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NON RUMINANT NUTRITION

The apparent ileal digestibility and the apparent total tract digestibility of carbohydrates and energy in hybrid rye are different from some other cereal grains when fed to growing pigs

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Abstract

An experiment was conducted to determine the apparent ileal digestibility (AID) and the apparent total tract digestibility (ATTD) of energy, starch, and total dietary fiber (TDF) in two varieties of hybrid rye and compare these values with values obtained for barley, wheat, corn, and sorghum. It was hypothesized that there are no differences in AID and ATTD of energy and nutrients among hybrid rye, barley, wheat, and sorghum. Twenty-four ileal cannulated barrows (initial body weight = 28.1 ± 3.0 kg) were randomly allotted to a two-period experimental design with six diets and four replicate pigs in each period for a total of eight replicate pigs per diet. Diets consisted of 97% of each grain, and each pig received a different diet in each period. The initial 5 d of each period were considered the adaptation period, whereas urine and fecal materials were collected from the feed provided from day 6 to 10, and ileal digesta were collected on days 12 and 13 of each period. Results indicated that the metabolizable energy (ME) on a dry matter (DM) basis was greatest (P < 0.05) in corn and wheat (3,732 and 3,641 kcal/kg DM), and least (P < 0.05) in barley (3,342 kcal/kg DM), whereas the two hybrid ryes contained 3,499 and 3,459 kcal/kg DM, respectively. The ME values in hybrid rye were not different from values determined for barley and sorghum (3,573 kcal/kg DM). In all grains, the AID of starch was greater than 90%, and the ATTD of starch was nearly 100%. Barley contained more TDF than the other cereal grains, and the two hybrid ryes had concentrations of soluble dietary fiber that were close to the concentration in barley but greater than in wheat, corn, and sorghum. The AID of TDF was less than 35% for all cereal grains, but the ATTD of TDF was greater (P < 0.05) in the two hybrid ryes (68% and 70%) than in the other ingredients (56% to 58%). In conclusion, feeding hybrid rye to pigs resulted in reduced pre-cecal absorption of energy compared with wheat, corn, and sorghum, but because hindgut fermentation of fiber was greater in hybrid rye than in other cereal grains, the content of ME in hybrid rye was not different from barley and sorghum but less than in corn and wheat.

Key words: cereal grains, energy digestibility, fiber, hybrid rye, pigs, starch

Introduction

Production of hybrid rye in North America is currently increasing, particularly in Western Canada and in the upper Midwestern United States. Due to greater yields, good overwintering ability, and improved drought tolerance, hybrid rye can be an attractive alternative to growing barley, wheat, or sorghum, especially on poor soil (Geiger and Miedaner, 2009). Hybrid rye can be used in the human food industry for

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Abbreviations

ADF	acid detergent fiber
AID	apparent ileal digestibility
ATTD	apparent total tract digestibility
DE	digestible energy
DM	dry matter
GE	gross energy
HGD	hindgut disappearance
IDF	insoluble dietary fiber
ME	metabolizable energy
NDF	neutral detergent fiber
SDF	soluble dietary fiber
TDF	total dietary fiber

baking and distilling, in biogas production, or in the feeding of livestock. However, there are currently no published values for metabolizable energy (ME) in hybrid rye when fed to pigs, and it has been demonstrated that the digestible nutrient compositions of new hybrids of rye are different from older cultivars of rye (Strang et al., 2016; McGhee and Stein, 2018). The fiber composition of hybrid rye is different from barley, wheat, corn, and sorghum (Rodehutscord et al., 2016; McGhee and Stein, 2018), but the extent of fermentation of fiber from hybrid rye in the small and large intestine of growing pigs is not well documented. Rye has greater concentrations of arabinoxylans and fructooligosaccharides than barley, wheat, corn, and sorghum, and a greater concentration of mixedlinked β -glucans than wheat, corn, and sorghum (Rodehutscord et al., 2016; McGhee and Stein, 2018). It is hypothesized that the fiber fraction in rye is fermented differently than fiber in other cereal grains, which may provide health benefits to animals (Bach Knudsen et al., 2005, 2016, 2017). However, at this time, digestion and fermentation of energy and fiber in hybrid rye fed to pigs have not been reported. Therefore, it was the objective of this experiment to determine the apparent ileal digestibility (AID) and the apparent total tract digestibility (ATTD) of starch, energy, and dietary fiber in hybrid rye and compare these values with values obtained for barley, wheat, corn, and sorghum. It was hypothesized that the digestion and fermentation of carbohydrates and other nutrients in hybrid rye will result in digestible energy (DE) and ME in hybrid rye that are not different from values obtained for barley, wheat, and sorghum. Due to an expected greater concentration of starch in corn, it was hypothesized that corn has greater DE and ME than hybrid rye.

Materials and Methods

The experiment was conducted at the Swine Research Center at the University of Illinois following a protocol that was approved by the Institutional Animal Care and Use Committee at the University of Illinois (#15196).

Animals, housing, and experimental design

Twenty-four growing barrows (initial body weight = 28.1 ± 3.0 kg) that were the offspring of PIC Line 359 boars and Camborough sows (Pig Improvement Company, Henderson, TN) were prepared with a T-cannula in the distal ileum (Stein et al., 1998). Pigs were housed individually in metabolism crates that were equipped with a self-feeder, a nipple waterer, and slatted floors to allow for the total, but separate, collection of urine and fecal materials. Throughout the experiment, pigs had free access to

water. Following a 7-d recovery period from surgery, animals were allotted to a two-period experimental design with six diets. There were four replicate pigs per diet in each period for a total of eight replicate pigs per diet. All pigs received a different diet in the second period than they received in the first period.

Two sources of hybrid rye (KWS Lochow GmbH, Bergen, Germany) and one source of barley, wheat, corn, and sorghum were ground through a hammer mill (model WA-8-H; Schutte Buffalo LLC, Buffalo, NY) with a 1.59-mm screen, and each source of grain was used in one diet (Table 1). One of the hybrids of rye was grown in Canada in 2017, but all other grains used in the experiment were grown in the United States in 2017. Vitamins and minerals were included in all diets to meet or exceed the estimated nutrient requirements for 25 to 50 kg growing pigs (NRC, 2012). Diets also contained 0.50% titanium dioxide as an indigestible marker.

Feeding and sample collection

Pigs were limit fed at 3.2 times the estimated ME requirement for maintenance (i.e., 197 kcal ME per kg body weight^{0.60}; NRC, 2012), which was provided each day in two equal meals at 0800 and 1700 hours. Values for ME in each grain were assumed to be as indicated by NRC (2012) and the value for hybrid rye was assumed to be similar to the value for conventional rve. Orts were collected daily prior to feeding the morning meal, pooled for the duration of the collection period, and weighed at the conclusion of the experiment. Feed consumption was recorded daily, and diets were fed for 13 d in each period. The initial 5 d were considered the adaptation period to the diet, whereas urine and fecal materials were collected from feed provided during the following 4 d according to the standard procedures using the marker-to-marker approach (Adeola, 2001). The start marker for the fecal collection was included in the morning meal on day 6, and the stop marker was included in the morning meal on day 10. Ileal digesta samples were collected on days 12 and 13 as previously described (Stein et al., 1998). Urine was collected in urine buckets over a preservative of 50 mL of 6N HCl. Fecal samples, orts, 20% of the collected urine, and ileal digesta were stored at -20 °C immediately after collection.

Chemical and physical analyses

At the conclusion of the experiment, urine and ileal digesta samples were thawed and mixed within animal and diet, and a subsample was lyophilized. Urine samples were filtered through a Whatman grade 4 filter paper prior to being lyophilized and analyzed, and ileal digesta samples were finely ground using a coffee grinder. Fecal samples and orts were dried in a forced-air oven, and fecal samples were ground using a 1-mm screen in a Wiley mill (model 4; Thomas Scientific, Swedesboro, NJ).

All diets, ingredients, fecal samples, and ileal digesta samples were analyzed for dry matter (DM; method 930.15; AOAC International, 2007). Diet and ingredient samples were analyzed for ash (method 942.05; AOAC International, 2007) and for crude protein (method 990.03; AOAC International, 2007) using a Leco Nitrogen Determinator (model FP628, Leco Corp., St. Joseph, MI). Ingredient samples were analyzed for acid detergent fiber (ADF) and neutral detergent fiber (NDF) with residual ash included using Ankom Technology methods 12 and 13, respectively, following pretreatment with heat-stable alpha-amylase (Ankom 2000 Fiber Analyzer, Ankom Technology, Macedon, NY). After ADF analysis, acid detergent lignin was determined using Ankom Technology method 9 (Ankom Daisy II Incubator, Ankom Technology, Macedon, NY).

Table 1.	Composition	of experimental	l diets, as-fed basis
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Item	Hybrid rye 1	Hybrid rye 2	Barley	Wheat	Corn	Sorghum
Ingredient, %						
Cereal grain	96.85	96.85	96.95	97.10	96.70	96.85
Ground limestone	1.05	1.05	0.95	1.20	0.80	1.05
Dicalcium phosphate	1.05	1.05	1.05	0.65	1.45	1.05
Titanium dioxide	0.50	0.50	0.50	0.50	0.50	0.50
Sodium chloride	0.40	0.40	0.40	0.40	0.40	0.40
Vitamin-mineral premix ¹	0.15	0.15	0.15	0.15	0.15	0.15
Analyzed composition						
DM, %	90.55	90.13	92.41	90.68	87.68	88.36
GE, kcal/kg	3,762	3,702	3,855	3,793	3,656	3,705
Crude protein, %	10.25	8.84	10.14	10.28	7.19	9.48
Ash, %	4.47	4.59	5.19	4.28	4.15	4.00
Total starch, %	50.20	51.71	50.79	54.29	56.08	60.12
Resistant starch, %	2.61	0.59	1.50	0.79	2.77	7.37
IDF, %	12.20	15.10	15.90	10.30	8.50	8.10
SDF, %	1.30	3.20	3.10	0.50	ND^2	0.70
TDF, %	13.60	18.30	19.10	10.80	8.50	8.80
Arabinose, %	2.84	3.11	1.82	1.77	1.06	0.86
Xylose, %	5.31	4.24	4.28	2.70	1.67	1.98
Fructooligosaccharides, %	9.35	9.42	5.31	2.26	1.29	0.52
β-glucan, %	3.84	4.15	4.55	2.63	2.20	0.44

¹The vitamin–micromineral premix provided the following quantities of vitamins and micro minerals per kg of complete diet: vitamin A as retinyl acetate, 11,150 IU; vitamin D_3 as cholecalciferol, 2,210 IU; vitamin E as selenium yeast, 66 IU; vitamin K as menadione nicotinamide bisulfate, 1.42 mg; thiamin as thiamine mononitrate, 1.10 mg; riboflavin, 6.59 mg; pyridoxine as pyridoxine hydrochloride, 1.00 mg; vitamin B_{12} , 0.03 mg; D-pantothenic acid as D-calcium pantothenate, 23.6 mg; niacin, 44.1 mg; folic acid, 1.59 mg; biotin, 0.44 mg; Cu, 20 mg as copper chloride; Fe, 125 mg as iron sulfate; I, 1.26 mg as ethylenediamine dihydriodide; Mn, 60.2 mg as manganese hydroxychloride; Se, 0.30 mg as sodium selenite and selenium yeast; and Zn, 125.1 mg as zinc hydroxychloride. ²ND, not detected.

Diet, ingredient, ileal digesta, and fecal samples were analyzed for insoluble dietary fiber (IDF) and soluble dietary fiber (SDF) on an Ankom Total Dietary Fiber Analyzer (Ankom Technology, Macedon, NY) using method 991.43 (AOAC International, 2007). Total dietary fiber (TDF) was calculated as the sum of IDF and SDF. The gross energy (GE) in diets, ingredients, fecal samples, urine samples, and ileal digesta samples were measured using an isoperibol bomb calorimeter (model 6400, Parr Instruments, Moline, IL) with benzoic acid used as the standard for calibration. Urine was dripped onto cotton balls and prepared for GE analysis as previously described (Kim et al., 2009). Ingredient samples were analyzed for total acid-hydrolyzed ether extract by acid hydrolysis using 3N HCl (Ankom^{HCl}, Ankom Technology, Macedon, NY) prior to fat extraction with petroleum ether (Ankom^{XT15}, Ankom Technology, Macedon, NY). Ingredients were also analyzed for amino acids on a Hitachi Amino Acid Analyzer, Model No. L8800 (Hitachi High Technologies America, Inc; Pleasanton, CA) using ninhydrin for post-column derivatization and norleucine as the internal standard. Prior to analysis, samples were hydrolyzed with 6N HCl for 24 h at 110 °C (method 982.30 E[a]; AOAC International, 2007). Methionine and Cys were determined as Met sulfone and cysteic acid after cold performic acid oxidation overnight before hydrolysis (method 982.30 E[b]; AOAC International, 2007). Tryptophan was determined after NaOH hydrolysis for 22 h at 110 °C (method 982.30 E[c]; AOAC International, 2007). The titanium dioxide concentration was determined in diets and ileal digesta samples following the procedure by Myers et al. (2004).

The concentration of total starch in diets, ingredients, ileal digesta, and fecal samples was analyzed by the glucoamylase procedure (method 76-13; AACC., 2007), which

yields the enzymatically hydrolyzed starch in the samples. The concentration of resistant starch in diet samples was also determined (method 2002.02; AOAC International, 2002) using a commercial enzyme kit (K-RSTAR; Megazyme Int., Bray, Ireland). The concentration of mixed-linked β -glucans in diet samples was analyzed using a commercial enzyme kit (K-BGLU; Megazyme Int., Bray, Ireland). Hydrolyzed arabinose and xylose concentrations were determined by high-performance liquid chromatography following the procedure by Bourquin et al. (1990) and Hoebler et al. (1989) and corrected for free arabinose and xylose, which were determined following the procedure by Smiricky et al. (2002). The concentration of fructooligosaccharides was determined using a two-step procedure described by Call et al. (2018). In the first step, free extractable sugars (glucose, fructose, sucrose, and raffinose) were analyzed by high-pressure ion chromatography. In the second step, samples were hydrolyzed using 3N trifluoroacetic acid prior to analysis. The concentration of fructooligosaccharides was calculated by correcting the hydrolyzed fructose concentration for the concentration of free/extractable sugars and calculated fructose equivalents of hydrolyzed raffinose and sucrose. Therefore, values for fructooligosaccharides include both short-chain and long-chain fructooligosaccharides. Mycotoxin analysis on all cereal grains was performed at Trilogy Analytical Laboratories (Washington, MO) using liquid chromatography-tandem mass spectroscopy. The concentration of ergot alkaloids was determined by refractive index high-performance liquid chromatography using Phenomenex Strata-X-CW (Phenomenex, Inc., Torrance, CA) weak cation exchange and reversed-phase column. The particle size of ground ingredients was analyzed with a Ro-Tap Sieve Shaker (W.S. Tyler, Mentor, OH) with 13 sieves of sieve

opening sizes 53 to 3,360 µm (procedure S319.4, ANSI/ASAE, 2008).

Calculations and statistical analyses

The DE and ME in diets were calculated by subtracting the GE in the feces and the GE in the feces and urine, respectively, from the GE in the diet (NRC, 2012). The DE and ME in the ingredients were calculated by dividing the DE and ME in the diets by the ingredient inclusion rate, which was approximately 97% in all diets. The ATTD of DM, GE, starch, and TDF was calculated for each diet using the following equation (Adeola, 2001):

$$\text{ATTD}_{\text{nutrient}}, \ \% \ = \left(\frac{\text{Nutrient}_{\text{intake}} - \text{Nutrient}_{\text{feces}}}{\text{Nutrient}_{\text{intake}}}\right) \times 100$$

The AID of DM, GE, starch, and TDF was calculated for each diet using the following equation (Stein et al., 2007):

$$AID_{nutrient}, \ \% \ = 100 - \left[\left(\frac{Nutrient_{digesta}}{Nutrient_{feed}} \right) \times \left(\frac{Ti_{feed}}{Ti_{digesta}} \right) \right] \times 100$$

Hindgut disappearance (HGD) of DM, GE, starch, and TDF was calculated using the following equation (Högberg and Lindberg, 2004):

HGD_{nutrient},
$$\% = ATTD_{nutrient}$$
, $\% - AID_{nutrient}$, $\%$

Data were analyzed using the MIXED procedure of SAS (SAS Institute Inc., Cary, NC). The pig was the experimental unit for all analyses. An outlier was defined as an observation with a studentized residual of greater than 3 or less than -3 and was subsequently removed from further statistical analysis. One extreme outlier from the sorghum treatment group was detected and removed from all variable analyses. An additional replicate was removed from the sorghum treatment for the variables ATTD of TDF and HGD of TDF. Thus, statistical analyses for ATTD and HGD of TDF were conducted using six replicates for the sorghum treatment and eight replicates for all other treatments. Statistical analyses for all other variables were conducted using seven replicates from the sorghum treatment and eight replicates from the hybrid rye, barley, wheat, and corn treatments. PROC UNIVARIATE and PROC GPLOT were used to check model assumptions. The statistical model in PROC MIXED included source of grain as the fixed effect and pig and period as random effects. The model was fitted with the restricted maximum likelihood method and the degrees of freedom were estimated using the Kenward-Rogers approach. Least squares means were estimated and separated using the PDIFF statement with Tukey-Kramer adjustment in PROC MIXED. Results were considered significant at P \leq 0.05 and considered a trend at P ≤ 0.10.

Results

Nutrient compositions of diets were in agreement with formulated values. GE in hybrid rye was 3,866 and 3,837 kcal/kg in each source, respectively, and ranged among ingredients from 3,824 kcal/kg in corn to 3,974 kcal/kg in barley (Table 2). One source of rye contained 56.56% starch, and the other source contained 54.90%. The concentration of TDF in barley was 19.0% and the two sources of hybrid rye contained 15.2% and 18.1% TDF, respectively, whereas wheat, corn, and sorghum contained less than 12% TDF. The mean particle size of the grains ranged from

222 to 431 μ m with the two hybrid ryes having average particle sizes of 309 and 313 μ m, respectively (Table 3). The second source of hybrid rye, as well as barley and corn, contained 0.9, 0.2, and 0.1 mg/kg deoxynivalenol, respectively, and corn also contained 0.3 μ g/kg of fumonisin B1 and 28.9 μ g/kg zearalenone (Table 4). The two hybrid ryes contained 0.22 and 0.08 mg/kg ergot alkaloids, whereas the other ingredients had concentrations of ergot alkaloids below the detectable limit of 10 μ g/kg.

All pigs recovered from surgery without complications and consumed their diets throughout the experiment without apparent problems. Total orts during the collection period ranged from 0.21 to 2.35 kg, with a mean of 1.00 ± 0.61 kg. Pigs fed the two sources of hybrid rye consumed 4,535 and 4,973 kcal GE/d, respectively, which was less (P < 0.05) than consumed daily by pigs fed barley, but not different from what was consumed by pigs fed wheat or corn (Table 5). The GE in feces was greatest (P < 0.05) for barley (1,111 kcal/d) and least for corn (468 kcal/d), whereas the GE in feces from each hybrid of rye was 668 and 773 kcal/d, respectively. The GE in urine was not different among cereal grains and ranged from 130 to 185 kcal/d. The AID of GE was greater (P < 0.05) in wheat, corn, and sorghum than in hybrid rye and barley. The ATTD of GE was greater (P < 0.05) in corn than in all other grains except wheat. There were no differences in the ATTD of GE between the two hybrids of rye and sorghum; however, the ATTD of GE was less (P < 0.05) in barley than in all other cereal grains and hybrid rye 1 did not differ from sorghum. The HGD of GE was greater (P < 0.05) in one source of hybrid rye than in barley, wheat, corn, and sorghum, but the second source of hybrid rye did not differ from barley, wheat, or corn.

On a DM basis, concentrations of DE and ME were greater (P < 0.05) in corn and wheat than in hybrid rye and barley. The DE in sorghum was less (P < 0.05) than in corn but not different from the DE in wheat and one of the sources of hybrid rye. The ME in sorghum was also less (P < 0.01) than in corn, but not different from wheat or the two hybrid ryes. The DE in barley was less (P < 0.05) than in all other ingredients, and the ME in barley was less (P < 0.05) than in all cereal grains except in one source of hybrid rye. The AID of DM was greater (P < 0.05) in wheat, corn, and sorghum than in the two hybrids of rye and barley (Table 6). The AID of starch was greater than 90% in all cereal grains, with wheat having greater (P < 0.05) AID of starch than one source of hybrid rye. The AID of TDF was less than 35% in all grains, but the AID of TDF in one hybrid of rye was less (P < 0.05) than in all other grains. The AID of arabinose ranged from 16.9% in corn to 48.3% in sorghum. There was also a tendency (P < 0.10) for sorghum to have greater AID of xylose compared with other grains.

The ATTD of DM in hybrid rye was intermediate (P < 0.05) between corn and barley, and did not differ from wheat or sorghum, but barley had ATTD of DM that was (P < 0.05) less than in all other grains. The ATTD of starch was nearly 100% for all grains, but the ATTD of starch was greater (P < 0.05) in corn than in barley. The ATTD of TDF was greater (P < 0.05) in the two hybrids of rye than in the other grains, with digestibility values of 68.3% and 70.8%. The ATTD of TDF in the other grains ranged from 56.1% in barley to 58.2% in wheat. Corn had reduced (P < 0.05) ATTD of arabinose and xylose compared with hybrid rye, and hybrid rye had greater (P < 0.05) ATTD of arabinose than wheat and corn, and greater (P < 0.05) ATTD of xylose than barley and corn.

The HGD of DM was greater (P < 0.05) in one source of hybrid rye than in all other cereal grains. One source of hybrid rye, which had reduced (P < 0.05) AID of starch compared with wheat, had greater (P < 0.05) HGD of starch than wheat; however,

Table 2. Analyzed composition of two sources of hybrid rye, barley, wheat, corn, and sorghum, as-fed basis

Item	Hybrid rye 1	Hybrid rye 2	Barley	Wheat	Corn	Sorghum
DM, %	90.09	90.32	92.62	89.98	87.72	88.03
GE, kcal/kg	3,866	3,837	3,974	3,870	3,824	3,844
Crude protein, %	10.81	9.25	10.56	10.06	7.62	9.44
Ash, %	1.42	1.70	2.55	1.67	1.35	1.19
Acid-hydrolyzed ether extract, %	1.28	1.21	2.16	1.87	3.11	2.83
Total starch, %	56.56	54.90	51.74	57.07	57.98	62.30
ADF ¹ , %	2.58	3.49	5.78	2.79	2.31	3.40
NDF ¹ , %	17.38	17.94	19.75	10.74	8.80	9.10
Acid detergent lignin, %	0.81	1.05	1.05	0.74	0.34	0.64
IDF, %	13.5	15.4	16.5	10.6	10.3	7.9
SDF, %	1.7	2.7	2.5	0.8	ND^2	0.1
TDF, %	15.2	18.1	19.0	11.3	10.3	8.0
Indispensable amino acids, %						
Arg	0.51	0.45	0.51	0.51	0.36	0.30
His	0.23	0.20	0.23	0.23	0.21	0.18
Ile	0.39	0.32	0.39	0.36	0.27	0.34
Leu	0.66	0.55	0.70	0.67	0.84	1.06
Lys	0.41	0.37	0.43	0.37	0.28	0.21
Met	0.17	0.16	0.16	0.16	0.14	0.13
Phe	0.49	0.38	0.51	0.44	0.36	0.42
Thr	0.34	0.31	0.33	0.30	0.27	0.26
Trp	0.09	0.10	0.10	0.11	0.06	0.07
Val	0.50	0.42	0.53	0.45	0.36	0.40
Total	3.79	3.26	3.89	3.60	3.15	3.37
Dispensable amino acids, %						
Ala	0.44	0.40	0.48	0.39	0.54	0.74
Asp	0.70	0.65	0.65	0.57	0.52	0.54
Cys	0.25	0.23	0.24	0.26	0.17	0.16
Glu	2.53	1.85	2.46	2.59	1.30	1.64
Gly	0.46	0.41	0.43	0.44	0.31	0.27
Pro	1.01	0.71	1.04	0.86	0.65	0.66
Ser	0.41	0.34	0.39	0.41	0.33	0.34
Tyr	0.21	0.19	0.26	0.26	0.22	0.24
Total	6.01	4.78	5.95	5.78	4.04	4.59
Total amino acids, %	9.99	8.23	10.03	9.56	7.39	8.13

 $^1\mathrm{ADF}$ and NDF included residual ash. NDF was measured after pretreatment with heat-stable alpha-amylase. $^2\mathrm{ND}$, not detected.

Table 3. Particle size of two sources of hybrid rye, barley, wheat, corn, and sorghum

Item	Hybrid rye 1	Hybrid rye 2	Barley	Wheat	Corn	Sorghum
Particle size mean, µm	309	313	310	222	274	431
Particle size SD, µm	3.46	3.48	2.96	3.12	2.76	2.90
Surface area, cm²/g	317.5	316.1	264.2	391.0	278.3	186.1
Distribution of particles, %						
Sieve opening, µm						
3,360	0.00	0.05	0.06	0.02	0.00	0.01
2,380	0.01	0.03	0.02	0.02	0.00	0.00
1,680	0.10	0.12	0.15	0.07	0.07	0.18
1,191	7.22	9.09	4.65	2.09	3.85	9.42
841	21.75	21.45	13.98	9.61	11.06	26.89
595	16.52	13.90	16.56	14.57	14.45	19.18
420	8.83	8.91	14.07	12.20	12.57	9.25
297	6.17	7.13	11.17	9.73	9.68	5.51
210	4.87	5.43	8.52	7.89	8.09	4.18
149	3.95	3.98	5.93	6.21	7.80	3.60
105	2.99	2.73	3.79	5.00	8.62	5.26
74	2.12	1.87	2.47	3.80	8.95	5.58
53	1.70	1.47	1.91	3.21	8.75	2.93
44	23.76	23.85	16.72	25.59	6.12	8.00

Toxin	Hybrid rye 1	Hybrid rye 2	Barley	Wheat	Corn	Sorghum
Deoxynivalenol, mg/kg	ND^2	0.9	0.2	ND	0.1	ND
Fumonisin B1, µg/kg	ND	ND	ND	ND	0.3	ND
Zearalenone, µg/kg	ND	ND	ND	ND	28.9	ND
Ergot, μg/kg	215.5	75.4	ND	ND	ND	ND

Table 4. Mycotoxin concentrations in two sources of hybrid rye, barley, wheat, corn, and sorghum, as-fed basis¹

¹Concentrations of the following mycotoxins were below detectable limits in all cereal grains, unless specified in the table: aflatoxin B1 (1 μ g/kg), aflatoxin B2 (1 μ g/kg), aflatoxin G1 (1 μ g/kg), aflatoxin G2 (1 μ g/kg), deoxynivalenol (0.1 mg/kg), fumonisin B1 (1 μ g/kg), fumonisin B2 (1 μ g/kg), fumonisin B3 (1 μ g/kg), aflatoxin G1 (1 μ g/kg), ochratoxin A (1 μ g/kg), 3-acetyl deoxynivalenol (0.1 mg/kg), 15-Acetyl deoxynivalenol (0.1 mg/kg), transition (0.1 mg/kg), not mg/kg), not mg/kg), not mg/kg), mosolaniol (0.1 mg/kg), diacetoxyscirpenol (0.1 mg/kg), HT-2 toxin (5 μ g/kg), T-2 toxin (5 μ g/kg), and ergot alkaloids (10 μ g/kg).

Table 5. AID, ATTD, and HGD of GE and concentration of DE, ME, and net energy in two sources of hybrid rye, and in barley, wheat, corn, and sorghum

Item	Hybrid rye 1	Hybrid rye 2	Barley	Wheat	Corn	Sorghum	SE	P-value
GE intake, kcal/d	4,535 ^{bc}	4,973 ^b	5,773ª	4,826 ^b	4,460 ^{bc}	4,060°	213.34	<0.001
GE in feces, kcal/d	668 ^{bc}	773 ^b	1,111ª	626 ^{bc}	468 ^d	565 ^{cd}	47.58	< 0.001
GE in urine, kcal/d	185	146	155	161	130	151	17.78	0.339
AID of GE, %	58.1 ^b	65.4 ^b	65.6 ^b	74.3ª	76.5ª	77.4ª	2.02	< 0.001
ATTD of GE, %	85.4 ^{bc}	84.7°	80.7 ^d	87.4 ^{ab}	89.5ª	86.0 ^{bc}	0.64	< 0.001
HGD of GE, %	27.0ª	19.6 ^{ab}	15.1 ^{bc}	13.2 ^{bc}	13.0 ^{bc}	8.6°	2.02	< 0.001
DE, kcal/kg DM	3,682 ^{cd}	3,583 ^d	3,464°	3,796 ^{ab}	3,858ª	3,738 ^{bc}	27.40	< 0.001
ME, kcal/kg DM	3,499°	3,459 ^{cd}	3,342 ^d	3,641 ^{ab}	3,732ª	3,573 ^{bc}	35.89	<0.001

^{a-d}Means within a row without a common superscript differ (P < 0.05).

there were no differences among the other grains. One source of hybrid rye also had greater (P < 0.05) HGD of TDF than all other grains, but there were no differences in HGD of TDF among the second source of hybrid rye and barley, wheat, and corn. The HGD of arabinose in sorghum was less (P < 0.05) than in one hybrid of rye, but the HGD of xylose did not differ among grains.

Discussion

Concentrations of starch and GE in each of the cereal grains were within expected ranges (NRC, 2012; Cervantes-Pahm et al., 2013; Evonik Industries, 2016; Rodehutscord et al., 2016; Rostagno et al., 2017), although some variation was observed. The concentration of crude protein in both hybrid ryes was less than previously reported for older cultivars of rye (NRC, 2012), but very close to published values for hybrid rye (Strang et al., 2016; McGhee and Stein, 2018). The concentration of TDF differed slightly from some reported values (NRC, 2012; Cervantes-Pahm et al., 2013; Lærke et al., 2015; Strang et al., 2016; McGhee and Stein, 2018). For example, the TDF in sorghum is reported to be 4.93% and starch is reported to be 70.05% (NRC, 2012); however, in the present experiment, and in other publications (Cervantes-Pahm et al., 2013; McGhee and Stein, 2018), the concentration of TDF in sorghum was 8% to 9% and starch was 62% to 67%. Likewise, reported concentrations of dietary fiber in rye range from 11% to 20%, so it is likely that the concentration of TDF and starch differs among conventional rye (Bach Knudsen, 1997; Salmenkallio-Marttila and Hovinen, 2005; Cervantes-Pahm et al., 2013) and hybrid rye cultivars (Strang et al., 2016; McGhee and Stein, 2018).

The analyzed concentrations of fructooligosaccharides are greater than previously reported (McGhee and Stein, 2018), but this is likely due to the different analytical methods used. In the present experiment, the concentration of

fructooligosaccharides was determined by measuring acidhydrolyzed fructose monomers and correcting for free fructose, sucrose, and raffinose, whereas in the previous experiment, the concentration of three specific inulin-type short-chain fructooligosaccharides containing 2, 3, or 4 fructose molecules was determined by high-performance liquid chromatography. Because fructooligosaccharides vary in chain length, the method used in the present experiment is more likely to include fructooligosaccharides of all chain lengths, whereas the method used previously likely underestimated the total concentration of fructooligosaccharides in cereal grains. Although fructooligosaccharides are considered highly fermentable and may have prebiotic effects in the hindgut of animals (Karppinen et al., 2003; Bouhnik et al., 2007; Zhao et al., 2013), they are largely excluded from AOAC method 991.43 dietary fiber analysis (McCleary et al., 2012) and, therefore, are not reflected in the fiber digestibility values that were calculated.

Mycotoxin analyses were conducted to identify potential confounding factors that may influence feed intake, digestibility, or health of pigs. There were no indications of mycotoxin toxicity in pigs and analyses confirmed that all grains had mycotoxin concentrations below recommended upper limits for pig feed (e.g., 1 mg/kg deoxynivalenol (FDA, 2010), 10 mg/kg fumonisin (FDA, 2001), and 0.1 mg/kg zearalenone (European Union, 2006). The concentration of ergot was also well below the 4 to 6 mg/kg threshold for ergot alkaloids in swine feed (Coufal-Majewski et al., 2016).

The AID of starch in all cereal grains was in agreement with published data (Cervantes-Pahm et al., 2013; Lærke et al., 2015; Rojas and Stein, 2015), with the exception that the AID of starch in wheat was somewhat greater than reported by Rosenfelder-Kuon et al. (2017). The observation that the AID of starch was greater than 90% in all grains used in the present experiment is likely due to the small particle size of the ingredients, as

Item	Hybrid rye 1	Hybrid rye 2	Barley	Wheat	Corn	Sorghum	SE	P-value
AID, %								
DM	59.5°	66.9 ^b	65.2 ^{bc}	75.0ª	76.4ª	75.4ª	1.70	< 0.001
Starch	91.2 ^b	95.9 ^{ab}	94.4 ^{ab}	97.8ª	95.2 ^{ab}	95.8 ^{ab}	1.47	< 0.001
TDF	-5.7 ^d	28.8 ^{ab}	20.9 ^{abc}	11.8°	13.6 ^{bc}	33.6ª	4.43	< 0.001
Arabinose	25.4 ^b	34.7 ^{ab}	35.7 ^{ab}	24.3 ^b	16.9 ^b	48.3ª	7.85	0.001
Xylose	49.7	39.5	48.2	39.3	31.5	69.3	10.23	0.072
ATTD, %								
DM	87.6 ^b	86.8 ^b	82.5°	88.7 ^{ab}	90.2ª	87.8 ^b	0.49	0.001
Starch	99.0 ^{ab}	99.1 ^{ab}	98.8 ^b	99.3 ^{ab}	99.5ª	99.2 ^{ab}	0.15	0.044
TDF	68.3ª	70.8ª	56.1 ^b	58.2 ^b	57.9 ^b	58.0 ^b	1.74	< 0.001
Arabinose	70.2ª	66.4ª	64.2 ^{ab}	53.2 ^{bc}	51.8°	61.3 ^{abc}	4.17	< 0.001
Xylose	75.2ª	68.9ª	55.3 ^{bc}	63.7 ^{ab}	46.4°	68.8ª	4.97	< 0.001
HGD, %								
DM	27.9ª	20.4 ^b	17.2 ^{bc}	13.9 ^{bc}	13.8 ^{bc}	12.2°	1.79	< 0.001
Starch	7.9ª	3.3 ^{ab}	4.4 ^{ab}	1.5 ^b	4.2 ^{ab}	3.4 ^{ab}	1.47	0.028
TDF	73.3ª	42.1 ^{bc}	35.7 ^{bc}	46.6 ^b	45.5 ^b	25.5°	5.98	< 0.001
Arabinose	39.5ª	25.9 ^{ab}	22.9 ^{ab}	23.2 ^{ab}	29.0 ^{ab}	7.3 ^b	8.37	0.007
Xylose	20.5	24.2	2.0	19.3	9.6	-5.6	14.88	0.218

Table 6. AID, ATTD, and HGD of DM and carbohydrates in two sources of hybrid rye and in barley, wheat, corn, and sorghum

^{a-c}Means in a row without a common superscript differ (P < 0.05).

reducing the particle size of cereal grains increases the AID of starch (Rojas and Stein, 2015). The AID of starch in rye and wheat is sometimes reported to be nearly 100% in pigs fed rye or wheat bread, but baking increases starch gelatinization, and therefore also increases the speed and extent of starch digestion compared with raw cereal-based diets (Cummings and Englyst, 1995; Bach Knudsen et al., 2005; Le Gall et al., 2010). Thus, the physical form and particle size of cereal grains should be taken into consideration when comparing starch digestibility values among publications.

The structure of starch in rye differs from wheat, which may result in slower hydrolysis and reduced AID of starch (Juntunen et al., 2003; Bach Knudsen et al., 2005; Le Gall et al., 2010), although the AID of starch was only markedly reduced in one hybrid of rye. The reduced AID of starch observed in one hybrid of rye compared with wheat may be due to increased intestinal viscosity (Bach Knudsen et al., 2005; Le Gall et al., 2010; Lærke et al., 2015). In rye, high extract viscosity is a primary breeding goal because it improves bread-baking quality, but it may have negative consequences on the digestibility of nutrients (Jürgens et al., 2012). Increased viscosity from fiber can increase waterbinding capacity and reduce digesta passage rate, endogenous enzyme efficacy, and glucose absorption, although the effects are more pronounced in poultry than in pigs (Antoniou et al., 1981; Lærke et al., 2008; Le Gall et al., 2009; Jürgens et al., 2012; Zuber et al., 2016). If intestinal viscosity is not the main reason for reduced digestion of starch in the rye, it may be due to arabinoxylans resisting degradation in the small intestine, which may reduce the digestion of starch by blocking enzyme accessibility to starch and other nutrients (Le Gall et al., 2009, 2010; Kasprzak et al., 2012).

The concentrations of arabinoxylans, mixed-linked β -glucans, and total non-starch polysaccharides are negatively correlated with AID of starch in rye (Rosenfelder-Kuon et al., 2017), but in the present experiment, the hybrid of rye with the lower AID of starch also had reduced concentrations of arabinoxylans, mixed-linked β -glucans, and TDF. Crystallinity of starch, amylose to amylopectin ratio, and granule size may also influence starch digestibility (Rosenfelder-Kuon et al., 2017). The analyzed concentration of resistant starch was greater

in the hybrid with reduced AID of starch, which indicates that the composition of the starch itself had more impact on starch digestibility than non-starch components of the grain. Differences in starch composition and digestibility exist among genotypes of the same species (Singh et al., 2010; Rodehutscord et al., 2016; Rosenfelder-Kuon et al., 2017), and the same is true among sources of the same genotype grown under different environmental conditions (Copeland et al., 2009). The hybrids of rye used in this experiment were of different genotypes and were grown geographically far from each other (Western Canada and New York), so it is not possible to discern if genotype or environment is more responsible for the observed differences in composition and digestibility of starch.

Soluble fiber content, structure of arabinoxylans, formation of cross-linkages between fiber and other macromolecules, and extract viscosity are all influenced by growing and harvesting conditions, as well as the genotype of the plant (Drews and Seibel, 1976; Bengtsson et al., 1992; Ragaee et al., 2001; Hansen et al., 2003; Jürgens et al., 2012; Laidig et al., 2017). The fiber structure and fermentability depend on the location in the grain because fiber from the endosperm is more fermentable than fiber from the pericarp or testa (Glitsø et al., 1999). If the chemical composition of fiber and/or gross structure of the grain varied greatly between the two hybrids of rye used in the present experiment, these factors may explain the differences observed for AID of DM and TDF between the two hybrids of rye (Bach Knudsen et al., 2005; Le Gall et al., 2009). The disappearance of fiber prior to the cecum may be due to the partial degradation of arabinoxylans and β -glucans and subsequent absorption or fermentation of glucose, arabinose, and xylose. However, absorbed xylose and arabinose have limited energetic value because they will mostly be excreted in the urine (Schutte et al., 1991; Yule and Fuller, 1992; Huntley and Patience, 2018a, 2018b; Abelilla and Stein, 2019). Therefore, even though the AID of TDF and arabinose was greater in sorghum and one source of hybrid rye than in other grains, pre-cecal degradation of fiber does not necessarily result in increased energy for the pig (Abelilla and Stein, 2019).

Although microbial fermentation occurs throughout the gastrointestinal tract, most microbial fermentation of TDF and

subsequent short-chain fatty acid synthesis occurs in the cecum and colon, so ATTD, rather than AID, of TDF is a more meaningful estimation of fiber fermentation (Jensen and Jørgensen, 1994; Jaworski and Stein, 2017). The greater ATTD of TDF in hybrid rye than in the other grains, the greater ATTD of arabinose in hybrid rye than in wheat and corn, and the greater ATTD of xylose in hybrid rye than in barley and corn indicate that more microbial fermentation of fiber occurred in pigs fed rye. The arabinoxylans in rye are generally more soluble and fermentable than the arabinoxylans in other cereal grains due to their structure (Karppinen, 2003; Le Gall et al., 2009, 2010), and rye and barley contain considerable amounts of fermentable mixed-linked β-glucans (Bach Knudsen and Hansen, 1991; Bach Knudsen, 1997; Rodehutscord et al., 2016). Furthermore, the AID of DM was less in one source of hybrid rye than in wheat, corn, and sorghum; hence, more substrate was available to microbes in the large intestine. Therefore, the fermentability of rye fiber, in combination with greater amounts of unabsorbed material entering the hindgut, explains why the HGD of DM, starch, and TDF was greater in one hybrid of rye than most of the other cereal grains.

Dietary fiber in rye primarily consists of arabinoxylans, fructooligosaccharides, mixed-linked β -glucans, and cellulose, and fermentation of rye fiber results in increased synthesis of butyrate, a preferred source of energy for colonocytes and a promoter of gut health (Glitsø et al., 1998; Bach Knudsen et al., 2005; Le Gall et al., 2009). In the present experiment, not only was a greater proportion of fiber in hybrid rye degraded (as evidence by the greater ATTD of TDF than in all other grains), but hybrid rye also contained more TDF than wheat, sorghum, and corn, so the total amount of fiber fermented was greater as well. In contrast, barley had the greatest amount of TDF, but a lower ATTD of DM and TDF than hybrid rye, so when pigs were fed barley, more fiber was excreted in the feces than if pigs were fed rye.

On a DM basis, the values obtained for the DE and ME in hybrid rye were within 100 kcal/kg of most previously published values for rye, and the same was true for barley (NRC, 2012; Evonik Industries, 2016; Rostagno et al., 2017). The reason the AID of GE, ATTD of GE, and ME are greater in corn and wheat than in one hybrid of rye and in barley is likely that corn and wheat contain more starch and less fiber, and starch provides more energy to the animal than fiber. Microbial fermentation of fiber results in the synthesis and absorption of short-chain fatty acids; however, endogenous enzymatic digestion of starch is more efficient and yields more energy than fiber fermentation (Nelson and Cox, 2004). Fiber may also form cross-linkages with cell wall proteins or interfere with bile acid formation and thereby reduce the digestibility of amino acids and lipids, and consequently GE as well (Bach Knudsen et al., 2005; Le Gall et al., 2009; Urriola et al., 2013). Barley and rye contain more TDF than the other cereal grains, but only limited fermentation of fiber occurs in the small intestine (Jensen and Jørgensen, 1994; Nitrayová et al., 2009; Lærke et al., 2015). Therefore, when barley or rye is fed to pigs, more fiber, as well as more endogenous material (Cunningham et al., 1962; Souffrant, 2001; Cervantes-Pahm et al., 2014; Montoya et al., 2015; Agyekum and Nyachoti, 2017), will exit the small intestine, thus increasing the analyzed GE in ileal digesta and reducing the AID of GE. Although the AID of GE was markedly reduced in barley and rye compared with wheat, corn, and sorghum, the HGD of GE was greater in one of the rye hybrids than in barley, wheat, corn, and sorghum, and this is the reason there was no difference in the ATTD of GE among the hybrid of rye and wheat and sorghum. The greater HGD of GE that occurred in hybrid rye as a result of microbial

fiber fermentation partially compensated for the reduced prececal energy digestibility, and thus, the ME in hybrid rye was not different from sorghum or barley.

Conclusions

The ME for hybrid rye did not differ from published values for conventional rye. Inclusion of hybrid rye in diets for pigs results in reduced pre-cecal absorption of energy compared with wheat, corn, and sorghum, but hindgut fermentation of fiber is greater in rye than in other cereal grains. The greater HGD of DM, starch, TDF, and GE in hybrid rye than in other grains demonstrates that a greater proportion of the energy from rye is obtained from hindgut fermentation when pigs are fed hybrid rye compared with other grains. Overall, feeding hybrid rye will provide ME that is not different from that provided by barley or sorghum, but less than by wheat and corn, so diets should be formulated accordingly to account for the different amounts of energy contributed by different cereal grains.

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Conflict of interest statement

The authors declare that they have no conflicts of interest.

Literature Cited

- Abelilla, J. J., and H. H. Stein. 2019. Fate of pentoses in the small intestine and hindgut of growing pigs. J. Anim. Sci. 97(Suppl. 2):95. (Abstr.) doi:10.1093/jas/skz122.171
- Adeola, O. 2001. Digestion and balance techniques in pigs. In Lewis, A. J., and L. L. Southern, editors. *Swine Nutrition*. 2nd ed. New York (NY): CRC Press; p. 903–916.
- Agyekum, A. K., and C. M. Nyachoti. 2017. Nutritional and metabolic consequences of feeding high-fiber diets to swine: a review. Eng. 3:716–725. doi:10.1016/J.ENG.2017.03.010
- ANSI/ASAE. 2008. R2012. Method of determining and expressing fineness of feed materials by sieving. St. Joseph (MI): American Society of Agricultural and Biological Engineers.
- Antoniou, T., R. R. Marquardt, and P. E. Cansfield. 1981. Isolation, partial characterization, and antinutritional activity of a factor (pentosans) in rye grain. J. Agric. Food Chem. **29**:1240– 1247. doi:10.1021/jf00108a035
- AOAC International. 2002. Official methods of analysis. 17th ed. Gaithersburg (MD): Association of Official Analytical Chemists.
- AOAC International. 2007. Official methods of analysis. 18th ed. Gaithersburg (MD): Association of Official Analytical Chemists.
- Bach Knudsen, K. E. 1997. Carbohydrate and lignin contents of plant materials used in animal feeding. Anim. Feed Sci. Technol. 67:319–338. doi:10.1016/S0377-8401(97)00009-6
- Bach Knudsen, K. E., and I. Hansen. 1991. Gastrointestinal implications in pigs of wheat and oat fractions. Br. J. Nutr. 65:217–232. doi:10.1079/BJN19910082
- Bach Knudsen, K. E., H. Jørgensen, and P. K. Theil. 2016. Changes in short-chain fatty acid plasma profile incurred by dietary fiber composition. J. Anim. Sci. 94:476–479. doi:10.2527/ jas.2015–9786
- Bach Knudsen, K. E., N. P. Nørskov, A. K. Bolvig, M. S. Hedemann, and H. N. Lærke. 2017. Dietary fibers and associated phytochemicals in cereals. Mol. Nutr. Food Res. 61:1600518. doi:10.1002/mnfr.201600518

- Bach Knudsen, K. E., A. Serena, A. K. Kjaer, H. Jørgensen, and R. Engberg. 2005. Rye bread enhances the production and plasma concentration of butyrate but not the plasma concentrations of glucose and insulin in pigs. J. Nutr. 135:1696–1704. doi:10.1093/jn/135.7.1696
- Bengtsson, S., R. Andersson, E. Westerlund, and P. Åman. 1992. Content, structure and viscosity of soluble arabinoxylans in rye grain from several countries. J. Sci. Food Agric. 58:331–337. doi:10.1002/jsfa.2740580307
- Bouhnik, Y., L. Achour, D. Paineau, M. Riottot, A. Attar, and F. Bornet. 2007. Four-week short chain fructo-oligosaccharides ingestion leads to increasing fecal bifidobacteria and cholesterol excretion in healthy elderly volunteers. Nutr. J. 6:42. doi:10.1186/1475-2891-6-42
- Bourquin, L. D., K. A. Garleb, N. R. Merchen, and G. C. Fahey Jr. 1990. Effects of intake and forage level on site and extent of digestion of plant cell wall monomeric components by sheep. J. Anim. Sci. 68:2479–2495. doi:10.2527/1990.6882479x
- Call, L. M., D'Amico, S., Grausgruber, H., Schönlechner, R. 2018. Fruktane in alten und neuen österreichischen Weizensorten. Getreide Mehl und Brot. vol. 1; p. 2–6. [accessed July 24, 2020] Available from file:///C:/Users/hstein/Downloads/Fruktane_ Getreide_Mehl-und-Brot.pdf.
- Cervantes-Pahm, S. K., Y. Liu, A. Evans, and H. H. Stein. 2014. Effect of novel fiber ingredients on ileal and total tract digestibility of energy and nutrients in semi-purified diets fed to growing pigs. J. Sci. Food Agric. **94**:1284–1290. doi:10.1002/jsfa.6405
- Cervantes-Pahm, S. K., Y. Liu, and H. H. Stein. 2013. Comparative digestibility of energy and nutrients and fermentability of dietary fiber in eight cereal grains fed to pigs. J. Sci. Food Agric. 94:841–849. doi:10.1002/jsfa.6316
- Copeland, L., J. Blazek, H. Salman, and M. C. Tang. 2009. Form and functionality of starch. Food Hydrocoll. 23:1527–1534. doi:10.1016/j.foodhyd.2008.09.016
- Coufal-Majewski, S., K. Stanford, T. McAllister, B. Blakley, J. McKinnon, A. V. Chaves, and Y. Wang. 2016. Impacts of cereal ergot in food animal production. Front. Vet. Sci. 3:15. doi:10.3389/fvets.2016.00015
- Cummings, J. H., and H. N. Englyst. 1995. Gastrointestinal effects of food carbohydrate. Am. J. Clin. Nutr. 61(4 Suppl):938S–945S. doi:10.1093/ajcn/61.4.938S
- Cunningham, H. M., D. W. Friend, and J. W. G. Nicholson. 1962. The effect of age, body weight, feed intake, and adaptability of pigs on the digestibility and nutritive value of cellulose. *Can. J. Anim. Sci.* **42**:167–175. doi:10.4141/cjas62-027
- Drews, E., and W. Seibel. 1976. Bread-baking and other uses around the world. In: Bushuk, W. editor. Rye: production, chemistry and technology. St. Paul (MN): American Association of Cereal Chemists; p. 127–178.
- European Union (EU) 2006. Commission Recommendation 2006/576/EC. Commission recommendation of 17 August 2006 on the presence of deoxynivalenol, zearalenone, ochratoxin A, T-2 and HT-2 and fumonisins in products intended for animal feeding. *Off. J. Eur. Union* **L229**:7–9.
- Evonik Industries. 2016. AMINODat 5.0 Platinum version. Hanau-Wolfgang (Germany): Evonik Degussa GmbH.
- FDA (Food and Drug Administration). 2001. Guidance for Industry: fumonisin levels in human foods and animal feeds. Available from https://www.fda.gov/regulatory-information/ search-fda-guidance-documents/guidance-industryfumonisin-levels-human-foods-and-animal-feeds. [accessed June 11, 2020].
- FDA (Food and Drug Administration). 2010. Guidance for Industry and FDA: advisory levels for deoxynivalenol (DON) in finished wheat products for human consumption and grains and grain by-products used for animal feed. Available from https://www.fda.gov/regulatory-information/search-fdaguidance-documents/guidance-industry-and-fda-advisorylevels-deoxynivalenol-don-finished-wheat-products-human. [accessed June 11, 2020].

- Geiger, H. H., and T. Miedaner. 2009. Rye (Secale cereale L.). In: Carena, M. J., editor. Cereals. Handbook of plant breeding no. 3. New York (NY): Springer US; p. 157–181.
- Glitsø, L. V., G. Brunsgaard, S. Højsgaard, B. Sandström, and K. E. Bach Knudsen. 1998. Intestinal degradation in pigs of rye dietary fibre with different structural characteristics. Br. J. Nutr. 80:457–468. doi:10.1017/S0007114598001536
- Glitsø, L. V., H. Gruppen, H. A. Schols, S. Højsgaard, B. Sandström, and K. E. Bach Knudsen. 1999. Degradation of rye arabinoxylans in the large intestine of pigs. J. Sci. Food Agric. 79:961–969. doi:10.1002/ (SICI)1097-0010(19990515)79:7<961::AID-JSFA311>3.0.CO;2-1
- Hansen, H. B., C. V. Rasmussen, K. E. Bach Knudsen, and Å. Hansen. 2003. Effects of genotype and harvest year on content and composition of dietary fibre in rye (Secale cereale L.) grain. J. Sci. Food Agric. 83:76–85. doi:10.1002/jsfa.1284
- Hoebler, C., J. Barry, A. David, and J. Delort Laval. 1989. Rapid acid hydrolysis of plant cell wall polysaccharides and simplified quantitative determination of their neutral monosaccharides by gas-liquid chromatography. J. Agric. Food Chem. 37:360–367. doi:10.1021/jf00086a020
- Högberg, A., and J. E. Lindberg. 2004. Influence of cereal nonstarch polysaccharides on digestion site and gut environment in growing pigs. Livest. Prod. Sci. 87:121–130. doi:10.1016/j. livprodsci.2003.10.002
- Huntley, N. F., and J. F. Patience. 2018a. The effect of xylose on water and energy balance in pigs. J. Anim. Sci. **96**(Supp 2):162– 163. (Abstr.) doi:10.1093/jas/sky073.299
- Huntley, N. F., and J. F. Patience. 2018b. Xylose: absorption, fermentation, and post-absorptive metabolism in the pig. J. Anim. Sci. Biotechnol. 9:4. doi:10.1186/s40104-017-0226-9
- Jaworski, N. W., and H. H. Stein. 2017. Disappearance of nutrients and energy in the stomach and small intestine, cecum, and colon of pigs fed corn-soybean meal diets containing distillers dried grains with solubles, wheat middlings, or soybean hulls. J. Anim. Sci. **95**:727–739. doi:10.2527/jas.2016.0752
- Jensen, B. B., and H. Jørgensen. 1994. Effect of dietary fiber on microbial activity and microbial gas production in various regions of the gastrointestinal tract of pigs. Appl. Environ. Microbiol. 60:1897–1904. doi:10.1128/AEM.60.6.1897-1904.1994
- Juntunen, K. S., D. E. Laaksonen, K. Autio, L. K. Niskanen, J. J. Holst, K. E. Savolainen, K. H. Liukkonen, K. S. Poutanen, and H. M. Mykkänen. 2003. Structural differences between rye and wheat breads but not total fiber content may explain the lower postprandial insulin response to rye bread. Am. J. Clin. Nutr. 78:957–964. doi:10.1093/ajcn/78.5.957
- Jürgens, H.-U., G. Jansen, and C. B. Wegener. 2012. Characterisation of several rye cultivars with respect to arabinoxylans and extract viscosity. J. Agric. Sci. 4:1–12. doi:10.5539/jas.v4n5p1
- Karppinen, S. 2003. Dietary fiber components of rye bran and their fermentation in vitro [Doctoral dissertation]. Helsinki (Finland): University of Helsinki.
- Karppinen, S., O. Myllymäki, P. Forssell, and K. Poutanen. 2003. Fructan content of rye and rye products. Cereal Chem. 80:168–171. doi:10.1094/CCHEM.2003.80.2.168
- Kasprzak, M. M., H. N. Lærke, and K. E. Knudsen. 2012. Effects of isolated and complex dietary fiber matrices in breads on carbohydrate digestibility and physicochemical properties of ileal effluent from pigs. J. Agric. Food Chem. 60:12469–12476. doi:10.1021/jf303326d
- Kim, B. G., G. I. Petersen, R. B. Hinson, G. L. Allee, and H. H. Stein. 2009. Amino acid digestibility and energy concentration in a novel source of high-protein distillers dried grains and their effects on growth performance of pigs. J. Anim. Sci. 87:4013– 4021. doi:10.2527/jas.2009-2060
- Lærke, H. N., S. Arent, S. Dalsgaard, and K. E. Bach Knudsen. 2015. Effect of xylanases on ileal viscosity, intestinal fiber modification, and apparent ileal fiber and nutrient digestibility of rye and wheat in growing pigs. J. Anim. Sci. 93:4323–4335. doi:10.2527/jas.2015-9096

- Lærke, H. N., C. Pedersen, M. A. Mortensen, P. K. Theil, T. Larsen, and K. E. B. Knudsen. 2008. Rye bread reduces plasma cholesterol levels in hypercholesterolaemic pigs when compared to wheat at similar dietary fibre level. J. Sci. Food Agric. 88:1385–1393. doi:10.1002/jsfa.3229
- Laidig, F., H.-P. Piepho, D. Rentel, T. Drobek, U. Meyer, and A. Huesken. 2017. Breeding progress, variation, and correlation of grain and quality traits in winter rye hybrid and population varieties and national on-farm progress in Germany over 26 years. Theor. Appl. Genet. 130:981–998. doi:10.1007/s00122-017-2865-9
- Le Gall, M., K. L. Eybye, and K. E. Bach Knudsen. 2010. Molecular weight changes of arabinoxylans of wheat and rye incurred by the digestion processes in the upper gastrointestinal tract of pigs. Livest. Sci. **134**:72–75. doi:10.1016/j.livsci.2010.06.101
- Le Gall, M., A. Serena, H. Jørgensen, P. K. Theil, and K. E. Bach Knudsen. 2009. The role of whole-wheat grain and wheat and rye ingredients on the digestion and fermentation processes in the gut–a model experiment with pigs. Br. J. Nutr. 102:1590–1600. doi:10.1017/S0007114509990924
- McCleary, B. V., J. W. DeVries, J. I. Rader, G. Cohen, L. Prosky, D. C. Mugford, and K. Okuma. 2012. Determination of insoluble, soluble, and total dietary fiber (CODEX definition) by enzymatic-gravimetric method and liquid chromatography: collaborative study. J. AOAC Int. 95:824–844. doi:10.5740/ jaoacint.cs2011_25
- McGhee, M. L., and H. H. Stein. 2018. Apparent and standardized ileal digestibility of AA and starch in hybrid rye, barley, wheat, and corn fed to growing pigs. J. Anim. Sci. **96**:3319–3329. doi:10.1093/jas/sky206
- Montoya, C. A., S. M. Rutherfurd, and P. J. Moughan. 2015. Nondietary gut materials interfere with the determination of dietary fiber digestibility in growing pigs when using the Prosky method. J. Nutr. **145**:1966–1972. doi:10.3945/jn.115.212639
- Myers, W. D., P. A. Ludden, V. Nayigihugu, and B. W. Hess. 2004. Technical Note: A procedure for the preparation and quantitative analysis of samples for titanium dioxide. J. Anim. Sci. 82:179–183. doi:10.2527/2004.821179x
- Nelson, D. L., and M. M. Cox. 2004. Lehninger principles of biochemistry lecture. 4th ed. New York (NY): WH Freeman & Co.
- Nitrayová, S., J. Heger, P. Patráš, H. Kluge, and J. Brož. 2009. Effect of xylanase on apparent ileal and total tract digestibility of nutrients and energy of rye in young pigs. Arch. Anim. Nutr. 63:281–291. doi:10.1080/17450390903020455
- NRC. 2012. Nutrient requirements of swine. 11th rev. ed. Washington (DC): The National Academies Press.
- Ragaee, S. M., G. L. Campbell, G. J. Scoles, J. G. McLeod, and R. T. Tyler. 2001. Studies on rye (Secale cereale L.) lines exhibiting a range of extract viscosities. 1. Composition, molecular weight distribution of water extracts, and biochemical characteristics of purified water-extractable arabinoxylan. J. Agric. Food Chem. 49:2437–2445. doi:10.1021/jf001227g
- Rodehutscord, M., C. Rückert, H. Maurer, H. Schenkel, W. Schipprack, K. E. Bach Knudsen, M. Schollenberger, M. Laux, M. Eklund, W. Siegert, et al. 2016. Variation in chemical composition and physical characteristics of cereal grains from different genotypes. Arch. Anim. Nutr. 70:87–107. doi:10.1080/1745039X.2015.1133111
- Rojas, O. J., and H. H. Stein. 2015. Effects of reducing the particle size of corn grain on the concentration of digestible and

metabolizable energy and on the digestibility of energy and nutrients in corn grain fed to growing pigs. *Livest. Sci.* **181**:187–193. doi:10.1016/j.livsci.2015.09.013

- Rosenfelder-Kuon, P., E. J. P. Strang, H. K. Spindler, M. Eklund, and R. Mosenthin. 2017. Ileal starch digestibility of different cereal grains fed to growing pigs. J. Anim. Sci. 95:2711–2717. doi:10.2527/jas.2017.1450
- Rostagno, H. S., L. F. T. Albino, J. L. Donzele, P.C. Gomes, R. F. de Oliveira, D. C. Lopez, A. S. Ferreira, S. L. T. Barreto, and R. F. Euclides. 2017. In: Rostagno, H. S., editor. Brazilian tables for poultry and swine: Composition of feedstuffs and nutritional requirements. 4th ed. Viçosa, MG (Brazil): Federal University of Viçosa; p. 482.
- Salmenkallio-Marttila, M., and S. Hovinen. 2005. Enzyme activities, dietary fibre components and rheological properties of wholemeal flours from rye cultivars grown in Finland. J. Sci. Food Agric. **85**:1350–1356. doi:10.1002/jsfa.2128
- Schutte, J. B., J. de Jong, R. Polziehn, and M. W. Verstegen. 1991. Nutritional implications of D-xylose in pigs. Br. J. Nutr. 66:83– 93. doi:10.1079/bjn19910012
- Singh, J., A. Dartois, and L. Kaur. 2010. Starch digestibility in food matrix: a review. Trends Food Sci. Technol. 21:168–180. doi:10.1016/j.tifs.2009.12.001
- Smiricky, M. R., C. M. Grieshop, D. M. Albin, J. E. Wubben, V. M. Gabert, and G. C. Fahey Jr. 2002. The influence of soy oligosaccharides on apparent and true ileal amino acid digestibilities and fecal consistency in growing pigs. J. Anim. Sci. 80:2433–2441. doi:10.2527/2002.8092433x
- Souffrant, W. B. 2001. Effect of dietary fibre on ileal digestibility and endogenous nitrogen losses in the pig. Anim. Feed Sci. Technol. **90**:93–102. doi:10.1016/S0377-8401(01)00199-7
- Stein, H. H., B. Sève, M. F. Fuller, P. J. Moughan, and C. F. M. de Lange. 2007. Invited Review: Amino acid bioavailability and digestibility in pig feed ingredients: terminology and application. J. Anim. Sci. 85:172–180. doi:10.2527/jas.2005–742
- Stein, H. H., C. F. Shipley, and R. A. Easter. 1998. Technical Note: A technique for inserting a T-cannula into the distal ileum of pregnant sows. J. Anim. Sci. 76:1433–1436. doi:10.2527/1998.7651433x
- Strang, E. J., M. Eklund, P. Rosenfelder, N. Sauer, J. K. Htoo, and R. Mosenthin. 2016. Chemical composition and standardized ileal amino acid digestibility of eight genotypes of rye fed to growing pigs. J. Anim. Sci. 94:3805–3816. doi:10.2527/ jas.2016-0599
- Urriola, P. E., S. Cervantes-Pahm, and H. H. Stein. 2013. Fiber in Swine Nutrition. In: Chiba, L. I., editor. Sustainable swine nutrition. Ames (IA): Wiley-Blackwell; p. 255–276.
- Yule, M. A., and M. F. Fuller. 1992. The utilization of orally administered D-xylose, L-arabinose and D-galacturonic acid in the pig. Inter. J.Food Sci. Nutr. **43**:31–40. doi:10.3109/09637489209027530
- Zhao, P. Y., J. P. Wang, and I. H. Kim. 2013. Evaluation of dietary fructan supplementation on growth performance, nutrient digestibility, meat quality, fecal microbial flora, and fecal noxious gas emission in finishing pigs. J. Anim. Sci. 91:5280– 5286. doi:10.2527/jas.2012-5393
- Zuber, T., T. Miedaner, P. Rosenfelder, and M. Rodehutscord. 2016. Amino acid digestibility of different rye genotypes in caecectomised laying hens. Arch. Anim. Nutr. **70**:470–487. doi: 10.1080/1745039X.2016.1226035