). Bovine serum albumin (Fraction V), p-nitrophenyl phosphate, D-mannitol, Trizma-HCI, HEPES, phenylmethylsulfonyl fluoride (**PMSF**), and other chemicals were purchased from Sigma Chemical Co. (St. Louis, MO).

Small Intestinal Morphometry and Isolation of Mucosal Scrapings

At 1, 3, 5, and 9 wk of age, 6, 6, 4, and 4 pigs, respectively, were i.m. injected with ketamine (Fort Dodge Laboratories Inc., Fort Dodge, IA), Telazol (Fort Dodge Laboratories Inc.), and xylazine (Bayer Corp., Shawnee Mission, KS) at doses of 4, 2.2, and 2.2 mg/kg of BW, respectively. After the pre-anesthetic procedure, halothane was administered to the pigs at a 5% concentration via a facemask to achieve a surgical plane of anesthesia. While the pigs were under anesthesia, their abdomens were opened, and the entire small intestine was transected 5 cm from both the pylorus and ileocecal sphincter. The intestinal lumen was flushed with ice-cold saline solution (154 m*M* NaCl, 100 n*M* PMSF, Trizma-HCI; pH 7.4). For 1-wk-old pigs, the entire length of the small intestine was divided into 3 equal-length segments. For 3-, 5-, and 9-wk-old pigs, gut morphology was used to identify intestinal segments, and the entire duodenum (from 5 cm posterior to the pylorus to the junction with jejunum), jejunum (from the junction with duodenum to the junction with ileum), and ileum (from the junction with jejunum to the junction with cecum) were transected. The total weight, mucosa weight, length, and surface area (minus amplification by villi and microvilli using the width × length approach) of the duodenum, jejunum, and ileum were determined for the different age groups. These isolated intestinal segments were divided into sections. The sections were opened longitudinally, and mucus was removed by patting with paper towels. The mucosa was collected by scraping the luminal surfaces firmly with glass slides that were placed over ice. The mucosal scrapings were pooled within the defined duodenal, jejunal, and ileal segments for the same pig, divided, and placed in screw-capped plastic tubes. The tubes were capped, frozen in liquid N_2, and stored at –70°C.

Preparation of Intestinal Brush-Border Membrane Vesicles

Brush-border membrane vesicles were prepared from 5-wk-old pig jejunal mucosa according to the modified Mg^{2+} precipitation procedure adapted from Maenz and Patience (1993). Approximately 50 g of mucosa scrapings was thawed in ice-cold homogenate buffer (50 m*M* D-mannitol, 10 m*M* Trizma-HCl, 100 u*M* PMSF; pH 7.4 adjusted with Trizma-base). The thawed tissue and homogenate buffer were divided into eight 45-mL plastic tubes and homogenized with an Omni 2000 polytron homogenizer (Omni International Inc., Waterbury, CT) with a 10-mm diameter generator at a speed of 20,000 rpm for 1 min. The resulting homogenates were pooled and centrifuged at 2,000 × *g* for 15 min with a preparative ultracentrifuge (Beckman Model L5-65; Beckman Instruments, Inc., Palo Alto, CA). After removing the top foam layer and discarding the pellets, the supernatant fraction was mixed with 1 *M* $MgCl_2$ solution to achieve 10 m*M* $MgCl_2$, stirred for 15 min, and then centrifuged at 2,400 × *g* for 15 min. The top foam layer and pellets were removed, and the resulting supernatant fraction was centrifuged at 19,000 × *g* for 30 min to generate crude brush-border membrane pellets. The supernatant fraction was poured off, and 1 mL of resuspension buffer (300 m*M* D-Mannitol, 50 m*M* HEPES; pH 7.4 adjusted with Trizma-base) was added to the pellets. The pellets were resuspended by repeated passage through a 26-gauge needle and pooled among the centrifuge tubes. The resultant crude brush-border membrane vesicle suspension was transferred into cryogenic vials in 2-mL aliquots (Nalgene Company, Rochester, NY) and frozen in liquid N_2 until use. For a given hydrolase assay, a suitable number of aliquots of brush-border membrane vesicle suspensions was thawed in the vesicle resuspension buffer (150 m*M* D-mannitol, 200 m*M* KSCN, 50 m*M* HEPES; pH 7.4 adjusted with Trizma-base). The resuspended crude vesi-

Downloaded from www.journalofanimalscience.org at Coastal Plain 55293 on May 28, 2014

cles were then homogenized in a prechilled glass Wheaton tissue grinder (Wheaton, Millville, NJ) with 8 strokes before centrifugation at 39,000 × *g* for 30 min to generate the brush-border membrane pellets. The pellets were resuspended with a 26-gauge needle in a suitable volume of vesicle resuspension buffer (150 m*M* D-mannitol, 200 m*M* KSCN, 50 m*M* HEPES; pH 7.4 adjusted with Trizma-base) to give the final brush-border membrane vesicle suspension, which was analyzed for protein and hydrolase.

Protein and Hydrolase Assays

Protein concentrations of the homogenates and brush-border suspensions were determined colorimetrically with a DU-640 spectrophotometer at 595 nm (Beckman Instruments, Inc., Fullerton, CA) according to the method of Bradford (1976).

Sucrase (EC 3.2.1.48) activity was determined according to the procedure of Dahlqvist (1964). The intestinal mucosal homogenate or brush-border membrane vesicles were incubated with sucrose at 38°C, and the liberated glucose was measured by a glucose-specific hexokinase reaction. Alkaline phosphatase (EC 3.1.3.1) was assayed according to the method of Engstrom (1964). The intestinal mucosal homogenate or brush-border membrane vesicles were incubated with p-nitrophenyl phosphate at 38°C. Enzyme activities were normalized to protein content. Total jejunal hydrolase activities (μmol hydrolyzed/min) over the entire jejunal segment were estimated as enzyme activity per unit of mucosal homogenate protein × homogenate protein content per gram mucosa × total jejunum mucosa weight (Zhang et al., 1997).

Statistical Analyses

Statistical analyses were preformed using the GLM procedures of SAS (SAS Inst., Inc., Cary, NC) as a completely randomized design; individual pig was the experimental unit. Gender effect was tested in the model; however, no gender effects were detected. Means were separated using the LSD procedure at a significance level of $P < 0.05$.

RESULTS

Body Weights and Small Intestinal Morphometry

Body weights and small intestinal weights, length, and area presented in Table 1 show the expected increase ($P < 0.05$) from 1 to 9 wk postnatal. There was a 7-fold increase in BW from 2.7 kg at 1 wk to 23.32 kg at 9 wk. Weight gains averaged 111, 388, and 486 g/d from 1 to 3 wk, 3 to 5 wk, and 5 to 9 wk, respectively. Body weight gains were greater ($P < 0.05$) from wk 3 to 5 than from wk 1 to 3. Total intestinal weights and intestinal mucosa weights increased more rapidly from 3 to 5 wk than from 1 to 3 wk; the slowest rate of increase was from 5 to 9 wk. Intestinal length and surface area decreased relative to gain as pigs grew during the 3- to 9-wk postnatal period. Intestinal weight as a proportion of BW was greatest ($P < 0.05$) at 5 wk for the age groups studied.

Weights of the duodenum, jejunum, and ileum increased ($P < 0.05$) as pigs grew from 3 to 9 wk (Table 2). Weights of the mucosa in each section of the small intestine were greater ($P < 0.05$) at 9 wk than at 1, 3, or 5 wk of age. The length of jejunum was greater ($P < 0.05$) in pigs at 9 wk than at 5 wk, which was greater than in those at 3 wk of age. Surface area of each section of the small intestine increased ($P < 0.05$) from 3 to 9 wk (Table 2). Between the ages of 3 to 9 wk, the increase in mucosa weight was greatest for the jejunum followed by the duodenum and the ileum. Similarly, the increase was greatest for the duodenum followed by the jejunum and then the ileum when mucosal weight was expressed per unit of the appropriate intestinal segment weight (Table 2).

Jejunal Mucosa Protein Content and Hydrolase Activities

Table 3 shows the jejunal mucosa protein content and hydrolase activities of the pigs. Mucosal homogenate protein concentrations of the harvested jejunums did not differ among the age groups studied. There were large variations in enzyme activities among pigs. Sucrase activity was detectable, but very low, at 1 wk of age. There was a 55-fold increase in jejunal sucrase activity from 1 to 9 wk; the greatest rate of increase occurred between 5 and 9 wk. Total jejunal sucrase activity, total jejunal sucrase activity expressed per unit of jejunal mucosa weight, and total sucrase activity expressed per unit of jejunal surface area did not differ among pigs of ages 1, 3, and 5 wk but was greater ($P < 0.05$) at 9 wk of age. Alkaline phosphatase activity was numerically greater at 3 wk, but it was not different from that at 1, 5, or 9 wk of age. Total jejunal ALP in pigs at 9 wk was greater ($P < 0.05$) than activity at 5 wk, which was greater than that at 1 wk of age. Total ALP activity normalized to mucosa weight of the jejunum was greater ($P < 0.05$) at 3 wk than at other ages (Table 3). The quality and purity of the brush-border membrane vesicles assessed by characterization of mucosal hydrolase showed that relative to the intestinal homogenate, the final brush-border membrane preparations from the 1-, 3-, 5-, and 9-wk-old pigs had respective enrichments of 18-, 26-, 38-, and 5-fold in sucrase activity. Corresponding numbers for ALP were 4-, 5-, 8-, and 10-fold in enrichments in ALP activities, respectively (data not shown).

DISCUSSION

The interaction of genetics, nutrition, endogenous regulatory mechanisms, and environment directs functional development of organ systems including the gas-

Downloaded from www.journalofanimalscience.org at Coastal Plain 55293 on May 28, 2014

Table 1. Body weights and small intestine morphometrics of pigs, fresh tissue basis

	Age, wk				
Item	1	3	5	9	SD
No. of pigs	6	6	4	4	
BW, kg	2.72[a]	4.28[b]	9.70[c]	23.32[d]	0.980
Intestinal weight, g	110.48[a]	184.62[b]	461.45[c]	896.95[d]	40.123
Intestinal length, cm	421.6[a]	764.5[b]	946.6[b]	1,354.5[c]	127.69
Intestinal area, cm^2	810[a]	1,890[b]	3,356[c]	5,475[d]	588.2
Intestinal weight/BW, g/kg	40.5[a]	43.3[ab]	47.7[b]	38.7[a]	4.16
Mucosa weight, g	92.68[a]	137.02[b]	367.17[c]	721.38[d]	20.045
Mucosa weight/intestinal weight, g/kg	837.6[b]	739.1[a]	798.7[ab]	806.2[ab]	47.77
Mucosa weight/BW, g/kg	33.9[a]	32.1[a]	38.0[b]	31.1[a]	3.92
Intestinal length/BW, cm/kg	155.4[c]	179.4[c]	97.2[b]	58.23[a]	18.13
Intestinal area/BW, cm^2/kg	297.3[a]	443.6[b]	345.4[b]	235.1[a]	73.97

[a–d]Means in the same row that do not have common superscripts differ, $P < 0.05$.

trointestinal tract. Development of the gastrointestinal tract in the pig commences early in fetal life and rapidly progresses after birth, during which time a significant stride in the ontogeny of the gastrointestinal tract occurs in providing the neonate with nutrients and protection by processes of digestion and absorption (Cranwell, 1995). Rapid growth and development during the early postnatal period significantly affects subsequent growth and thereby pig productivity. In the current study, developmental patterns of small intestine digestive capacity in pigs between 1 and 9 wk of age were investigated. The pig's intestinal weight increased in direct proportion to its BW. In contrast, rabbit intestinal weight increased disproportionately slowly (Buddington and Diamond, 1990), and rat intestinal weight increased disproportionately rapidly (Tolza and Diamond, 1992) relative to BW. However, both studies reported disproportionate changes in small intestinal lengths and nominal surface areas to BW as in the pig. Moreover, in the cat, a strict carnivore, intestinal weight increased disproportionately slower to BW, whereas intestinal length and nominal surface area increased in proportion to BW (Buddington and Diamond, 1992). During the early postnatal period in life of the cat, its small intestine undergoes no significant increase in weight, length, or nominal surface area (Buddington and Diamond, 1992), whereas in the pig, an omnivore, the intestine undergoes intense hyperplasia within the first 24 h after birth (Widdowson et al., 1976). Indeed, a 126% increase in pig mucosal homogenate protein has been reported during the first 6 h after parturition (Zhang et al., 1997). In another study, Tarvid et al. (1994) observed that intestinal weight and length increased in direct proportion to BW in pigs from

Table 2. Morphometrics of the small intestinal regions of pigs, fresh tissue basis

	Age, wk[1]				
Item	1	3	5	9	SD
No. of pigs	6	6	4	4	
Duodenum					
Weight, g	36.28[c]	19.15[b]	22.30[b]	76.28[d]	10.214
Mucosa weight, g	32.23[c]	12.93[b]	19.53[b]	62.03[d]	9.969
Length, cm	140.6[d]	79.2[c]	80.8[c]	99.1[c]	15.11
Surface area, cm^2	243[c]	170[b]	271[c]	393[d]	24.3
Jejunum					
Weight, g	40.15[b]	137.20[c]	401.30[d]	708.20[e]	43.527
Mucosa weight, g	33.60[b]	103.70[c]	318.35[d]	576.30[e]	21.335
Length, cm	140.6[b]	593.5[c]	770.9[d]	1,137.6[e]	116.18
Surface area, cm^2	259[b]	1,520[c]	2,744[d]	4,602[e]	563.2
Ileum					
Weight, g	34.05[bc]	28.26[b]	37.85[c]	112.46[d]	6.736
Mucosa weight, g	26.85[b]	20.38[b]	29.30[b]	83.05[c]	8.304
Length, cm	140.6[c]	90.3[b]	94.5[b]	117.5[bc]	19.28
Surface area, cm^2	323[c]	214[b]	331[c]	495[d]	73.2

[b–e]Means in the same row that do not have common superscripts differ, $P < 0.05$.

[1]For 1-wk-old pigs, the small intestine was divided into 3 equal-length segments of proximal, middle, and distal for duodenum, jejunum, and ileum, respectively. For 3-, 5-, and 9-wk-old pigs, gut morphology was used to identify intestinal segments including duodenum (from 5 cm posterior to the pylorus to the junction with jejunum), jejunum (from the junction with duodenum to the junction with ileum), and ileum (from the junction with jejunum to the junction with cecum).

Downloaded from www.journalofanimalscience.org at Coastal Plain 55293 on May 28, 2014

Table 3. Mucosal protein and hydrolase activities in jejunum (identified by gut morphology from the junction with duodenum to the junction with ileum) of pigs, fresh tissue basis

	Age, wk[1]				
Item	1	3	5	9	SD
No. of pigs	6	6	4	4	
Protein/mucosa, mg/g	89.20	102.74	86.87	86.87	9.959
Sucrase activity, nmol/(mg protein·min)	2.41[c]	6.18[c]	11.88[c]	135.38[d]	7.569
Total sucrase, umol/min	8.08[c]	67.22[c]	331.19[c]	6,764.82[d]	311.769
Total sucrase/mucosa, umol/(min·g)	0.24[c]	0.65[c]	1.04[c]	11.74[d]	0.658
Total sucrase/area, nmol/(min·cm^2)	32.30[c]	44.22[c]	120.87[c]	1,470.61[d]	78.774
ALP[2] activity, umol/(mg protein·min)	4.21	6.43	3.45	3.48	2.081
Total ALP, mmol/min	11.8[c]	68.3[cd]	94.4[d]	169.6[e]	35.16
Total ALP/mucosa, mmol/(min·g)	0.35[c]	0.71[d]	0.38[c]	0.36[c]	0.17
Total ALP/area, nmol/(min·cm^2)	47.2[d]	44.9[cd]	34.4[c]	36.7[cd]	2.62

[c–e]Means in the same row that do not have common superscripts differ, $P < 0.05$.

[1]For 1-wk-old pigs, the small intestine was divided into 3 equal-length segments of proximal, middle, and distal for duodenum, jejunum, and ileum, respectively. For 3-, 5-, and 9-wk-old pigs, gut morphology was used to identify intestinal segments including duodenum (from 5 cm posterior to the pylorus to the junction with jejunum), jejunum (from the junction with duodenum to the junction with ileum), and ileum (from the junction with jejunum to the junction with cecum).

[2]ALP = alkaline phosphatase.

1 to 3 wk of age. During growth between 1 to 9 wk in the current study, BW, small intestine weight, and small intestine length increased 8.5-, 8.1-, and 3.2-fold, respectively. Furthermore, associated with the increase in tissue weight was a significant increase in weight of the mucosa from 1 to 9 wk of age. This finding is an indication that, during the first 9 wk of age, the small intestine of pigs undergoes substantial increases in physical size to accommodate the processing of ingested nutrients. Intestinal weight and length expressed per unit of BW reported for 1- and 3-wk-old pigs by Tarvid et al. (1994) were similar to observations in the current study.

Anatomical distinction of duodenum, jejunum, and ileum at 1 wk of age is fraught with technical problems; thus, the small intestine was divided into three equal-length segments for 1-wk-old pigs. As a result, wk 1 morphometric data for duodenum (segment 1), jejunum (segment 2), and ileum (segment 3) may not truly represent each of these 3 segments. This uncertainty probably explains some of the observations of heavier and longer segment 1, 2, or 3 at wk 1 than of the duodenum, jejunum, and ileum at wk 3. The differential changes in weights among the duodenum, jejunum, and ileum were evident in mucosa weight. It has been reported the duodenum, jejunum, and ileum represent 4 to 5%, 88 to 91%, and 4 to 5%, respectively, of length of the small intestine in the fully grown pig (Yen, 2001). Observations from the current study indicate that the duodenum accounts for approximately 10, 9, and 7% of the length of the small intestine in 3-, 5-, and 9-wk-old pigs, respectively. Corresponding numbers for the jejunum are approximately 78, 81, and 84% with values of 12, 10, and 9% for the ileum. The jejunum, therefore, represents more of the length of the small intestine as the pig grows.

Digestive actions of mucosal enzymes occur on the brush-border surface of enterocytes compared with pancreatic enzymes, whose digestive actions take place in the intestinal lumen. Postnatal increases in pancreatic enzymes during the first 6 to 8 wk of life in pigs have been reported (Lindemann et al., 1986; Owsley et al., 1986). The current study examined postnatal changes in jejunal brush-border membrane-bound enzymes sucrase and ALP. Jejunum was selected because it represents >75% of the entire small intestine. Brush-border maltase and sucrase that serve as the final step in small intestinal digestion of starch (linear regions of its structure) to glucose were recently shown to have a common ancestral gene with shared exon structures and peptide domains (Nichols et al., 2003). The current study confirms the presence of sucrase at 1 wk of age and, thus, the potential for sucrose hydrolysis in pigs. Previously, sucrase activities generally have been found to be absent from fetal pigs (Buddington and Malo, 1996) and present at very low levels at birth (Manners and Stevens, 1972; Zhang et al., 1997). Furthermore, sucrase activity was found to be virtually nonexistent in the pig jejunum until 6 d after birth; a marked increase occurred at the second week of postnatal life (James et al., 1987). Manners and Stevens (1972) reported that maximum sucrase activity was found at the 20 and 40% sites from the proximal duodenum in younger pigs (1 to 8 wk) and at a wider range of sites 40, 60, and 80% from the proximal duodenum in older pigs (17 to 19 wk). Those researchers concluded that a trend toward extension of sucrase in a proximal to distal direction along the small intestine existed as the pigs aged. The 10-fold increase in jejunal mucosa brush-border sucrase activity between 5 and 9 wk of age is more than twice the increase from 1 to 3 wk of age, which perhaps reflects the switch in dietary carbohy-

Downloaded from www.journalofanimalscience.org at Coastal Plain 55293 on May 28, 2014

drate from predominantly lactose to starch. This hypothesis is based on the known substrate effects on enzyme production in the digestive tract, which in the current situation would be expected to increase the production of sucrase for the hydrolysis of digestion products of starch by amylase. Age-related developmental changes in brush-border sucrase have been observed in ducks (King et al., 2000), pigs (Fan et al., 2002), and rats (Pacha et al., 2003; Sabat and Veloso, 2003). There was no significant change in intestinal brush-border ALP activity of pigs among the age groups examined in the current study. This observation is similar to those reported for ducks and rats (King et al., 2000; Pacha et al., 2003) but different from the findings of Fan et al. (2002), who observed that ALP was greatest in 28-d-old pigs. Indeed, ALP was numerically greatest in 3-wk-old pigs in the current study, but high variation in ALP data masked statistical detection of the difference.

The magnesium-precipitation method used in the current study produced stable preparations of purified porcine jejunal brush-border membrane vesicles. The purity of intestinal membrane preparations is usually assessed in terms of enrichments of marker enzymes. The enzymes used are anchored in the brush-border membranes of the small intestine. Traditionally, disaccharidases (sucrase and maltase), peptidases (aminopeptidase), and ALP (Salloum et al., 1993) have been used as marker enzymes for enzyme enrichment. The sucrase enrichment in the current study was greater than the 20-fold enrichment reported in rat and rabbit jejunum (Hopfer, 1987). The 8-fold ALP enrichment in the present study for 5-wk-old, 10-kg pigs was less than the 21-fold enrichment reported for 15-kg pigs by Maenz and Patience (1993) and the 13-fold enrichment reported by Fan et al. (1998) for 110-kg pigs. The different enrichment values reported in the literature are suggestive of species- and age-related enzyme-specific ontogenetic patterns of biosynthesis and insertion into brush-border membranes of the small intestine (Buddington and Malo, 1996).

In conclusion, relative BW, intestinal weight, and mucosa weight normalized to BW in pigs were significantly greater from 3 to 5 wk than from 1 to 3 wk, but specific jejunal sucrase and ALP activities were unchanged from 1 to 5 wk. In avian species, it was proposed that whole body growth rates are determined in part by the allocation of tissue to the gastrointestinal tract (Obst and Diamond, 1992). This assertion also might be true in mammals because in the present study, the most rapid intestinal growth rates correlated with the greatest whole body growth rates. These results support the premise that age-related increases in intestinal brush-border enzymes support developmental changes in hydrolytic capacity and that amplified intestinal growth is observed during postnatal growth in the pig.

LITERATURE CITED

Biviano, A. B., C. Martinez del Rio, and D. L. Phillips. 1993. Ontogenesis of intestinal morphology and intestinal disaccharidases in chicken (*Gallus gallus*) fed contrasting purified diets. J. Comp. Physiol. B 163:508–518.

Bradford, M. 1976. A rapid and sensitive method for the determination of microgram quantities of protein utilizing the principles of protein-dye binding. Anal. Biochem. 72:248–254.

Buddington, R. K., and J. M. Diamond. 1990. Ontogenetic development monosaccharide and amino acid transporters in rabbit intestine. Am. J. Physiol. 259:G544–555.

Buddington, R. K., and J. M. Diamond. 1992. Ontogenetic development of nutrient development in cat intestine. Am. J. Physiol. 263:G605–616.

Buddington, R. K., and C. Malo. 1996. Intestinal brush-border membrane enzyme activities and transport functions during prenatal development of pigs. J. Pediatr. Gastroenterol. Nutr. 23:51–64.

Cranwell, P. D. 1995. Development of the neonatal gut and enzyme systems. Pages 99–154 in The Neonatal Pig: Development and Survival. M. A. Varley, ed. CAB International, Wallingford, UK.

Dahlqvist, A. 1964. Method for assay of intestinal disaccharides. Anal. Biochem. 7:18–25.

Engstrom, L. 1964. Studies on bovine-liver alkaline phosphatase, purification, phosphate incorporation. Biochem. Biophys. Acta 92:71–78.

Fan, M. Z., O. Adeola, E. K. Asem, and D. King. 2002. Postnatal ontogeny of kinetics of porcine jejunal brush border membrane-bound alkaline phosphatase, aminopeptidase N and sucrase activities. Comp. Biochem. Physiol. Part A 132:599–607.

Fan, M. Z., O. Adeola, M. I. McBurney, and C. I. Cheeseman. 1998. Kinetic analysis of L-glutamine transport into porcine jejunal enterocyte brush-border membrane vesicles. Comp. Biochem. Physiol. Part A 121:411–422.

Ferraris, R. P., S. A. Villenas, and J. Diamond. 1992. Regulation of brush-border enzymes activities and enterocyte migration rates in mouse small intestine. Am. J. Physiol. 262:G1047–G1059.

Hopfer, U. 1987. Membrane transport mechanisms for hexoses and amino acids in the small intestine. Pages 1499–1526 in Physiology of the Gastrointestinal Tract. L. R. Johnson, ed. Raven Press, New York, NY.

James, P. S., M. W. Smith, D. R. Tivey, and T. J. G. Wilson. 1987. Epidermal growth factor selectively increases maltase and sucrase activities in neonatal piglet intestine. J. Physiol. 393:583–594.

King, D. E., E. K. Asem, and O. Adeola. 2000. Ontogenetic development of intestinal digestive functions in White Pekin ducks. J. Nutr. 130:57–62.

Lindemann, M. D., S. G. Cornelius, S. M. El Kandelgy, R. L. Moser, and J. E. Pettigrew. 1986. Effect of age, weaning, and diet on digestive enzyme levels in the piglet. J. Anim. Sci. 62:1298–1307.

Maenz, D. D., and J. F. Patience. 1993. L-threonine transport in pig jejunal brush border membrane vesicles. J. Biol. Chem. 267:22079–22086.

Manners, M. J., and J. A. Stevens. 1972. Changes from birth to maturity in the pattern of distribution of lactase and sucrase activity in the mucosa of the small intestine of pigs. Br. J. Nutr. 28:113–127.

Matasushita, S. 1985. Development of sucrase in the chicken small intestine. J. Exp. Zool. 233:377–383.

Nichols, B. L., S. Avery, P. Sen, D. M. Swallow, D. Hahn, and E. Sterch. 2003. The maltose-glucoamylase gene: Common ancestry to sucrase-isomaltase with complementary starch digestion activities. Proc. Natl. Acad. Sci. USA 100:1432–1437.

NRC. 1998. Nutrient Requirements of Swine. 10th ed. Natl. Acad. Press, Washington, DC.

Obst, B. S., and J. M. Diamond. 1992. Ontogenesis of intestinal nutrient transport in domestic chickens (*Gallus gallus*) and its relation to growth. Auk 109:451–464.

Owsley, W. F., D. E. Orr, and L. R. Tribble. 1986. Effects of age and diet on the development of the pancreas and the synthesis and secretion of pancreatic enzymes in the young pig. J. Anim. Sci. 63:497–504.

Downloaded from www.journalofanimalscience.org at Coastal Plain 55293 on May 28, 2014

Pacha, J., R. Vagnerova, and J. Bryndova. 2003. Carbenoxolone accelerates maturation of rat intestine. Pediatr. Res. 53:808–813.

Sabat, P., and C. Veloso. 2003. Ontogenic development of intestinal disaccharidases in the precocial rodent *Octodon degus* (Octodontidae). Comp. Biochem. Physiol. Part A 134:393–397.

Salloum, R. M., B. R. Stevens, G. S. Shultz, W. W. Souba. 1993. Regulation of the small intestinal glutamine transport by epidermal growth factor. Surgery 113:552–559.

Soriano, M. E., and J. M. Planas. 1998. Developmental study of a-methyl -D-glucoside and L-proline uptake in the small intestine of chicken. Poult. Sci. 77:1347–1353.

Tarvid, I., P. D. Cranwell, L. Ma, and R. Vavala. 1994. The early postnatal development of protein digestion in pigs. II. Small intestinal enzymes. Pages 181–184 in Proc. VIth Int. Symp. Dig. Physiol. Pigs. W. B. Souffrant and H. Hagemeister, ed. EEAP Publ. No. 80, Rostock, Germany.

Tolza, E. M., and J. Diamond. 1992. Ontogenetic development of nutrient transport in rat intestine. Am. J. Physiol. 263:G593–G604.

Yen, J. T. 2001. Anatomy of the digestive system and nutritional physiology. Pages 32–63 in Swine Nutrition. A. J. Lewis and L. L. Southern, ed. CRC Press, Boca Raton, FL.

Widdowson, E. M., V. E. Colombo, and C. A. Artavanis. 1976. Changes in the organs of pigs in response to feeding for the first 24 h after birth. Biol. Neonate 28:272–281.

Zhang, H., C. Malo, and R. Buddington. 1997. Sucking induces rapid intestinal growth and changes in brush-border digestive functions of newborn pigs. J. Nutr. 127:418–426.

Downloaded from www.journalofanimalscience.org at Coastal Plain 55293 on May 28, 2014

References This article cites 26 articles, 7 of which you can access for free at:
http://www.journalofanimalscience.org/content/84/1/112#BIBL

Citations This article has been cited by 7 HighWire-hosted articles:
http://www.journalofanimalscience.org/content/84/1/112#otherarticles

Downloaded from www.journalofanimalscience.org at Coastal Plain 55293 on May 28, 2014