



Effects of yeast products on the intestinal morphology, barrier function, cytokine expression, and antioxidant system of weaned piglets*

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Abstract: The goal of this study was to evaluate the effects of a mixture of yeast culture, cell wall hydrolysates, and yeast extracts (collectively “yeast products,” YP) on the performance, intestinal physiology, and health of weaned piglets. A total of 90 piglets weaned at 21 d of age were blocked by body weight, sex, and litter and randomly assigned to one of three treatments for a 14-d feeding experiment, including (1) a basal diet (control), (2) 1.2 g/kg of YP, and (3) 20 mg/kg of colistin sulfate (CSE). No statistically significant differences were observed in average daily feed intake, average daily weight gain, or gain-to-feed ratio among CSE, YP, and control piglets. Increased prevalence of diarrhea was observed among piglets fed the YP diet, whereas diarrhea was less prevalent among those fed CSE. Duodenal and jejunal villus height and duodenal crypt depth were greater in the control group than they were in the YP or CSE groups. Intraepithelial lymphocytes (IEL) in the duodenal and jejunal villi were enhanced by YP, whereas IEL in the ileal villi were reduced in weaned piglets fed YP. Secretion of jejunal and ileal interleukin-10 (IL-10) was higher and intestinal and serum antioxidant indexes were affected by YP and CSE. In YP- and CSE-supplemented animals, serum D-lactate concentration and diamine oxidase (DAO) activity were both increased, and intestinal mRNA expressions of *occludin* and *ZO-1* were reduced as compared to the control animals. In conclusion, YP supplementation in the diets of weaned piglets appears to increase the incidence of diarrhea and has adverse effects on intestinal morphology and barrier function.

Key words: Yeast products, Weaned piglet, Intestinal morphology, Barrier function, Antioxidant system
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1 Introduction

Weaned piglets face numerous challenges, including diarrhea, impaired growth rates, and low feed intake (Blecha and Charley, 1990; Pluske *et al.*, 1996; Kang *et al.*, 2012). Antibiotics have long been incorporated into the diets of piglets to solve post-weaning problems; however, their use increases the potential for antibiotic residues to persist in pork products, and bacterial resistance could be transferred to humans (van den Bogaard and Stobberingh, 2000). As such, many countries have banned the inclusion of antibiotics in the diets of pigs. To maintain the health status and growth performance of weaned piglets, there has been increasing demand to identify safe alternatives to antibiotics. Yeast culture (YC) is a dried product that contains live yeast cells and several metabolic by-products, including enzymes, vitamins, other nutrients, and important co-factors, which are produced during the yeast fermentation process. Previous studies have tested the effects of YC, Calcofluor white-hypersensitive (CWH), and yeast products (YP) on the performance of weaned piglets, demonstrating that they exert positive effects on intestinal function and health and enhance the immune response of piglets. Because YC, CWH, and yeast extracts (YE) exhibit differential effects on weaning piglets, a mixture of the three YP may therefore have synergistic effects on piglet health. In the present study, we hypothesized that dietary supplementation with YP may have positive effects on the intestinal physiology and health of weaned piglets; thus, the objective of the present study was to examine the growth performance, incidence of diarrhea, intestinal morphology, barrier function, immune response, and antioxidant system of weaned piglets fed a diet supplemented with YP.

2 Materials and methods

2.1 Animals, experimental treatments, and incidence of diarrhea

A total of 90 Duroc×Landrace×Yorkshire piglets were weaned at 21 d of age (average body weight (BW)=(7.86±0.22) kg), and were blocked by BW, sex, and litter and randomly assigned to one of three treatments, including (1) a basal diet, (2) the basal diet

supplemented with 1.2 g/kg of YP (Shintsen Biological Technology Co., Ltd., Hubei, China), and (3) the basal diet supplemented with 20 mg/kg of colistin sulfate (CSE), for 14 d. The yeast used was *Saccharomyces cerevisiae*, and yeast cells were isolated from YC by centrifugation; cell walls were also isolated by centrifugation after the yeast cell was broken. Isolated cell walls were then hydrolyzed by the enzyme mannase. After drying, all the YC, CWH, and YE of a batch fermentation were mixed together to form the YP, the chemical composition of which is presented in Table 1. The cereal-based basal diet (Table 2) met the National Research Council (NRC) nutrient specifications for pigs in the 10–20 kg BW range (NRC, 2012). The YP group was fed the basal diet supplemented with 1.2 g/kg of YP, and the control and CSE groups were both fed the basal diet supplemented with 0.6 g/kg of wheat and 0.6 g/kg of soybean meal. There were six pens per experimental diet, with five piglets per pen. Piglets were allowed free access to feed and drinking water at all times during the study (Wu *et al.*, 2010). At 21 and 35 d of age, piglets were weighed immediately before feeding. Troughs were weighed and feed was added daily to determine pen feed intake. The average daily feed intake (ADFI), average daily gain (ADG), and gain-to-feed ratio (G:F) were calculated per pen, and the incidence of diarrhea in piglets was monitored and recorded daily by the same individual over the course of the study (Yin *et al.*, 2010). The incidence of diarrhea was defined as described by Liu *et al.* (2008). The incidence of diarrhea was also calculated according to the formula: $\text{diarrhea incidence} = \frac{\text{total number of pigs with diarrhea}}{(\text{total number of pigs} \times \text{experimental days})} \times 100\%$, where “total number of pigs with diarrhea” was defined as the number of pigs with diarrhea observed each day (Liu *et al.*, 2008).

Table 1 Chemical composition of the yeast products (YP)

Component	YP (%)
Moisture	10.13
Crude protein	22.84
Crude fat	2.31
Crude fiber	7.27
Calcium	0.17
Phosphorus	0.63
Ash	3.88

Table 2 Ingredient and chemical composition of the basal diet (as-fed basis)

Ingredient	Content (%)
Extruded corn	28.5
Wheat	24.5
Extruded soybean	13.8
Soybean meal	10.3
Spray-dried whey	10.0
Fish meal	4.5
Soy oil	3.0
Limestone	0.6
Monocalcium phosphate	0.6
L-Lys·HCl	0.4
Salt	0.3
Vitamin and mineral premix ^a	3.5
Calculated analysis	
ME (MJ/kg)	13.55
CP	20.00
Total Lys	1.40
Total Met	0.35
Total Thr	0.87
Ca	0.70
Available P	0.43

^a The vitamin-mineral premix supplied per kg of feed: 10 000 IU of vitamin A; 1000 IU of vitamin D₃; 80 IU of vitamin E; 2.0 mg of vitamin K₃; 0.03 mg of vitamin B₁₂; 12 mg of riboflavin; 40 mg of niacin; 25 mg of D-pantothenic acid; 0.25 mg of biotin; 1.6 mg of folic acid; 3.0 mg of thiamine; 2.25 mg of pyridoxine; 300 mg of choline chloride; 150 mg of Fe (FeSO₄); 100 mg of Zn (ZnO); 30 mg of Mn (MnSO₄); 25 mg of Cu (CuSO₄); 0.5 mg of I (KIO₃); 0.3 mg of Co (CoSO₄); 0.3 mg of Se (Na₂SeO₃); and 4.0 mg of ethoxyquin

2.2 Sample collection and serum anti-oxidation index, D-lactate, and diamine oxidase analysis

BW of the piglets was determined at 35 d of age. Six piglets (three females and three males) from each diet (one piglet per pen) were randomly selected for collection of blood and tissue samples, according to the protocol described by He *et al.* (2011). Blood samples were collected by jugular venipuncture using 10-ml tubes, and centrifuged at 3000g at 4 °C for 10 min to recover serum (Yin *et al.*, 2010). Serum samples were then stored at -80 °C until required for further analyses of D-lactate, diamine oxidase (DAO), and the anti-oxidation index. Piglets were then anesthetized (with C₃H₂ClF₅O) and euthanized by intravenous administration (jugular vein) of 4% sodium pentobarbital solution (40 mg/kg BW) (Yang *et al.*, 2012). The gastrointestinal tract of euthanized piglets was immediately resected and divided into stomach,

duodenum, jejunum, ileum, cecum, and colon. Approximately 20 cm of intestinal segments were aseptically isolated from the middle sections of the duodenum, jejunum, and ileum. The isolated intestinal segments were then flushed with phosphate-buffered saline and each segment was divided into two sections. One section (about 2 cm in length) was fixed using a 10% formaldehyde-phosphate buffer and kept at 4 °C, whereas the other section (approximately 18 cm in length) was used for mucosal sampling (Wu *et al.*, 2015). Immediately after collection, the mucosal tissue samples were frozen in liquid nitrogen and stored at -80 °C until required for further analysis of cytokines, anti-oxidation index, and mRNA expression (Tan *et al.*, 2011; Yang *et al.*, 2013). Serum D-lactate content was measured using a commercial kit (Beijing Leadman Biochemistry Co., Beijing, China) and a Beckman CX4 Chemistry Analyzer (Beckman Coulter, Brea, CA, USA). The serum anti-oxidation index and DAO activity were determined using corresponding reagent kits (Jiancheng Bioengineering Institute, Nanjing, China) according to the protocol described by Yin *et al.* (2013).

2.3 Small intestinal morphology analysis

The fixed intestinal segments were embedded using low-melt paraffin wax. Three cross-sections of each intestinal segment (5 μm in thickness) were stained with hematoxylin and eosin. Villus height and crypt depth of each intestinal segment were measured at 40× magnification using an image processing and analysis system (Version 1, Leica Imaging Systems Ltd., Cambridge, UK). At least ten well-oriented intact villi and their associated crypts were examined in each intestinal section of each piglet. The mean villus height and crypt depth of each section were then calculated per piglet and used for further analysis (Tan *et al.*, 2009).

2.4 Measurement of cytokines and the anti-oxidation index in intestinal mucosa

Levels of interleukin-1β (IL-1β), IL-2, and IL-10 in the intestinal mucosa of piglets were measured using commercially available swine enzyme-linked immunosorbent assay (ELISA) kits according to the manufacturer's instructions (Cusabio Biotech Co., Ltd., Hubei, China). The minimum detectable doses for IL-1β, IL-2, and IL-10 were 3.9 pg/ml, 15.6 pg/ml,

and 6.25 pg/ml, respectively. The total antioxidant capacity (T-AOC) of the intestinal mucosa (A015), catalase (CAT) (A007-1) and superoxide dismutase (SOD) (A001-3) activities, and malondialdehyde (MDA) (A003-1) and glutathione (GSH) (reduced, A006-1) contents were assessed using corresponding reagent kits according to the instructions of the manufacturer (Jiancheng Bioengineering Institute) (Ren *et al.*, 2012). Protein concentration was determined by bicinchoninic acid assay (Beyotime Biotechnology, Beijing, China), according to the instructions of the manufacturer. Concentrations of the intestinal mucosal cytokines and the anti-oxidation index were standardized to the concentration of protein in each sample.

2.5 RNA extraction and cDNA synthesis

Approximately 100 mg of intestinal mucosa was pulverized using liquid nitrogen, according to the protocol described by Yang *et al.* (2013). Total RNA was then isolated from the homogenate by the TRIzol[®] reagent (Invitrogen, Carlsbad, CA, USA) using 100 mg tissue per milliliter TRIzol. The integrity of the RNA was checked using agarose gel electrophoresis with ethidium bromide as the staining agent. The quantity and quality of RNA were determined by ultraviolet spectroscopy using a spectrophotometer (NanoDrop ND-1000; Thermo Fisher Scientific, DE, USA). The RNA had an OD₂₆₀:OD₂₈₀ ratio (OD₂₆₀ and OD₂₈₀ are the optical densities at 260 and 280 nm, respectively) between 1.8 and 2.0. The RNA (10 µg) was incubated with DNase I (Invitrogen) according to the manufacturer's instructions and the treated RNA was then quantified using NanoDrop ND-1000 (Thermo Fisher Scientific). After quantification, 1 µg of DNA-free RNA was used for complementary DNA (cDNA) synthesis. First-strand cDNA was synthesized using oligo (dT) primer and Superscript II Reverse Transcriptase (Invitrogen).

2.6 Relative quantification of mRNA expression of *occludin* and *ZO-1*

Oligo 6.0 software (Molecular Biology Insights, Cascade, CO, USA) was used to design primers, which are listed in Table 3. Real-time quantitative PCR (RT-PCR) analyses were performed using the ABI 7900HT Fast Real-Time PCR System (Applied Biosystems, Carlsbad, CA, USA). Total volume for each PCR was 10 µl, comprising 5 µl SYBR Green mix, 1 µl 4× diluted cDNA, 0.2 µl each of forward and reverse primers, and 0.2 µl ROX Reference Dye (50×). Following a pre-denaturation process (10 s at 95 °C), a total of 40 cycles of amplification (each cycle consisting of 95 °C for 5 s and 60 °C for 20 s) were conducted, which was followed by a melting curve program (from 60 °C to 99 °C with a heating rate of 0.1 °C/s, following which the fluorescence was collected). In each sample, glyceraldehyde-3-phosphate dehydrogenase (*GAPDH*) and *β-actin* were used as the reference genes to normalize the expressions of the genes of interest. The relative mRNA expression ratio (*R*) of each gene of interest was calculated by the following equation: $R = 2^{-\Delta\Delta C_T}$, where $-\Delta\Delta C_T = (C_{T \text{ sample gene of interest}} - C_{T \text{ reference sample}}) - (C_{T \text{ control gene of interest}} - C_{T \text{ reference control}})$.

The C_T of reference was the mean C_T value of *GAPDH* and *β-actin*. The efficiency of RT-PCR was determined by amplifying a dilution series of cDNA according to the equation $10^{(-1/\text{slope})}$. The mRNA of reference and interest genes was amplified with comparable efficiencies. In negative controls, the cDNA sample was replaced with water.

2.7 Statistical analysis

All data were subjected to one-way analysis of variance (ANOVA) using SAS software (Version 9.2; SAS Institute Inc., Cary, NC, USA). The pen was used as the experimental unit for the analysis of growth

Table 3 Primer sequences for real-time PCR analysis

Gene	Direction	Sequence (5'→3')	GenBank accession number	Product size (bp)
<i>Occludin</i>	Forward	ATGCTTTCTCAGCCAGCGTA	NM_001163647.2	176
	Reverse	AAGGTTCCATAGCCTCGGTC		
<i>ZO-1</i>	Forward	GAGGATGGTCACACCGTGGT	XM_003353439.2	169
	Reverse	GGAGGATGCTGTTGTCTCGG		
<i>β-actin</i>	Forward	TGCGGGACATCAAGGAGAAG	XM_003357928.1	216
	Reverse	AGTTGAAGGTGGTCTCGTGG		
<i>GAPDH</i>	Forward	AAGGAGTAAGAGCCCCTGGA	NM_001206359.1	140
	Reverse	TCTGGGATGGAACTGGAA		

performance and incidence of diarrhea, and the piglet was used as the experimental unit for the analysis of the anti-oxidation index, concentrations of D-lactate and cytokines, DAO activity, intestinal morphology, and mRNA expression. Probability values <0.05 were used to indicate statistical significance among means.

3 Results

3.1 Growth performance, incidence of diarrhea, and small intestinal morphology

Dietary supplementation with CSE and YP from Days 1 to 14 post-weaning had no significant effect on ADG, ADFI, or G:F in weaned piglets (Table 4). The incidence of diarrhea in weaned piglets was

Table 4 Effects of dietary supplementation with YP on growth performance and incidence of diarrhea in weaned piglets

Group	ADG (g/d)	ADFI (g/d)	G:F (g/g)	Diarrhea rate (%)
Control	261.90	378.63	0.69	4.48 ^b
YP	255.95	359.32	0.71	8.65 ^a
CSE	229.76	346.07	0.64	2.84 ^c
SEM	30.62	28.07	0.04	1.29
<i>P</i> -value	0.560	0.580	0.190	0.010

ADG: average daily gain; ADFI: average daily feed intake; G:F: gain-to-feed ratio; YP: yeast products; CSE: colistin sulfate; SEM: standard error of the mean. ^{a, b, c} Means in the same column with different superscript letters are significantly different ($P < 0.05$)

increased ($P < 0.05$) following dietary supplementation with YP, but reduced ($P < 0.05$) following dietary supplementation with CSE. Dietary supplementation with CSE and YP reduced ($P < 0.05$) villus height in the duodenum and jejunum, as well as crypt depth in the duodenum; however, no significant differences in villus height, or crypt depth in the ileum, or crypt depth in the jejunum were observed among the various treatments (Table 5). The number of goblet cells per 100 enterocytes was lower ($P < 0.05$) in the duodenal villi of animals fed a CSE-supplemented diet compared to those fed the control or YP-supplemented diets, whereas that in the ileal villi was higher ($P < 0.05$). No significant differences were observed in the number of goblet cells per 100 enterocytes in the jejunal villi (Table 5). The number of Intraepithelial lymphocytes (IEL) per 100 enterocytes was higher ($P < 0.05$) in the duodenal villi of piglets fed YP-supplemented diets in comparison to those fed control or CSE-supplemented diets. The number of IEL per 100 enterocytes was also higher ($P < 0.05$) in the jejunal villi of piglets fed the YP-supplemented diet in comparison to those fed the control diet. However, piglets fed the control diet had a higher ($P < 0.05$) number of IEL per 100 enterocytes in the ileal villi in comparison to those fed CSE- or YP-supplemented diets (Table 5).

3.2 Intestinal cytokines

Concentrations of IL-1 β and IL-2 were increased ($P < 0.05$) in the ileal mucosa of piglets fed

Table 5 Effects of YP supplementation on the morphology of the small intestine of weaned piglets

Group	Villus height (μm)			Crypt depth (μm)			VH:CD ($\mu\text{m}:\mu\text{m}$)		
	Duodenum	Jejunum	Ileum	Duodenum	Jejunum	Ileum	Duodenum	Jejunum	Ileum
Control	521.13 ^a	465.59 ^a	368.71	318.12 ^a	266.07	205.05	1.64	1.75	1.80
YP	458.39 ^b	367.09 ^b	351.82	256.22 ^b	253.73	219.28	1.79	1.45	1.60
CSE	439.94 ^b	360.81 ^b	389.74	256.02 ^b	242.97	225.54	1.72	1.49	1.73
SEM	25.85	29.58	27.72	26.71	14.28	10.30	0.10	0.10	0.13
<i>P</i> -value	0.030	0.010	0.590	0.030	0.340	0.320	0.330	0.080	0.140
Group	Goblet cells ¹			Intraepithelial lymphocytes ²					
	Duodenum villi	Jejunum villi	Ileum villi	Duodenum villi	Jejunum villi	Ileum villi			
Control	6.58 ^a	3.92	4.17 ^b	5.42 ^b	9.83 ^b	21.92 ^a			
YP	7.25 ^a	2.92	4.42 ^b	9.42 ^a	11.25 ^a	12.92 ^b			
CSE	4.60 ^b	3.70	6.33 ^a	6.67 ^b	10.75 ^{ab}	12.75 ^b			
SEM	0.68	0.37	0.48	0.68	0.42	1.95			
<i>P</i> -value	0.030	0.120	0.002	0.002	0.050	0.005			

VH:CD: villus height: crypt depth; YP: yeast products; CSE: colistin sulfate; SEM: standard error of the mean. ^{a, b} Means in the same column with different superscript letters are significantly different ($P < 0.05$). ¹ Goblet cells per 100 enterocytes. ² Intraepithelial lymphocytes per 100 enterocytes

CSE-supplemented diets in comparison to those fed the control or YP-supplemented diets. Treatment effects on duodenal and jejunal IL-1 β and IL-2 concentrations were not observed. The concentration of IL-10 was higher ($P<0.05$) in the duodenal mucosa of piglets fed CSE-supplemented diets than that in those fed the control or YP-supplemented diets. Concentrations of IL-10 were significantly higher ($P<0.05$) in the jejunal mucosa of piglets fed CSE- and YP-supplemented diets in comparison to those fed the control diet, and concentrations of IL-10 were significantly higher ($P<0.05$) in the ileal mucosa of piglets fed YP-supplemented diets in comparison to those fed the control diet (Table 6).

3.3 Anti-oxidation index

Duodenal, ileal, and serum T-AOC was increased ($P<0.05$) in piglets fed CSE- and YP-supplemented diets in comparison to those fed the

control diet; however, piglets fed the CSE-supplemented diet had a higher ($P<0.05$) jejunal T-AOC than those fed the YP-supplemented diet. An increase ($P<0.05$) in duodenal and jejunal CAT was observed in piglets fed the YP-supplemented diet compared to those fed the control or CSE-supplemented diets. Serum CAT was also higher ($P<0.05$) in animals fed the YP-supplemented diet compared to those fed the control diet. Jejunal SOD was decreased ($P<0.05$) following dietary supplementation with YP. Piglets that were fed YP- or CSE-supplemented diets yielded greater levels of ($P<0.05$) serum SOD than those fed the control diet. Dietary supplementation with YP increased ($P<0.05$) ileal GSH in weaned piglets. No differences in duodenal, jejunal, and serum GSH were observed among the various treatments. The concentrations of MDA in the jejunum and ileum declined ($P<0.05$) in piglets fed YP- and CSE-supplemented diets compared to those

Table 6 Effects of YP supplementation on intestinal IL-1 β , IL-2, and IL-10 concentrations in weaned piglets

Group	IL-1 β (pg/g of protein)			IL-2 (pg/g of protein)			IL-10 (pg/g of protein)		
	Duodenum	Jejunum	Ileum	Duodenum	Jejunum	Ileum	Duodenum	Jejunum	Ileum
Control	83.89	13.50	11.57 ^b	117.24	120.18	117.81 ^b	205.30 ^b	87.57 ^b	178.64 ^b
YP	82.81	12.30	13.06 ^b	121.25	128.71	119.67 ^b	214.49 ^b	126.46 ^a	241.51 ^a
CSE	95.46	15.91	20.25 ^a	116.84	117.03	135.60 ^a	275.98 ^a	124.14 ^a	211.08 ^{ab}
SEM	6.34	1.68	1.48	3.19	6.06	5.10	17.62	9.62	15.02
P-value	0.550	0.340	0.020	0.610	0.140	0.040	0.040	0.010	0.040

YP: yeast products; CSE: colistin sulfate; SEM: standard error of the mean. ^{a, b} Means in the same column with different superscript letters are significantly different ($P<0.05$)

Table 7 Effects of YP supplementation on serum and intestinal mucosal anti-oxidation index of weaned piglets

Group	Total antioxidant capacity (U/g of protein)				Catalase (U/g of protein)				Superoxide dismutase (U/g of protein)	
	Duodenum	Jejunum	Ileum	Serum ¹	Duodenum	Jejunum	Ileum	Serum ²	Duodenum	Jejunum
Control	246.39 ^c	487.57 ^{ab}	486.33 ^b	1.66 ^c	412.85 ^b	294.66 ^b	276.95	22.81 ^b	240.86	260.88 ^a
YP	454.43 ^b	413.88 ^b	581.83 ^a	3.74 ^a	539.63 ^a	405.11 ^a	298.49	30.61 ^a	224.79	212.02 ^b
CSE	583.27 ^a	574.32 ^a	659.07 ^a	2.87 ^b	445.34 ^b	241.28 ^b	289.15	25.73 ^{ab}	248.43	252.22 ^a
SEM	37.90	55.41	40.52	0.24	35.90	42.14	30.53	2.12	21.46	12.64
P-value	0.001	0.030	0.040	0.001	0.030	0.020	0.780	0.050	0.610	0.010

Group	Superoxide dismutase (U/g of protein)		Glutathione (μ mol/g of protein)				Malondialdehyde (nmol/g of protein)			
	Ileum	Serum ¹	Duodenum	Jejunum	Ileum	Serum ³	Duodenum	Jejunum	Ileum	Serum ⁴
Control	208.73	44.11 ^b	1.59	1.46	1.68 ^b	3.59	92.49	97.97 ^a	93.22 ^a	5.19 ^a
YP	189.17	72.03 ^a	1.78	1.54	2.21 ^a	3.30	89.50	74.66 ^b	59.32 ^b	3.36 ^b
CSE	161.71	76.41 ^a	1.62	1.36	1.67 ^b	3.93	73.57	65.96 ^b	69.30 ^b	4.83 ^a
SEM	22.81	6.76	0.17	0.15	0.18	0.31	8.16	7.28	6.23	0.35
P-value	0.210	0.003	0.630	0.650	0.040	0.250	0.150	0.010	0.003	0.003

YP: yeast products; CSE: colistin sulfate; SEM: standard error of the mean. ^{a, b, c} Means in the same column with different superscript letters are significantly different ($P<0.05$). ¹ U/ml; ² U/L; ³ μ mol/L; ⁴ nmol/ml

fed the control diet, and animals fed the YP-supplemented diet had lower ($P<0.05$) concentrations of serum MDA than those fed the control or CSE-supplemented diets (Table 7).

3.4 Intestinal barrier function

Serum D-lactate concentration and DAO activity were both increased ($P<0.05$) following dietary supplementation with YP and CSE (Table 8). The expression levels of *occludin* were reduced ($P<0.05$) in the jejunum and ileum of piglets fed CSE- and YP-supplemented diets, respectively, in comparison to those fed the control diet. Jejunal *ZO-1* expression was also down-regulated ($P<0.05$) by YP and CSE supplementation, and piglets fed the YP-supplemented diet yielded a lower ($P<0.05$) expression level of ileal *ZO-1* than did those fed the control and CSE-supplemented diets (Table 8).

Table 8 Effects of YP supplementation on serum D-lactate concentration, DAO activity, and intestinal *occludin* and *ZO-1* mRNA expression in weaned piglets

Group	D-Lactate ($\mu\text{g/ml}$)	DAO (U/L)	<i>Occludin</i>		<i>ZO-1</i>	
			Jejunum	Ileum	Jejunum	Ileum
Control	8.90 ^b	13.15 ^b	1.00 ^a	1.00 ^a	1.00 ^a	1.00 ^a
YP	10.90 ^a	16.41 ^a	0.81 ^{ab}	0.78 ^b	0.78 ^b	0.74 ^b
CSE	10.67 ^a	15.83 ^a	0.73 ^b	0.92 ^{ab}	0.65 ^c	0.91 ^a
SEM	0.46	0.77	0.06	0.06	0.05	0.05
<i>P</i> -value	0.001	0.005	0.010	0.030	0.001	0.010

DAO: diamine oxidase; YP: yeast products; CSE: colistin sulfate; SEM: standard error of the mean. ^{a, b} Means in the same column with different superscript letters are significantly different ($P<0.05$)

4 Discussion

At 2 weeks post-weaning, no significant differences were observed in ADG, ADFI, and G:F among piglets fed the CSE, YP, and control diets. Although several studies have shown that the inclusion of YC, YE, or yeast cell products has positive effects on the ADG of weaned piglets (Maribo and Spring, 2003; Carlson et al., 2005; Hahn et al., 2006; Kogan and Kocher, 2007; Shen et al., 2009), van der Peet-Schwering et al. (2007) reported that the ADG of weaned piglets is not significantly affected by antibiotics and YC+cell wall products at 2 weeks post-weaning. We speculate that the effects of YC and yeast cell wall products on ADG were attenuated

after being combined in the YP mixture. Moreover, dietary supplementation with YP increased the incidence of diarrhea in weaning piglets, and to our knowledge, no reports about the influence of YC, YE, or CWH on the incidence of diarrhea in weaning piglets have been published. The reduction of the positive effects of YC, YE, and CWH on the growth performance of piglets could be attributed to the fact that the gut health of piglets was likely adversely affected by the mixture of YC, YE, and CWH. Future studies should be conducted to test the interactions among YC, YE, and CWH. Although CSE has been widely accepted as a growth promoter in swine production, the present results demonstrate that it does not significantly affect the growth performance of weaning piglets. This finding could be attributed to colistin resistance or the fact that the dosage of CSE administered in the present study was very low (20 mg/kg), which was below the minimum dosage to improve growth performance. Moreover, although there were no statistically significant differences in growth performance among CSE, YP, and control groups, the G:F in the CSE group was about 5% and 7% lower than the control and YP groups, respectively. The lower G:F of CSE piglets was probably due to the fact that CSE animals had the lower feed intake and lower ADG.

Diarrhea usually follows some form of intestinal dysfunction arising from significant post-weaning changes in intestinal morphology, including an increase in crypt depth and a reduction in villus height, as has been observed in several studies (Boudry et al., 2004; Montagne et al., 2007; Verdonk et al., 2007). Atrophy of the villi could be attributed to an increase in cell apoptosis, which is induced by cellular factors or endogenous stressors, and further regulates crypt height by promoting crypt cell proliferation (Jiang et al., 2000; Fleck and Carey, 2005). Shen et al. (2009) reported that dietary YC increased villus height and the villus: crypt ratio in the jejunum of weaned piglets; however, van der Peet-Schwering et al. (2007) observed no changes in jejunal morphology when YC or YC+cell wall products were included in the diets of piglets. In the present study, we observed that villus height in both the duodenum and jejunum, as well as the duodenal crypt depth, were reduced in piglets fed a diet supplemented with YP. The variable effects of YP in weaned piglets may be due to differences in the

live yeast contents of the diet, feeding environment, and piglet weaning age (van Heugten *et al.*, 2003). Although CSE and YP had similar effects on the intestinal morphology of weaned piglets, YP supplementation increased the incidence of diarrhea, whereas CSE supplementation had the opposite effect, possibly because CSE inhibits reproduction of the bacteria that cause diarrhea. Interspersed among the absorptive epithelial cells of the intestine, IEL and goblet cells are involved in preventing both bacterial overgrowth and the penetration of potential pathogens into epithelium. Because YC, yeast cell wall products, and antibiotics have been reported to affect the gastrointestinal bacterial community of weaned piglets (van der Peet-Schwering *et al.*, 2007; Shen *et al.*, 2009), variations in IEL and goblet cell abundance could occur in response to changes in the epithelium of the microbiota.

The epithelium of the intestinal mucosa acts as a physical barrier that helps to block pathogens, while allowing dietary nutrients to enter the body (Sun *et al.*, 1998). An intact intestinal mucosal barrier is therefore very important for proper intestinal function. D-Lactate and DAO are two important markers of mucosal integrity in the intestine, because serum D-lactate concentration increases and DAO activity intensifies when the mucosa is damaged (Luk *et al.*, 1980; Vella and Farrugia, 1998). Both serum D-lactate concentration and DAO activity were increased in YP-treated piglets, suggesting that the intestinal mucosal barrier was also damaged following dietary supplementation with YP, which is consistent with the changes observed in intestinal morphology and the incidence of diarrhea. The mRNA expression levels of the tight junction proteins *occludin* and *ZO-1* were also lower in piglets fed the YP-supplemented diet than in piglets fed the control diet. In a previous study, van der Peet-Schwering *et al.* (2007) reported that dietary supplementation with YP and YC did not affect the integrity of the small intestine, as indicated by levels of plasma intestinal fatty acid binding protein (I-FABP). The disparity in results between the two studies may be explained by differences in the age at weaning.

Weaning stress is associated with oxidative stress, which is considered a major factor affecting intestinal health and function (Kaplan *et al.*, 2007; Wang *et al.*, 2008). Antioxidant enzymes, such as

CAT, SOD, and GSH are important components of the antioxidant system, which is involved in protecting cells from oxidative stress (Irshad and Chaudhuri, 2002). Thus, functioning of the antioxidant system can be assessed by examining the activity of antioxidant enzymes and the concentration of GSH. Although dietary supplementation with YP exerted adverse effects on the incidence of diarrhea, intestinal morphology, and barrier function, the intestinal and serum antioxidant systems of weaned piglets (as indicated by the changes in T-AOC, antioxidant enzyme activities, and GSH and MDA concentrations in the intestinal mucosa and serum) were affected in piglets fed a diet supplemented with YP. These findings are consistent with previous reports of various *in vitro* and *in vivo* experimental models in which yeast polysaccharides exhibited antioxidant properties (Kogan *et al.*, 2005; Pourahmad *et al.*, 2011). As diarrhea is usually associated with oxidative stress, which activates the antioxidant system (Granot and Kohen, 2004), this activation in piglets fed the YP-supplemented diet may have resulted from the negative effects of YP on the gut health of weaned piglets. Early weaning results in a sudden cessation of passive immunity from the milk of sows, when the immune system of piglets is still immature, making them vulnerable to diseases such as diarrhea (Ushida *et al.*, 2008). Dietary supplementation with specific nutrients or immunomodulators could improve the performance and health of weaning piglets (Jiang *et al.*, 2009). Cytokines are small peptides that play important roles in the regulation of immune and inflammatory responses (Pié *et al.*, 2004). Proinflammatory cytokines (e.g., IL-1 β , IL-2, and tumor necrosis factor α (TNF α)) are necessary to initiate the inflammatory response during infection; however, overexpression of these cytokines can affect pathological responses (Clark, 2007; Zelnickova *et al.*, 2008). Anti-inflammatory cytokines (e.g., IL-10 and IL-4) are capable of inhibiting the overexpression of pro-inflammatory cytokines and other mediators that could lead to hyper-activation of immune responses in weaned piglets (King *et al.*, 2003; Schiepers *et al.*, 2005). Piglets fed a diet supplemented with YP exhibited lower levels of ileal IL-1 β and IL-2 than those fed a diet supplemented with CSE. In addition, the levels of IL-10 in the jejunum and ileum of piglets fed the YP-supplemented diet were greater than those of

piglets fed the control diet, suggesting that YP influences the immune response of weaned piglets. These results are consistent with previous reports of stimulation of the immune response of weaned piglets following dietary supplementation with yeast cell wall products or specific polysaccharides (Hahn *et al.*, 2006). Moreover, stimulation of the immune response by YP was very likely due to its effects on the intestinal health of weaned piglets, as those fed YP-supplemented diets yielded a higher incidence rate of diarrhea. In addition, the immune system was likely more reactive in piglets with diarrhea. As dysfunction of the large intestine is also a major cause of diarrhea, additional research is needed to test the effects of YP on the large intestine of weaned piglets.

5 Conclusions

The results of our study suggest that supplementation of YP in the diets of weaned piglets has negative effects on the incidence of diarrhea, intestinal morphology, and barrier function. Moreover, the mucosal immune system and antioxidant system in the small intestine of piglets were also affected by dietary supplementation with YP. Additional research that incorporates factors such as weaning age and the effects on the large intestine is warranted to gain a better understanding of the effects of YP on weaned piglets.

Compliance with ethics guidelines

Huan-sheng YANG, Fei WU, Li-na LONG, Tie-jun LI, Xia XIONG, Peng LIAO, Hong-nan LIU, and Yu-long YIN declare that they have no conflicts of interest.

All institutional and national guidelines for the care and use of laboratory animals were followed.

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中文概要

题目: 酵母产物对断奶仔猪肠道形态、屏障功能、细胞因子表达和抗氧化系统的影响

目的: 验证添加酵母混合物(酵母培养物、酵母细胞壁水解物和酵母提取物)对断奶仔猪生长性能、腹泻发生率、肠道形态、屏障功能、免疫反应和抗氧化系统的影响。

创新点: 考察酵母培养物、酵母细胞壁水解物和酵母提取物混合物对断奶仔猪的协同作用。

方法: 90头21日龄断奶仔猪随机分为3组,分别饲喂基础日粮(对照组),含1.2 g/kg的酵母混合物(YP组)及含20 mg/kg硫酸粘杆菌素日粮(CSE组)14天,比较三组间各项指标差异。

结论: 结果表明,三组之间平均日采食量、平均日增重和料肉比无显著差异。YP组腹泻发生率显著高于其它两组。对照组十二指肠和空肠的绒毛高度以及十二指肠的隐窝深度显著高于YP组和CSE组。相对于对照组或CSE组,YP组十二指肠和空肠绒毛淋巴细胞数目显著增加,而回肠绒毛内淋巴细胞数目显著降低。相对于对照组,YP组空肠和回肠内白介素-10(IL-10)的分泌增加,YP和CSE也显著影响了仔猪肠道和血清中抗氧化因子;YP和CSE组血清D-乳酸浓度和二胺氧化酶活性都增强;YP组或CSE组肠道occludin和ZO-1 mRNA表达降低。综上所述,酵母混合物添加会增加断奶仔猪腹泻发生率,并对断奶仔猪肠道形态学和屏障功能具有副作用。

关键词: 酵母产物;断奶仔猪;肠道形态;屏障功能;抗氧化系统