JOURNAL OF ANIMAL SCIENCE
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J Anim Sci 2006. 84:843-852.

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Effects of guar gum and cellulose on digesta passage rate, ileal microbial populations, energy and protein digestibility, and performance of grower pigs[1,2]

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ABSTRACT: Dietary guar gum and cellulose were studied as purified soluble and insoluble nonstarch polysaccharide (NSP) sources, respectively. A control diet containing 14% cornstarch was formulated. A 7% guar gum, a 7% cellulose, and a 7% guar gum + 7% cellulose diet were formulated by adding the NSP to the control diet at the expense of cornstarch (wt/wt), forming a 2 × 2 factorial arrangement. The objectives were to determine whether guar gum and cellulose altered 1) the passage rate of digesta through the small intestine and total tract; 2) the digestibility of energy and CP, characteristics of the digesta, and microbial populations in the ileum; 3) plasma glucose and ghrelin concentrations; and 4) short-term voluntary feed intake and growth performance of grower pigs. In Exp. 1, 12 pigs (27.0 ± 1.5 kg of BW) were fitted with an ileal T-cannula and were used in a 2-period change-over design, providing 6 observations per diet. Each period included 18 d: a 12-d acclimation period followed by 2-d feces, 3-d digesta, and 1-d venous blood collection periods. In Exp. 1, guar gum and cellulose slowed the passage rate of digesta through the small intestine by 26 and 18%, respectively ($P < 0.05$). Guar gum increased total tract retention time of the digesta by 14% ($P < 0.05$). Guar gum and cellulose increased the viscosity of ileal digesta by 72 and 76%, respectively ($P < 0.05$). Cellulose reduced ileal energy and CP digestibility ($P < 0.05$), but guar gum only tended to decrease ileal energy digestibility ($P < 0.10$). Guar gum and cellulose reduced total tract energy and CP digestibility ($P < 0.05$). At 60 min after feeding, guar gum decreased plasma glucose by 10% ($P < 0.10$). Guar gum interacted with cellulose to reduce plasma ghrelin before and after feeding ($P < 0.05$). Guar gum and cellulose interacted to increase ileal bifidobacteria and enterobacteria ($P < 0.05$); however, guar gum, but not cellulose, increased ileal clostridia ($P < 0.05$). In Exp. 2, 20 individually housed grower pigs (5 pigs per diet) had free access to the 4 diets used in Exp. 1 for 14 d. Guar gum and cellulose decreased ADG and reduced ADFI on d 0 to 14 ($P < 0.05$). In summary, increasing purified NSP in the diet reduced the passage rate of digesta, energy and protein digestibility, and feed intake, but increased ileal bifidobacteria and enterobacteria populations. The effects of cellulose were similar to those of guar gum. In conclusion, monitoring of dietary NSP is a critical factor to achieve predictable digestible nutrient intake and intestinal bacterial populations.

Key words: cellulose, feed intake, guar gum, passage rate, pig

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INTRODUCTION

The use of alternative feed ingredients to supplement or substitute conventional feed ingredients in swine diets can be attractive economically. Plant-based alternative feed ingredients may contain a broad range of nonstarch polysaccharide (**NSP**) in cell walls (Souffrant, 2001). These NSP are not digestible by porcine endogenous enzymes and may act as antinutrients (Stanogias and Pearce, 1985). Diets or ingredients with a high NSP content may compromise voluntary feed in-

[1] The Natural Sciences and Engineering Research Council of Canada and Danisco Animal Nutrition are acknowledged for funding the project. Pork producers of Saskatchewan, Manitoba, and Alberta and the Agriculture Development Fund of Saskatchewan Agriculture, Food, and Rural Revitalization are acknowledged for their strategic funding to Prairie Swine Centre Inc.

[2]Presented in part at the ASAS Midwestern Section Mtg., Des Moines, IA, March 15-17, 2004 (Abstr. 195 and 196).

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Received July 15, 2005.
Accepted November 22, 2005.

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take and nutrient digestibility or use in weaned and grower pigs (Kyriazakis and Emmans, 1995; Zijlstra et al., 1999, 2001).

The mechanisms relative to reduced voluntary feed intake attributable to some alternative feed ingredients seem complex and are poorly understood (de Lange et al., 2000a,b). Individual NSP fractions may play a key role in reducing voluntary feed intake and/or nutrient digestibility (Choct et al., 1999; Owusu-Asiedu et al., 2003; Zijlstra et al., 2004). Managing the negative effects of NSP on voluntary feed intake requires an understanding of the physical and chemical characteristics of NSP and the physiological changes occurring in pigs after inclusion of NSP fractions in the diet. Guar gum and cellulose are, respectively, regarded as purified sources of soluble and insoluble NSP (De Haan et al., 1989; Pluske et al., 1998). In the current study, guar gum and cellulose were used to test the hypothesis that increasing levels of soluble and insoluble NSP will alter the rate of digesta flow and microflora in the gastrointestinal tract of grower pigs.

The objectives of the current study were to determine the effects of guar gum and cellulose on 1) digesta passage rate through the small intestine and total tract; 2) energy and CP digestibility, digesta characteristics, and ileal microbial populations; 3) plasma glucose and ghrelin concentrations; and 4) short-term voluntary feed intake and growth performance in grower pigs.

MATERIALS AND METHODS

Experimental Design

Diets with and without guar gum and cellulose were studied in a 2 × 2 factorial arrangement for a total of 4 dietary treatments. Cornstarch as a purified starch source was replaced by purified guar gum and/or purified cellulose to achieve a clean comparison of carbohydrate sources.

Experimental Diets

A corn and soybean meal-based control diet containing 14% cornstarch (Nacan Product Ltd., Brampton, ON, Canada) was formulated. A guar gum diet and a cellulose diet were formulated by adding 7% guar gum (galactomannan: β(1-4)-linked D-mannopyranose with α(1-6) D-galactose branch points; Pangaea Sciences, Mississauga, ON, Canada) and cellulose (β(1,4)-linked glucose polymer; Dawns Food, Saskatoon, SK, Canada), respectively, to the control diet at the expense of cornstarch (wt/wt). A guar gum-cellulose diet was formulated by adding 7% guar gum and 7% cellulose to the control diet at the expense of 14% cornstarch. The control diet was formulated based on apparent ileal digestible AA and DE to contain 3.50 Mcal of DE/kg and 2.4 g of apparent digestible lysine/Mcal (PSCI, 2000; Table 1) using feed formulation software (Version 7, Brill Corporation, Norcross, GA). Diets were supplemented with synthetic AA to balance the ideal AA ratio and were fortified to exceed vitamin and minerals requirements (NRC, 1998). Acid-insoluble ash (Celite Corp., World Minerals Co., Lompoc, CA) was added as an indigestible marker to determine energy and protein digestibility.

Table 1. Ingredient composition of the experimental diets, as-fed basis[1]

Ingredient	Control	Guar gum	Cellulose	Guar gum and cellulose
			%	
Corn	61.97	61.97	61.97	61.97
Soybean meal	18.70	18.70	18.70	18.70
Cornstarch[2]	14.00	7.00	7.00	—
Guar gum[3]	—	7.00	—	7.00
Cellulose[4]	—	—	7.00	7.00
Dicalcium phosphate	1.75	1.75	1.75	1.75
Limestone	0.60	0.60	0.60	0.60
Acid-insoluble ash[5]	0.50	0.50	0.50	0.50
Vitamin premix[6]	0.50	0.50	0.50	0.50
Mineral premix[7]	0.50	0.50	0.50	0.50
Canola oil	0.50	0.50	0.50	0.50
Salt	0.40	0.40	0.40	0.40
L-Lysine·HCl	0.35	0.35	0.35	0.35
L-Threonine	0.13	0.13	0.13	0.13
DL-Methionine	0.06	0.06	0.06	0.06
L-Tryptophan	0.04	0.04	0.04	0.04
Analysed composition				
DM, %	88.6	88.6	88.5	88.4
Total NSP[8]	14.8	23.1	21.2	25.2
Soluble NSP	2.9	7.6	8.1	11.0
Insoluble NSP	11.9	15.4	13.1	14.2
CP, %	16.9	16.8	16.9	17.0
GE, Mcal/kg of DM	4.29	4.30	4.23	4.25
Water-holding capacity, g of water/g of DM	1.56	1.96	1.69	4.37

[1]Calculated composition of the control diet (%): DM, 87.6; CP, 14.4; ADF, 3.5; NDF, 9.2; lysine, 0.84; threonine, 0.51; methionine, 0.27; tryptophan, 0.15 [AA reported as apparent digestible]; Ca, 0.75; total P, 0.65; DE, 3.5 Mcal/kg; digestible lysine, 2.4 g/Mcal of DE (PSCI, 2000). The GE content of cornstarch, guar gum, and cellulose was 4.191, 4.227, and 3.498 Mcal/kg of DM, respectively.
[2]Nacan Product Ltd., Brampton, ON, Canada.
[3]Pangaea Sciences, Missisauga, ON, Canada.
[4]Dawn Food, Saskatoon, SK, Canada.
[5]Celite Corporation, World Minerals Co., Lompoc, CA.
[6]Provided per kilogram of the diet: vitamin A, 8,250 IU; vitamin D_3, 825 IU; vitamin E, 40 IU; niacin, 35 mg; D-pantothenic acid, 15 mg; riboflavin, 5 mg; menadione, 4 mg; folic acid, 2 mg; thiamine, 1 mg; D-biotin, 0.2 mg; vitamin B_{12}, 0.025 mg.
[7]Provided per kilogram of the diet: Zn, 100 mg as zinc sulfate; Fe, 80 mg as ferrous sulfate; Cu, 50 mg as copper sulfate; Mn, 25 mg as manganous sulfate; I, 0.5 mg as calcium iodate; Se, 0.1 mg as sodium selenite.
[8]NSP = nonstarch polysaccharide.

Experimental Procedures

The animal protocols were approved by the University of Saskatchewan Committee on Animal Care and Supply (protocol no. 19970019 and 20030009), followed principles established by the Canadian Council on Animal Care (CCAC, 1993), and were conducted at Prairie Swine Center Inc., Saskatoon, SK, Canada.

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In Exp. 1, 12 barrows (Camborough-22 × Line 65, PIC Canada Ltd., Airdrie, AB, Canada; initial BW = 27.0 ± 1.2 kg, mean ± SD) were fitted with a nylon T-cannula at the distal ileum and housed individually in metabolism pens with plastic-coated expanded metal floors and solid polyvinyl chloride-planked siding. The pens were 1.5 (length) × 1.5 (width) × 0.9 m (height) and allowed freedom of movement of pigs during the entire experiment. A single-space dry feeder and a bowl-drinker were located at the front of the pen. Cannulas, cannulation surgery, and pre- and postoperative care of animals were according to the procedure described by Wubben et al. (2001). After surgery, pigs were fed a standard diet for 7 d and were then switched to 1 of the 4 experimental diets in a 2-period change-over design (Peterson, 1985) with 3 groups of 4 pigs, resulting in 3 observations per diet per period for a total of 24 observations or 6 observations per diet. Each experimental period included 18 d: a 12-d acclimation to an experimental diet based on expected time required to alter intestinal microflora (Collier et al., 2003) followed by 1-d ileal digesta sampling for microbial assays (d 13), 2-d feces collection (d 14 and 15), 2-d ileal digesta collection (d 16 and 17), and 1 d of blood sampling (d 18). Daily feed allowance was equal among diets and was adjusted to 3 times maintenance (3 × 110 kcal of DE/kg of $BW^{0.75}$; NRC, 1998) based on the DE content of the control diet and was fed in 2 equal meals (0700 and 1500). Diets were provided as a dry mash, and pigs consumed the feed allowance within 30 min after feeding. Pigs were housed in an environmentally controlled room with an average temperature of 21°C and a 14-h light and 10-h dark cycle.

In Exp. 2, 20 pigs (Camborough-22 × Line 65, PIC Canada Ltd., 12 barrows and 8 gilts; initial BW = 26.0 ± 1.2 kg) were housed in individual pens to study short-term effects of NSP on voluntary feed intake and growth performance. The rectangular pens measured 0.91 × 1.83 m. The flooring was fully slatted, precast concrete slats. The penning consisted of solid plastic partitions between pens and at the front of the pens and a concrete wall with an opening at the back of the pens between 2 rows of pens. Pens were equipped with a nipple drinker and an adjustable single-space dry feeder. Pigs were housed in an environmentally controlled room with an average temperature of 18°C. Lights were on from 0700 to 1900. After a 7-d acclimation, pigs were fed 1 of 4 experimental diets for 14 d. Pigs had free access to water and feed in dry mash form. Five pens (3 barrows and 2 gilts) were assigned randomly to diets for a total of 5 pigs per diet. Pigs were weighed on d 0, 7, and 14 of the experiment, and feed disappearance was measured on d 7 and 14. Average daily gain, ADFI, and G:F were calculated.

Sample Collection Methods

For Exp. 1, feed was collected during the collection period and stored at –20°C. On d 13, digesta samples (200 to 250 mL) were collected every 15 min for 4 h under anaerobic conditions by attaching plastic bags filled with carbon dioxide to the stalk of the cannulas. Samples were stored on ice until bacterial enumeration, which was started within 2 h. Feces were collected quantitatively on d 14 and 15. By incorporating 1% ferric oxide in the morning feed on d 14, the total-tract retention time was measured by checking the pigs every 15 min and recording the time of first appearance of ferric oxide in feces. Collected feces were pooled over the collection period into 1 bag per pig and stored at –20°C.

Digesta were collected for 2 d (d 16 and 17). On d 16, 1% Cr_2O_3 was added to the morning feed (0700). Digesta were collected for subsequent 30-min periods (from 0730 to 1830 h), weighed, homogenized, subsampled, and stored at –20°C until analysis. Concentration of Cr_2O_3 was determined in each subsample. Aliquots of digesta collected for each pig on d 16 were pooled and homogenized with digesta collected on d 17. At the end of the collection, feces and digesta samples were thawed, homogenized, subsampled, and freeze-dried for further chemical analyses.

Blood was collected on d 18 by jugular vena puncture, 30 min before feeding for a baseline measurement and 30 and 60 min after feeding. Approximately 5 mL of blood was collected into heparinized tubes and immediately centrifuged at 1,500 × *g* for 15 min at 4°C; plasma was decanted into 2 vials [prepared with EDTA (1 mg/mL) and proteinase inhibitor (Trasylol, Bayer, Etobicoke, ON, Canada; 70 μg/mL)] per pig and stored at –20°C until analysis.

Bacterial Enumeration

Bacterial enumeration was performed according to standard enumeration procedures (Estrada et al., 2001). Briefly, digesta samples were weighed and diluted in peptone water to an initial 10^1 dilution. Ten-fold dilutions were plated in duplicate using an automated plater (Autoplate, Spiral Biotech Inc., Bethesda, MD) on the following media: trypticase soy agar (Difco Laboratories, Detroit, MI) containing 5% sheep blood for total aerobes; reinforced clostridium agar (Oxoid Ltd., Basingstoke, UK) containing 5% sheep blood agar for total anaerobes; MacConkey agar (Becton Dickinson Microbiology Systems, Cockeysville, MD) for enterobacteria; clostrisel agar (Becton Dickinson Microbiology Systems) for clostridia; and Beerens agar (Beerens, 1990) for bifidobacteria. Trypticase soy agar and MacConkey agar were incubated aerobically at 37°C for 24 h. Reinforced clostridium agar and Beerens agar plates were incubated anaerobically (Gas-Pak anaerobic system, Becton Dickinson Microbiology Systems) at 37°C for 48 h. Total aerobes, anaerobes, enterobacteria, clostridia, and bifidobacteria colonies were counted and recorded in colony-forming units per gram of wet digesta.

Chemical Analyses

Analyses were conducted in duplicate. Immediately after collection, digesta pH was determined using a pH

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meter, and digesta viscosity (expressed as centipoises) was measured using a digital viscometer (Model LVTDVCP-11, Brookfield Engineering Laboratories Inc., Stoughton, MA) maintained at 24°C (Bedford et al., 1992). Diets, freeze-dried digesta, and feces were finely ground through a 1-mm screen in a Retsch mill (Brinkman Instruments, Rexdale, ON, Canada). Samples were analyzed for CP (macro-Kjeldahl; N × 6.25), acid-insoluble ash (McCarthy et al., 1974), Cr_2O_3 using a spectrophotometer (Fenton and Fenton, 1979), GE via an adiabatic bomb calorimeter (IKA Calorimeter System C-5000, IKA Works Inc., Wilmington, NC), and DM by drying at 135°C in an airflow-type oven for 2 h (method 930.15; AOAC, 1990). Ileal and total-tract apparent digestibility coefficients of energy and CP were calculated using the indicator or index method (Adeola, 2001). Water-holding capacity of diets and freeze-dried digesta was measured using a centrifugation method (Eastwood et al., 1983) by separating water from hydrated material. Diet samples were analyzed for soluble and insoluble NSP using the method of Englyst and Hudson (1993) by fractionating moisture, starch, protein, and fat from the sample (= NSP) and measuring water solubility of this fraction.

Glucose and Ghrelin Analyses

Plasma glucose was determined using a Microtiter kit (Wako Chemicals Inc., Richmond, VA).

A modified double-antibody RIA procedure (Cummings et al., 2002) was used to measure plasma ghrelin. Ghrelin antiserum was generated in rabbits. Ghrelin (1 to 10; human/rat, PGH-3627-PI, Peptides International, Louisville, KY) was conjugated to succinylated keyhole limpet hemocyanin (H5654, Sigma, St. Louis, MO) with EDC (22980, Pierce Biotechnology, Inc., Rockford, IL). For immunization in rabbits, the conjugate was emulsified in Alhydrogel and Freund's incomplete adjuvant. Tyr11 ghrelin (1 to 11) was custom-synthesized (Peptidec Technologies Ltd., Pierrefonds, QB, Canada) and radioiodinated using the Chloramine-T method. Iodinated material was purified on a 9- × 30-cm column, G25 Sephadex-fine, and eluted with 0.05 *M* sodium acetate buffer and 0.1% BSA.

The RIA incubation buffer was 50 m*M* Na phosphate buffer (200 μL, pH 7.4) containing 0.5% BSA treated with N-ethylmaleimide, 80 m*M* NaCl, 25 m*M* EDTA, 0.05% NaN_3, and 0.5% Triton X-100 (Sigma). Ghrelin (1 to 10) standard (Peptides International) or diluted sample (100 μL) was incubated for 24 h with 100 μL of antighrelin antiserum (final dilution of 1:750,000). Radioiodinated ghrelin (100 μL; 10,000 to 15,000 cpm) was added, and the mixture was incubated at 4°C for 22 to 24 h. Subsequently, 100 μL of antirabbit gamma globulin (Calbiochem, San Diego, CA) diluted at 1:4 with incubation buffer and 100 μL of 0.5% normal rabbit serum (Calbiochem) were added and incubated at 4°C for 22 to 24 h. Free and bound ligands were separated by centrifugation at 2,000 × *g* at 4°C for 30 min. Supernatant was discarded, and the radioactive pellet was counted for 1 min on a Micromedic ICN gamma counter (IC, Micromedic Apex, model 28027, TitreTek, Huntsville, AL). Antiserum characterization showed excellent cross reactivity between the full human octanoyl ghrelin (1 to 28; Peptidec) and the ghrelin (1 to 10) standard. However, the antiserum does not recognize des-octanoyl ghrelin (1 to 28; Peptidec). Swine, cow, and sheep plasma showed good parallelism with respect to displacement of the ghrelin (1 to 10) standard in preliminary studies (data not shown). The ghrelin RIA has a lower detection limit of 28 pg/mL (80% binding) and a higher limit of 450 pg/mL (20% binding) with an intraassay CV of 10.9%.

Calculation of Digesta Passage Rate and Mean Retention Time

For digesta collected on d 16, Cr_2O_3 concentrations obtained at each time point were calculated from the linear relationship following first-order kinetics as described by the equation Y = a + bX, where Y is Cr_2O_3 concentration (g of Cr_2O_3/g of DM) and X is time (h). The slope (b) of the line is the rate constant (Cr_2O_3 excretion rate), which describes the rate of digesta passage. Mean retention time from mouth to ileum was determined with the concentration of Cr_2O_3, using the formula (Faichney, 1975): mean retention time = $\Sigma C_i t_i / \Sigma C_i$ (C_i is the concentration of Cr_2O_3 at time t_i). Time points for initial appearance of Cr_2O_3 in digesta and ferric oxide in feces were recorded (Entringer et al., 1975; Potkins et al., 1991).

Statistical Analyses

To compare differences in measured variables among diets, data were analyzed by ANOVA using the GLM procedures of SAS (SAS Inst., Inc., Cary, NC) as a 2 × 2 factorial arrangement. Pig was considered the experimental unit. The statistical model included main effects for guar gum and cellulose and their guar gum × cellulose interaction. Main effects were described and considered significant if $P < 0.05$. Means were reported as least squares means. Trends ($0.05 < P < 0.10$) were reported.

RESULTS

Dietary Energy, Protein, and NSP Content

The analyzed CP and GE contents did not differ among diets and ranged from 16.8 to 17.0% and from 4.23 to 4.29 Mcal/kg of DM, respectively (Table 1). The addition of guar gum increased average analyzed total, soluble, and insoluble NSP from 18.0 to 24.2%, 5.5 to 9.3%, and 12.5 to 14.8%, respectively. Also, the addition of cellulose increased average total and soluble NSP from 19.0 to 23.2% and from 5.3 to 9.6%, respectively, without a change (13.7%) in insoluble NSP (Table 1).

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Table 2. Effects of guar gum and cellulose on the passage rate and digesta characteristics in grower pigs, Exp. 1[1]

Variable	Control	Guar gum	Cellulose	Guar gum and cellulose	Pooled SEM	*P*-value: Guar gum	*P*-value: Cellulose	*P*-value: Guar gum × cellulose
Passage rate to ileum								
Passage rate, % of Cr_2O_3/h	1.37	1.01	1.12	0.64	0.09	<0.001	0.004	0.506
Mean retention time, h	4.48	4.70	4.62	4.89	0.12	0.077	0.121	0.819
Chromium appearance, h	2.15	2.39	2.33	3.17	0.24	0.931	0.931	0.002
Total tract retention time, h	24.5	28.0	24.6	27.0	0.63	<0.001	0.517	0.401
Ileal digesta characteristics								
Quantity collected, g/kg of feed DM	69.7	114.5	117.1	139.0	8.25	0.001	<0.001	0.180
Viscosity, cP	1.52	5.57	6.35	8.92	1.31	0.020	0.005	0.577
pH	6.61	6.46	6.58	6.24	0.15	0.126	0.441	0.547
Water-holding capacity, g of water/g of DM	3.26	2.67	2.45	2.39	0.18	0.097	<0.008	0.159

[1]Based on 6 pigs per treatment.

Thus, the 7% addition of guar gum increased total NSP by 6.2% with most of this increase occurring in soluble NSP, whereas the 7% addition of cellulose increased total NSP by 4.2% with all of increase occurring in soluble NSP and not insoluble NSP. These results indicate for the first time that purified cellulose might act as a soluble NSP.

Passage Rate and Digesta Characteristics

Health problems did not occur during Exp. 1; all pigs consumed their daily feed allowance and gained BW. Guar gum and cellulose decreased digesta passage rate in the small intestine by 0.42 and 0.30%/h, respectively ($P < 0.01$; Table 2) as indicated by Cr_2O_3 excretion rate in the ileum. Guar gum increased digesta retention time 0.25 h in the ileum ($P < 0.10$), but cellulose did not. Guar gum and cellulose interacted to increase the time interval for the initial appearance of Cr_2O_3 at the distal ileum ($P < 0.01$). The combined NSP delayed initial appearance by 1 h, whereas individual NSP did not affect initial appearance. Guar gum increased total-tract digesta retention time by 3 h ($P < 0.001$) as indicated by initial appearance of ferric oxide in feces; cellulose did not.

Guar gum and cellulose increased the quantity of digesta collected at the end of the ileum by 33 and 36 g/kg of feed, respectively ($P < 0.001$; Table 2). Guar gum and cellulose increased digesta viscosity in the ileum by 3.3 and 4.1 cP, respectively ($P < 0.01$). Guar gum and cellulose did not affect digesta pH in the ileum. Water-holding capacity of digesta was decreased 0.33 and 0.55 g of water/g of DM with guar gum ($P < 0.10$) and cellulose ($P < 0.01$), respectively.

Energy and Protein Digestibility

At the ileum, guar gum reduced energy digestibility by 9.4 percentage units and reduced DE content by 392 kcal/kg of DM, thereby increasing the amount of nondigested energy (GE – DE) by 25% ($P < 0.10$; Table 3). However, guar gum did not affect CP digestibility. Cellulose reduced energy digestibility by 22 percentage units, CP digestibility by 20 percentage units, and ileal DE content by 972 kcal/kg of DM, thereby increasing the amount of nondigested energy by 68% ($P < 0.01$).

For the total tract, guar gum and cellulose interacted to decrease energy and CP digestibility and DE content and to increase the amount of nondigested energy ($P < 0.001$; Table 3). Guar gum in diets without cellulose decreased energy and CP digestibility by 1.2 and 3.9 percentage units, whereas guar gum in diets with cellulose decreased energy and CP digestibility by 9.1 and 13.7 percentages units, respectively.

Plasma Glucose and Ghrelin

Guar gum did not affect plasma glucose before or 30 min after feeding (Table 4). Cellulose reduced plasma glucose by 9.5 mg/dL before feeding ($P < 0.05$). Guar gum, but not cellulose, lowered plasma glucose by 8.4 mg/dL 60 min after feeding ($P < 0.10$).

Neither the main effect of guar gum nor cellulose affected plasma ghrelin before or after feeding (Table 4). However, guar gum and cellulose interacted to alter plasma ghrelin levels before and 30 and 60 min after feeding ($P < 0.05$); guar gum and cellulose diets increased plasma ghrelin, whereas the guar gum-cellulose diet did not.

Ileal Bacteria Populations

Guar gum increased the populations of total anaerobes, total aerobes, lactobacilli, enterobacteria, and clostridia ($P < 0.05$) and bifidobacteria and enterococci ($P < 0.10$) in the ileum (Table 5). In contrast, cellulose increased populations of bifidobacteria and enterobacteria ($P < 0.05$) and total anaerobes and enterococci ($P < 0.10$), but not total aerobes, lactobacilli, and clostridia. Guar gum and cellulose interacted to increase the populations of bifidobacteria and enterobacteria in the ileum ($P < 0.05$).

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Table 3. Effects of guar gum and cellulose on the energy and protein digestibilities in grower pigs, Exp. 1[1]

Variable	Control	Guar gum	Cellulose	Guar gum and cellulose	Pooled SEM	*P*-value: Guar gum	*P*-value: Cellulose	*P*-value: Guar gum × cellulose
Ileal								
Energy digestibility, %	73.1	64.0	51.2	41.6	5.3	0.093	0.001	0.962
DE, kcal/kg of DM	3,106	2,722	2,142	1,742	223	0.095	<0.001	0.973
GE – DE, kcal/kg of DM[2]	1,145	1,533	2,039	2,447	223	0.090	0.001	0.964
CP digestibility, %	71.6	64.9	54.6	42.7	5.7	0.118	0.003	0.651
Total tract								
Energy digestibility, %	87.8	86.6	84.9	75.8	1.0	<0.001	<0.001	<0.001
DE, kcal/kg	3,734	3,685	3,548	3,174	42	<0.001	<0.014	0.009
GE – DE, kcal/kg of DM[2]	517	570	632	1,015	42	<0.001	<0.001	<0.001
CP digestibility, %	84.7	80.8	83.4	69.7	1.7	<0.001	<0.001	<0.001

[1]Based on 6 pigs per treatment.
[2]GE – DE = nondigested energy.

Performance Variables

Cellulose caused a 2.2-kg reduction in BW by d 7 ($P < 0.01$), but guar gum did not. However, by d 14, both guar gum and cellulose reduced BW by 2.3 and 2.8 kg, respectively ($P < 0.01$; Table 6). For d 0 to 7, guar gum and cellulose reduced ADG by 141 and 233 g/d, respectively ($P < 0.05$). For d 8 to 14, guar gum and cellulose interacted to decrease ADG ($P < 0.05$). For the entire experiment (d 0 to 14), guar gum and cellulose reduced ADG by 170 g/d ($P < 0.01$).

Guar gum and cellulose reduced ADFI for d 0 to 7 by 222 and 292 g/d, respectively ($P < 0.05$; Table 6). For d 8 to 14, cellulose reduced ADFI by 106 g/d ($P < 0.10$), but not guar gum. For the entire experiment (d 0 to 14), guar gum and cellulose decreased ADFI by 227 and 271 g/d, respectively ($P < 0.05$).

For d 0 to 7, cellulose tended to reduce G:F by 0.12 ($P < 0.10$; Table 6), but guar gum did not. For d 8 to 14, guar gum reduced G:F by 0.07 ($P < 0.05$), but cellulose did not. For the entire experiment (d 0 to 14), guar gum and cellulose did not affect G:F.

DISCUSSION

Understanding the effects of soluble and insoluble NSP on digestive physiology and voluntary feed intake is critical for optimal swine production. Structures and physicochemical characteristics of NSP, such as viscosity and water-holding capacity, differ widely among feed ingredients and affect the digestive processes (Bergner, 1980; Friere et al., 2000; Wenk, 2001). In the current study, guar gum and cellulose were used to simulate effects of soluble and insoluble NSP, respectively, in feed ingredients on digestive physiology, nutrient digestibility, and voluntary feed intake in grower pigs.

Purified guar gum and cellulose slowed digesta passage rate, and inversely, guar gum increased total-tract retention time in the current study. Similarly, soluble NSP present in sugar beet pulp increased digesta viscosity and delayed digestive transit in the porcine small intestine (Knudsen and Hansen, 1991), suggesting that purified soluble NSP may act in a manner similar to the soluble NSP enclosed in commodity feed ingredients

Table 4. Effects of guar gum and cellulose on plasma glucose and ghrelin in grower pigs, Exp. 1[1]

Variable	Control	Guar gum	Cellulose	Guar gum and cellulose	Pooled SEM	*P*-value: Guar gum	*P*-value: Cellulose	*P*-value: Guar gum × cellulose
Plasma glucose, mg/dL								
Before feeding	99.8	100.2	88.3	92.7	3.4	0.486	0.011	0.554
30 min after feeding	86.7	95.5	100.0	88.6	5.5	0.813	0.561	0.077
60 min after feeding	92.9	83.5	89.1	81.7	4.2	0.055	0.505	0.814
Plasma ghrelin, pg/mL								
Before feeding	185.5	238.9	250.3	168.9	22.5	0.542	0.909	0.007
30 min after feeding	173.9	242.7	228.9	162.7	25.1	0.960	0.623	0.014
60 min after feeding	148.9	217.2	199.9	147.5	24.8	0.745	0.715	0.024

[1]Based on 6 pigs per treatment.

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Table 5. Effects of guar gum and cellulose on ileal bacterial populations in grower pigs, Exp. 1[1]

Variable	Control	Guar gum	Cellulose	Guar gum and cellulose	Pooled SEM	*P*-value: Guar gum	*P*-value: Cellulose	*P*-value: Guar gum × cellulose
Ileal bacteria, $\log_{10}$ cfu/g of wet digesta								
Total anaerobes	7.87	8.12	8.00	9.02	0.27	0.031	0.073	0.175
Total aerobes	7.69	8.16	7.74	8.91	0.30	0.014	0.202	0.266
Lactobacilli	7.58	8.07	7.43	8.68	0.34	0.018	0.499	0.277
Enterococci	7.39	7.55	7.57	8.63	0.33	0.076	0.068	0.182
Bifidobacteria	7.04	7.04	7.45	8.60	0.27	0.053	<0.001	0.049
Enterobacteria	7.12	7.13	7.46	8.61	0.27	0.041	0.001	0.046
Clostridia	6.75	7.39	6.43	7.89	0.39	0.014	0.790	0.328

[1]Based on 6 pigs per treatment.

(Rainbird and Low, 1986). Bran and oatmeal by-product (insoluble NSP) increased digesta passage rates through the entire gastrointestinal tract (Latymer et al., 1985), but not guar gum and pectin (purified soluble NSP), relative to barley, indicating that effects of soluble and insoluble NSP on passage rate are not consistent among studies, but likely depend on the existence of interfering factors that may exist in nonpurified NSP sources. Thus, the use of purified NSP sources might assist to separate NSP-specific effects from ingredient-specific effects.

Guar gum and cellulose increased the quantity of nondigested digesta by the distal ileum in the current study, indicating that NSP increase gut fill because of reduced energy and protein digestibility. Therefore, reduced digestibility attributable to NSP overrides an expected marginal increase in energy and protein digestibility caused by the slower passage rate of digesta, i.e., increased contact time between nutrients and digestive enzymes. The increased digesta quantity in the distal ileum may also be the direct response of increased water binding and viscosity caused by soluble NSP (Van der Meulen and Bakker, 1991), a response that occurred for both guar gum and cellulose in the current study. The latter indicates that purified cellulose also possesses physicochemical characteristics that normally are attributed solely to soluble NSP but not insoluble NSP (Bedford and Schulze, 1998). Guar gum and cellulose did not change pH of ileal digesta in the current study, indicating that potential effects of NSP on gastric acid secretion and digesta pH (Van der Meulen and Bakker, 1991) were eliminated by the distal ileum.

In the current study, guar gum and cellulose reduced both CP and energy digestibility, which is similar to the results from other studies (Dierick et al., 1983; Fahey et al., 1990). The reduction in DE content and energy digestibility reflected the switch in purified carbohydrate sources. Purified guar gum and cellulose replaced

Table 6. Effects of guar gum and cellulose on performance variables of grower pigs, Exp. 2[1]

Variable	Control	Guar gum	Cellulose	Guar gum and cellulose	Pooled SEM	*P*-value: Guar gum	*P*-value: Cellulose	*P*-value: Guar gum × cellulose
BW, kg								
d 0	26.7	26.8	26.9	26.9	0.6	0.952	0.809	0.952
d 7	31.1	30.0	28.8	28.0	0.6	0.119	0.002	0.836
d 14	37.4	35.6	35.1	32.3	0.4	0.005	0.001	0.470
ADG, g/d								
d 0 to 7	617	463	371	243	64	0.044	<0.001	0.844
d 8 to 14	903	800	892	600	43	0.004	0.027	0.042
d 0 to 14	760	631	632	421	48	<0.001	<0.001	0.404
ADFI, g/d								
d 0 to 7	1,406	1,120	1,050	893	103	0.049	0.013	0.542
d 8 to 14	1,960	1,731	1,714	1,479	141	0.123	0.100	0.980
d 0 to 14	1,683	1,426	1,382	1,186	102	0.042	0.018	0.769
G:F								
d 0 to 7	0.440	0.420	0.375	0.250	0.056	0.219	0.056	0.367
d 8 to 14	0.480	0.460	0.525	0.400	0.033	0.045	0.823	0.133
d 0 to 14	0.440	0.460	0.450	0.375	0.030	0.396	0.253	0.153

[1]Based on 5 pigs per treatment.

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purified starch; thus, reduced CP digestibility resulted solely from negative effects of dietary NSP on protein digestion. Similarly, pectin included at either 50 (Dierick et al., 1983) or 75 g/kg (Mosenthin et al., 1994), which replaced cornstarch, decreased apparent ileal digestibility of CP and AA. Also, soluble NSP markedly increased endogenous losses of AA in chickens (Angkanaporn et al., 1994) and thereby reduced apparent energy and protein digestibility. The underlying hypothesis is that soluble, but not insoluble NSP, primarily cause the negative effects of NSP on ileal digestibility of nutrients in nonruminants by increasing digesta viscosity (Van Barneveld, 1997) and by reducing interactions between substrates and digestive enzymes (Bedford and Schulze, 1998). In contrast, results of the current study indicate a similar response for purified cellulose, suggesting that purified insoluble NSP influence energy and protein digestibility similarly as soluble NSP.

In the current study, guar gum and cellulose increased intestinal bacteria populations. Bacteria prefer specific substrates, including carbohydrates with a specific chemical structure. Therefore, feed ingredients differing in NSP that are digested at different rates (Dierick et al., 1983; Johansen et al., 1996) could promote the growth of specific bacterial populations. For example, resistant starch and soluble NSP (guar gum) altered microbial populations in weanling pigs relative to insoluble NSP (Durmic et al., 1998). Specifically, total anaerobes and *Bacteroides* spp. increased, but *Clostridium* spp., *Lactobacillus* spp., and *Enterobacteria* decreased in the colon of pigs fed resistant starch (Durmic et al., 1998). In contrast, increases in bacterial populations were similar for guar gum and cellulose in the current study, and these increases might impact intestinal health. For example, diets high in NSP and resistant starch have been associated with increased numbers of *Brachyspira hydysenteriae* and a higher incidence of clinical swine dysentery (Pluske et al., 1998). In the current study, the combination of guar gum and cellulose caused the greatest increase in bacterial populations, especially for bifidobacteria and enterobacteria.

The increased ileal microbial population caused by purified NSP in the current study might have been due to combined effects of increased digesta viscosity and reduced nutrient digestibility and might mimic changes observed in NSP content caused by the main cereal included in the diet (Drew et al., 2002). Soluble NSP increase digesta viscosity and change the physiology and ecosystem of the gut (Choct et al., 1996), thereby reducing the interaction between substrate and digestive enzymes or effective absorption of nutrients. Decreased CP and energy digestibility increase the amount of undigested protein and energy in the distal ileum, which act as substrate for the microflora. This then creates a fertile local environment for bacteria to proliferate. Moreover, a slower moving digesta with low oxygen tension provides a relatively stable environment in the small intestine, allowing the gut microflora to colonize and proliferate (Wagner and Thomas, 1978).

Soluble NSP can also affect systemic glucose concentrations caused by reduced intestinal absorption of nutrients and modified digesta transit and motility in the small intestine (Jørgensen and Just, 1988; Cherbut, 1995). Specifically, soluble NSP reduce gastric emptying, rates of starch hydrolysis, and glucose transport (Ellis et al., 1996). Thus, soluble NSP improve glucose tolerance and insulin sensitivity by reducing the glucose absorption rate (Cameron-Smith et al., 1997). In the current study, purified guar gum tended to reduce postprandial plasma glucose, which is likely related to reduced digesta flow, energy digestibility, and change in dietary carbohydrate. Similarly, oat gum and oat bran both lowered plasma glucose (Braaten et al., 1994). Consequently, NSP reduced movement of nutrients from the lumen to the mucosal epithelium, resulting in a slower or reduced intestinal absorption of energy (Ellis et al., 1996), thereby reducing plasma glucose level.

The effects of NSP on total extent and rate of nutrient digestion will be related to hormonal responses (Ellis et al., 1996). The gut secretes approximately 20 hormones or regulatory peptides that either enhance or decrease nutrient absorption (Unväs-Moberg, 1992). Feed components that affect endogenous protein secretion or gastric emptying are expected to affect hormonal secretions. Ghrelin is a 28-AA acylated peptide secreted primarily by the stomach and duodenum (Kojima et al., 1999) that has an orexigenic function with combined controls of energy expenditure, gastric motility, and acid secretion and influences endocrine pancreatic function and glucose metabolism (Kojima et al., 1999; Takahiro et al., 2001). A hypothesis for the current study was that ghrelin, a physiological mediator of feeding, is expected to function in the regulation of voluntary feed intake and digesta passage rate. Reduced feeding status of pigs has been related to a decreased serum ghrelin concentration (Salfen et al., 2003), but serum ghrelin did not change in continuously fed pigs. Guar gum and cellulose interacted to increase plasma ghrelin independently but not in combination in the current study, suggesting that soluble NSP affect gastrointestinal endocrine responses. However, increases in plasma ghrelin could not be related conclusively to a reduced digesta passage rate, and further study is needed to relate gastrointestinal endocrine responses to digestive physiology.

The short-term impact of NSP on performance variables was of specific interest, in light of the short-term negative effects of NSP on ADFI that were observed previously and could be alleviated using supplemental carbohydrase (Zijlstra et al., 2004). In the current study, guar gum and cellulose reduced ADG and ADFI during the initial 7 d of feeding a high NSP diet. The reduction in growth rate and voluntary feed intake was the direct result of increased NSP content in the diets, and increased gut fill for NSP diets would likely have overestimated the truly achieved BW gain. Therefore,

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the negative effects of NSP on energy digestibility itself (Zijlstra et al., 1999) do underestimate the overall negative effects of NSP on growth performance because DE intake is also reduced by reduced voluntary feed intake, although the pig and its microflora might adapt to high-fiber diets over a longer period. Increased dietary NSP reduced total-tract energy digestibility and voluntary feed intake and also caused a higher proportion of the energy to be digested in the large intestine (Just et al., 1983). Consequently, less energy is absorbed as monosaccharide from the small intestine, and relatively more of the energy is fermented by bacteria into and absorbed as VFA and lactic acid in the large intestine (Jørgensen et al., 1996), thereby reducing the NE content of diets further than expected based on a reduced DE content. Therefore, overall, NSP do drastically reduce the use of dietary energy by the pig in support of protein deposition via changes in energy and protein digestibility and intake.

IMPLICATIONS

Purified guar gum and cellulose were used as a model to mimic the impact of feed ingredients with a high nonstarch polysaccharide content. The results of the study indicate that high nonstarch polysaccharides negatively affected digestible energy and protein intake, increased intestinal bacterial populations, and reduced growth performance overall. The nonstarch polysaccharide content of ingredients should be monitored and managed to ensure that a predictable growth performance of grower-finished pigs is reached. Purified cellulose was used to mimic insoluble nonstarch polysaccharide, but it had similar physicochemical characteristics as guar gum, which was used to mimic soluble nonstarch polysaccharide.

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