The influence of feed ingredients on CP and starch disappearance rate in complex diets for broiler chickens

Naja Bloch Pedersen,[*] Mark Hanigan,[†] Faegheh Zaefarian,[‡] Aaron J. Cowieson,[§,1] Mette Olaf Nielsen,[#] and Adam Christian Storm[*]

[*]*Novozymes A/S, Animal Health and Nutrition, 2800 Lyngby, Denmark;* [†]*Department of Dairy Science, Virginia Tech, Blacksburg 24061, USA;* [‡]*Monogastric Research Centre, School of Agriculture and Environment, Massey University, Palmerston North 4442, New Zealand;* [§]*Animal Nutrition and Health, DSM Nutritional Products, Kaiseraugst, Switzerland; and* [#]*Department of Animal Science, Aarhus University, 8830 Tjele, Denmark*

ABSTRACT The influence of feed ingredients on digestion kinetics of N and starch in complex diets was investigated in the current experiment. A total of 34 diets with different inclusion levels of 10 commonly used feed ingredients (corn, wheat, sorghum, soybean meal, canola meal, full-fat soybean meal [**FFSB**], palm kernel meal, meat and bone meal, wheat distillers grain with solubles and wheat bran) were randomly allocated to 170 cages with 8 birds in each. Apparent jejunal and ileal digestibility of N and starch was determined on a cage level in broilers feed the experimental diets ad libitum from 21 to 24 d after hatch. Disappearance rate of N and starch from the intestine was estimated through a first-order decay function fitted to the digesta data from the jejunum and ileum. The fit of the decay functions was evaluated with root mean squared error as percentage of the observed mean. The influence of the feed ingredients on the disappearance rates were found through a linear regression model, including the effect of the single ingredients, 2-way and 3-way interactions and evaluated with a Student t test test. Starch digestion kinetics were in general faster than N digestion kinetics. The N disappearance rate was both influenced by single ingredients and interaction amongst ingredients, whereas starch disappearance rate mainly was influenced by single ingredients. A combination of FFSB and soybean meal decreased the N digestion rate by 22 to 25% compared with diets with only soybean meal or FFSB, respectively. These results indicate that nutrients from 1 feed ingredient can influence the rate of disappearance of nutrients from other feed ingredients in a complex diet. This highlights the importance of understanding nutrient digestion kinetics and how these are influenced both additively and nonadditively by different feed ingredients in complex diets.

Key words: broiler, starch, protein, disappearance rate, complex diet

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INTRODUCTION

Synchronization of starch and protein digestion rates can influence the feed conversion ratio (**FCR**) in broiler chickens (Liu and Selle, 2015). Several reports have shown that whole body protein synthesis and feed efficiency were affected by synchronized availability of amino acids and carbohydrates (Geiger, 1950; van den Borne et al., 2007). Efficient growth occurs when glucose and amino acids are available simultaneously at tissue level, thus supporting that starch and protein digestion should be viewed as dynamic processes rather than a single static process (Liu and Selle, 2015). Rate of starch digestion has been studied in diets with one or two ingredients as the main starch source, and starch sources could be divided into 3 groups as per their rate of digestion. Some of the starch sources had the same ileal digestibility but different digestion rates (Weurding et al., 2001). Difference in the starch digestion can be ascribed to starch granular structure, antinutritional factors, and coarse particles (Carré, 2004). Disappearance rates of both N and starch have been shown to be affected by viscosity of diets, indicating that ingredients can interact in complex diets in a nonadditive way (Matthiesen et al., In Press). However, how feed ingredients interact in complex diets and how this affects the digestion rate of starch and protein is not clear.

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[1]Corresponding author: aaron.cowieson@dsm.com

Feed digestion can be described by 3 rate limiting aspects. 1) digesta transit time, 2) rate of absorption of nutrient, and 3) rate of hydrolysis of nutrient (Selle and Liu, 2018). Transit time and rate of hydrolysis are highly influenced by the feed ingredients in the diet. Soluble nonstarch polysaccharides (**NSP**) increases diet viscosity, which not only hinders enzymatic hydrolysis and movement of nutrients to the epithelium for absorption but it also decreases transit time (van der Klis and van Voorst, 1993; Choct et al., 1999). Absorption of glucose, amino acids, and peptides in the small intestine couples substrate flux to movement of sodium into the epithelial cells (Daniel and Zietek, 2015). It is suggested that the absorption system can be overloaded, and intestinal uptake of glucose, amino acids and peptides in that case is compromised (Selle and Liu, 2018). Among factors affecting the rate of hydrolysis in the intestine, the level of protease inhibitors, phytate, and NSP are all known to decrease the rate of digestion. Protease inhibitors decrease proteolysis through inhibition of trypsin, chymotrypsin, and amylase in the small intestine (van der Poel, 1990). Phytate can likewise influence the digestibility of starch and proteins through direct and indirect complex formations (Selle et al., 2012). This explains why both starch and protein digestion was improved, when exogenous phytase was added to the diet of broilers fed a sorghum-based feed (Sultan et al., 2011a). In addition, the kinetics of starch digestion was improved by adding an exogenous phytase (Sultan et al., 2011b). Among other antinutritional factors that decreases diet digestibility are NSP. A significant depression of ileal starch digestibility and protein digestibility was observed when NSP were added to diets, and a clear correlation between the level of NSP and ileal digestibility of starch and protein was also observed (Choct and Annison, 1992). Collectively, all these factors influence the rate of nutrient digestion, and this influence might be owing to interactions among feed ingredients, as it was demonstrated in a study by Choct and Annison (1992).

Understanding the dynamics of starch and protein digestion is therefore an important step in the attempt to optimize broiler production in the future (Liu and Selle, 2015). We hypothesized that modeling of intestinal N and starch disappearance rates can reveal interactions between feed ingredients that account for impacts on digestion kinetics.

The objective of the present study was to determine the in vivo N and starch disappearance rate constants for 34 complex diets fed to broilers by fitting data from the jejunum and ileum to a first-order decay function.

MATERIALS AND METHODS

The study was conducted at Massey University, New Zealand. All experimental procedures complied with Massey University Animal Ethics Committee guidelines.

Diets

Ten feed ingredients were used to produce different feed mixtures, based on corn, wheat, and sorghum as cereal sources; soybean meal, palm kernel meal (**PKM**), canola meal, and full-fat soybean meal (**FFSB**) as protein sources; and meat and bone meal (**MBM**), wheat distillers dried grains with solubles (**DDGS**), and wheat bran as coproducts. The combination of feedstuffs resulted in a total of 34 diets. The dietary treatments were split into 4 subgroups. The first group was based on variable cereal sources, constant inclusion of protein sources, and coproduct sources (Table 1). The second group of dietary treatments was based on variable protein sources, constant inclusion of cereal sources, and coproduct sources (Table 1). The third group of dietary treatments was based on variable by-product sources, constant inclusion of protein sources, and cereal sources (Table 2). The fourth group of dietary treatments was based on standard diets, which contained combination of the 3 cereal sources and a constant level of soybean meal (Table 2).

All feed mixtures contained 5.0 g/kg titanium dioxide (TiO_2; Merck KGaA, Darmstadt, Germany) as an indigestible marker for the determination of apparent ileal and jejunal nutrient digestibility. All diets were steam-conditioned at 60°C for 30 s and pelleted through a pellet mill (Model Orbit 15; Richard Sizer Ltd., Kingston upon Hull, UK) capable of manufacturing 180 kg of feed/h and equipped with a die ring with 3-mm apertures and a depth of 35 mm.

Birds and Housing

A total of 1,550 1-day-old male broiler (Ross 308) chicks were obtained from a commercial hatchery and fed a pre-experimental starter diet from 1 to 21 d of age. This diet was formulated to contain 12.7 MJ/kg AME, 22.5% CP, 0.9% calcium, 0.45% available phosphorus, and 0.125% digestible lysine. The space allocation per bird in grower cages was 640 cm^2. The grower cages, with wire floors, were housed in an environmentally controlled room with 20 h of fluorescent illumination per day. Cages were equipped with feed troughs and nipple drinkers. Diets were offered ad libitum, and water was freely available.

On day 21, birds were allocated to 170 electrically heated battery brooder cages (8 birds in each) and offered 1 of the 34 dietary treatments until day 24 each. The 34 dietary treatments were randomly assigned to 5 replicate cages, in a randomized complete block design.

Total feed intake for each cage was measured during the 3-day treatment period from day 21 to 24. Data were handled as mean of each cage. In cages with dead birds, data were handled as mean of remaining birds and was then used in the decay functions equally to cages without dead birds.

Table 1. Composition of the diets in %.

	Cereal source							Protein source													
Ingredient	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U
Corn	**54**	**0**	**0**	**27**	**27**	**0**	**18**	18	18	18	18	18	18	18	18	18	18	18	18	18	18
Wheat	**0**	**54**	**0**	**27**	**0**	**27**	**18**	18	18	18	18	18	18	18	18	18	18	18	18	18	18
Sorghum	**0**	**0**	**54**	**0**	**27**	**27**	**18**	18	18	18	18	18	18	18	18	18	18	18	18	18	18
Soybean meal	7.5	7.5	7.5	7.5	7.5	7.5	7.5	**30**	**0**	**0**	**0**	**15**	**15**	**15**	**0**	**0**	**0**	**10**	**10**	**10**	**0**
Canola meal	7.5	7.5	7.5	7.5	7.5	7.5	7.5	**0**	**30**	**0**	**0**	**15**	**0**	**0**	**15**	**15**	**0**	**10**	**10**	**0**	**10**
Full-fat soybean	7.5	7.5	7.5	7.5	7.5	7.5	7.5	**0**	**0**	**30**	**0**	**0**	**15**	**0**	**15**	**0**	**15**	**10**	**0**	**10**	**10**
Palm kernel meal	7.5	7.5	7.5	7.5	7.5	7.5	7.5	**0**	**0**	**0**	**30**	**0**	**0**	**15**	**0**	**15**	**15**	**0**	**10**	**10**	**10**
Meat and bone meal	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
DDGS	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Wheat bran	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Soybean oil	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Sodium bicarbonate	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
Salt	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
Dicalcium phosphate	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
Limestone	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4
Titanium dioxide	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
Vitamin premix[1]	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Mineral premix[1]	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1

Bolded values indicate variable inclusion of ingredients amongst treatments. Non-bolded values indicate constant inclusion of ingredients amongst treatments.

Diet A-G have different inclusion levels of the cereal source and diet H-U have different inclusion levels of the protein source.

Abbreviation: DDGS, distillers dried grains with solubles.

[1]Supplied per kilogram of diet: antioxidant, 100 mg; biotin, 0.2 mg; calcium pantothenate, 12.8 mg; cholecalciferol, 60 µg; cyanocobalamin, 0.017 mg; folic acid, 5.2 mg; menadione, 4 mg; niacin, 35 mg; pyridoxine, 10 mg; trans-retinol, 3.33 mg; riboflavin, 12 mg; thiamine, 3.0 mg; dl-α-tocopheryl acetate, 60 mg; choline chloride, 638 mg; Co, 0.3 mg; Cu, 3.0 mg; Fe, 25 mg; I, 1 mg; Mn, 125 mg; Mo, 0.5 mg; Se, 200 µg; Zn, 60 mg.

Table 2. Composition of the diets in %.

	By-product source						Standard diets						
Ingredient	V	W	X	Y	Z	AA	AB	AC	AD	AE	AF	AG	AH
Corn	18	18	18	18	18	18	**60**	**0**	**0**	**30**	**30**	**0**	**20**
Wheat	18	18	18	18	18	18	**0**	**60**	**0**	**30**	**0**	**30**	**20**
Sorghum	18	18	18	18	18	18	**0**	**0**	**60**	**0**	**30**	**30**	**20**
Soybean meal	7.5	7.5	7.5	7.5	7.5	7.5	**33**	**33**	**33**	**33**	**33**	**33**	**33**
Canola meal	7.5	7.5	7.5	7.5	7.5	7.5	0	0	0	0	0	0	0
Full-fat soybean	7.5	7.5	7.5	7.5	7.5	7.5	0	0	0	0	0	0	0
Palm kernel meal	7.5	7.5	7.5	7.5	7.5	7.5	0	0	0	0	0	0	0
Meat and bone meal	**9**	**0**	**0**	**4.5**	**4.5**	**0**	0	0	0	0	0	0	0
DDGS	**0**	**9**	**0**	**4.5**	**0**	**4.5**	0	0	0	0	0	0	0
Wheat bran	**0**	**0**	**9**	**0**	**4.5**	**4.5**	0	0	0	0	0	0	0
Soybean oil	**3**	**3**	**3**	**3**	**3**	**3**	3	3	3	3	3	3	3
Sodium bicarbonate	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
Salt	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
Dicalcium phosphate	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
Limestone	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4
Titanium dioxide	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
Vitamin premix[1]	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Mineral premix[1]	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1

Bolded values indicate variable inclusion of ingredients amongst treatments. Non-bolded values indicate constant inclusion of ingredients amongst treatments.

Diet V-AA have different inclusion levels of by-product source and diet AB-AH have different inclusion levels of the cereal source and a constant level of soybean meal.

Abbreviation: DDGS, distillers dried grains with solubles.

[1]Supplied per kilogram of diet: antioxidant, 100 mg; biotin, 0.2 mg; calcium pantothenate, 12.8 mg; cholecalciferol, 60 µg; cyanocobalamin, 0.017 mg; folic acid, 5.2 mg; menadione, 4 mg; niacin, 35 mg; pyridoxine, 10 mg; trans-retinol, 3.33 mg; riboflavin, 12 mg; thiamine, 3.0 mg; dl-α-tocopheryl acetate, 60 mg; choline chloride, 638 mg; Co, 0.3 mg; Cu, 3.0 mg; Fe, 25 mg; I, 1 mg; Mn, 125 mg; Mo, 0.5 mg; Se, 200 µg; Zn, 60 mg.

Sample Collection

On day 24, six birds per cage were randomly selected and euthanized by intravenous injection (1 mL per 2 kg live weight) of sodium pentobarbitone (Provet NZ Pty Ltd., Auckland, New Zealand). Digesta samples were collected by gently flushing the intestine with distilled water into plastic containers. For jejunal digesta collection, the contents of the proximal half of the jejunum were collected. The ileum was defined as the portion of the small intestine extending from the Meckel's diverticulum to a point ∼40 mm proximal to the ileocecal junction. The ileum was then divided into 2 halves, and the digesta were collected from the lower half toward the ileocecal junction. Digesta from birds within a cage were pooled, lyophilized (Model 0610; Cuddon Engineering, Blenheim, New Zealand), ground to pass through a 0.5-mm sieve, and stored at 4°C until laboratory analysis.

Chemical Analyses

The diets and digesta samples were analyzed for DM, titanium, N, starch, fat, crude fiber, phytate, and gross energy content. DM was determined using standard procedures (methods 930.15 and 925.10; AOAC, 2005). Gross energy was determined by adiabatic bomb calorimetry (Gallenkamp Autobomb, London, UK) standardized with benzoic acid. Samples were assayed for titanium on a UV spectrophotometer following the method of Short et al. (1996). Nitrogen was determined by combustion (Method 968.06; AOAC, 2005) using a carbon nanosphere-200, CP, and sulfur auto analyzer (LECO Corporation, St. Joseph, MI). Total starch was determined by the Megazyme Total Starch Assay Procedure (Megazyme International Ireland Ltd., Wicklow, Ireland), which is based on thermostable α-amylase and amyloglucosidase. Fat was determined using the Soxhlet extraction procedure (method 991.36; AOAC, 2005). Crude fiber was measured using standard procedures (methods 962.09 and 978.10; AOAC, 2005). Phytate content was determined in all raw materials, and the feed matrix composition was used to calculate the phytate content in the different diets, based on the results from the raw materials. Phytate was analyzed on a high-performance ion chromatography system with a ICS5000 dual pump, VWD-3400RS absorbance detector, and a TC-IC column oven (Dionex Corp., Sunnyvale, CA), as per the procedure described by Pontoppidan et al. (2007).

Calculations of In Vivo Data

All data were expressed on a DM basis, and all calculations were made for each cage, which gives 5 independent replicates per treatment.

Rate of feed intake (g/h) per bird was calculated as per Equation 1 under the assumption that birds were eating only during the 20 h of fluorescent illumination per day.

$$Avarage\ feed\ intake\ per\ bird\left(\frac{g}{h}\right) = \frac{Total\ feed\ in\ take\ in\ cage}{3days * 20h * 8birds} \quad \text{Equation 1}$$

Equation 2 was used to calculate the amount of nutrients (N or starch) consumed daily or present in the

jejunum or ileum based on the concentration of nutrient in the sample (sample nutrient [%]):

$$Nutrient(g) = Sample\ DM(g) * Sample\ Nutrient(\%) \quad \text{Equation 2}$$

Protein and starch disappearance rates (k) were based on the disappearance of nutrient (g N or g starch) from the diet to digesta in the jejunum and ileum, fitted to Equation 3 for estimation of k:

$$Nutrien(t) = Nutrient_{initial} e^{-kt} \quad \text{Equation 3}$$

Samples from the jejunum and ileum were not described with a time of passage estimate but with an anatomic location. Diet and ileum were given the relative timepoints of zero and 2, respectively, and a decay function was fitted to each diet using varying time values for the jejunum to assess sensitivity to the relative time settings. The relative time point for the jejunum yielding the lowest root mean squared errors as percentage of observed mean was chosen as the time point for the jejunum. These calculations were made for the decay of starch, and the timepoint for the jejunum that had the best fit to the decay function, was also used for N. Starch was chosen as the standard because digestion of starch is not influenced by endogenous loss such as N digestion. A function was fitted to each cage, and the mean of disappearance rate for the 5 cages represented the disappearance rate of the diet.

Diets were divided into the 4 previously described groups, and the influence of the feed ingredients, which varied in concentration in each group, was tested. The influence of the different feed ingredients on the disappearance rate was tested through linear regression with a global model, ranking the best fitting models according to Akaike information criterion, which is based on log-likelihood. Within the 4 dietary treatment groups, the percentage of inclusion of each ingredient as independent parameters, all 2-way interactions, and 3-way interactions were tested as parameters in a linear regression model. The parameters of the best fitting model were tested for significance. The MuMIn packages of R were used for the calculations. To test if the interactions between feed ingredients were additive or nonadditive, a paired Student' t test was made between single ingredients and combinations which showed to influence the rate of N and starch disappearance. All calculations and statistical analysis were made using R 3.6.1 (R Core Team, 2019).

RESULTS

Feed Intake, Diets, and Digestibility Coefficients

Two birds died during the 3-day test period from day 21 to 24, the birds were feed diet G and H (see Table 1), while the rest of the birds remained healthy. A Tukey honestly significant difference test showed that there were no significant differences in overall feed intake among diets. The average feed intake per bird was 145 g/d ±1.48 (7.2 g/h ±0.1). The average N intake per bird was 4.89 g/d ±0.07 (0.24 g/h ±0.003). There was no difference between the N (g) intakes among diets except for K (2.78 g/d ±0.16), P(3.92 g/d ±0.21), and Q (4.12 g/d ±0.26), these diets contained PKM(15–30% of diet) and had lower N (g) contents. There was no difference between the starch (g) intakes among diets; the average starch intake per bird was 54.1 g/d ±0.58 (2.70 g/h ±0.03). Diets had an average content of N, starch, fat, crude fiber, and phytate of 38.0 ± 0.29, 374.1 ± 1.55, 73.4% ± 1.14, 41.7 ± 2.02, and 12.6 ± 0.26 g/kg DM, respectively, and a gross energy content of 18.96 ± 0.021 kJ/g (Table 3). The apparent N and starch digestibility coefficients were determined for all diets at the jejunum and the ileum sites. The mean N digestibility coefficients for the jejunum and ileum were 0.503 ± 0.008 and 0.722 ± 0.004, respectively. The mean starch digestibility coefficients for the jejunum and ileum were 0.874 ± 0.005 and 0.938 ± 0.002, respectively (Table 4).

Kinetic Modeling of Nutrient Disappearance

A time point of 1.4 for the jejunum was found to result in the lowest root mean squared errors as percentage of observed mean for the decay of starch. Thus, the 3

Table 3. Composition of nutrients in diets (g/kg DM).

Diet	N	Fat	Starch	CF[1]	Phytate	GE[2] kJ/g
A	33.5	78.6	379.9	46.4	11.4	19.17
B	33.4	74.8	349.0	55.3	11.7	18.97
C	32.9	83.7	374.3	48.6	13.9	19.24
D	33.2	78.1	357.1	57.4	11.6	18.98
E	32.1	81.0	363.6	47.2	12.7	19.04
F	33.1	76.8	359.6	49.6	12.8	19.08
G	32.3	79.1	367.7	45.4	12.3	19.02
H	39.7	54.3	366.1	32.8	13.6	18.71
I	33.1	58.6	356.4	61.2	16.4	18.71
J	33.9	116.8	363.0	35.1	10.4	19.84
K	23.0	74.8	367.2	68.1	9.0	18.78
L	35.2	63.1	361.7	50.3	15.0	18.76
M	36.2	89.6	353.4	30.7	12.0	19.27
N	31.2	65.9	372.3	40.8	11.3	18.71
O	33.3	90.4	369.7	38.2	13.4	19.31
P	28.3	70.1	364.0	52.7	12.7	18.75
Q	28.7	95.5	378.7	43.9	9.7	19.41
R	35.4	80.3	355.4	36.5	13.5	19.09
S	32.0	63.5	368.9	51.9	13.0	18.61
T	31.8	84.3	364.3	42.5	11.0	19.07
U	29.5	83.4	369.8	51.2	11.9	19.05
V	35.3	85.0	364.6	42.4	11.0	18.85
W	31.4	78.7	356.2	36.4	12.3	19.12
X	31.1	76.3	372.8	48.5	13.8	19.14
Y	33.1	82.0	360.2	45.6	11.6	19.01
Z	32.7	79.3	384.5	43.8	12.4	18.96
AA	30.6	77.9	363.5	42.8	13.0	19.09
AB	39.1	55.0	388.7	24.9	12.6	18.76
AC	41.3	47.8	383.7	30.5	12.9	18.69
AD	38.8	57.6	424.8	21.8	15.3	18.75
AE	37.7	53.4	421.1	20.4	12.7	18.56
AF	38.1	55.2	426.6	24.0	13.9	18.76
AG	39.4	51.4	409.5	24.9	14.1	18.67
AH	38.9	52.8	401.6	25.2	13.6	18.63

[1]Crude fiber.
[2]Gross energy.

Table 4. Jejunal and ileal digestibility coefficients of N and starch.

	Jejunal digestibility				Ileal digestibility			
Diet	N	Se	Starch	Se	N	Se	Starch	Se
A	0.608	0.039	0.942	0.018	0.761	0.014	0.969	0.015
B	0.629	0.023	0.916	0.014	0.699	0.024	0.946	0.005
C	0.500	0.031	0.816	0.022	0.676	0.017	0.929	0.009
D	0.540	0.053	0.919	0.020	0.674	0.023	0.945	0.019
E	0.456	0.030	0.866	0.018	0.714	0.018	0.974	0.005
F	0.560	0.045	0.899	0.029	0.719	0.015	0.956	0.006
G	0.424	0.029	0.867	0.017	0.738	0.003	0.941	0.004
H	0.490	0.051	0.820	0.017	0.668	0.020	0.963	0.011
I	0.396	0.040	0.837	0.020	0.749	0.004	0.960	0.004
J	0.538	0.047	0.811	0.011	0.763	0.007	0.948	0.011
K	0.356	0.033	0.958	0.007	0.731	0.012	0.920	0.017
L	0.497	0.043	0.856	0.026	0.738	0.019	0.960	0.009
M	0.359	0.080	0.778	0.033	0.701	0.016	0.935	0.012
N	0.506	0.035	0.903	0.005	0.752	0.015	0.938	0.009
O	0.459	0.062	0.866	0.016	0.707	0.021	0.937	0.005
P	0.491	0.041	0.896	0.010	0.757	0.017	0.917	0.013
Q	0.525	0.043	0.928	0.007	0.688	0.022	0.920	0.009
R	0.502	0.029	0.862	0.032	0.755	0.011	0.899	0.009
S	0.498	0.036	0.917	0.018	0.584	0.047	0.975	0.005
T	0.482	0.024	0.886	0.022	0.701	0.012	0.930	0.005
U	0.440	0.047	0.917	0.014	0.689	0.029	0.882	0.020
V	0.546	0.034	0.951	0.017	0.705	0.028	0.950	0.009
W	0.522	0.017	0.886	0.013	0.733	0.018	0.943	0.010
X	0.531	0.045	0.889	0.022	0.701	0.013	0.956	0.007
Y	0.448	0.018	0.895	0.009	0.731	0.016	0.973	0.003
Z	0.586	0.028	0.888	0.014	0.696	0.013	0.920	0.012
AA	0.472	0.059	0.904	0.034	0.697	0.019	0.937	0.009
AB	0.604	0.035	0.882	0.028	0.805	0.004	0.955	0.002
AC	0.582	0.045	0.882	0.017	0.775	0.018	0.962	0.004
AD	0.565	0.035	0.795	0.036	0.762	0.014	0.884	0.006
AE	0.527	0.023	0.880	0.009	0.764	0.018	0.953	0.006
AF	0.500	0.030	0.800	0.040	0.754	0.016	0.911	0.009
AG	0.486	0.040	0.803	0.022	0.730	0.016	0.895	0.005
AH	0.480	0.050	0.814	0.015	0.723	0.017	0.900	0.009

Table 5. N and starch disappearance rate constants from first-order decay functions.

		N		Starch	
Treatment	n	k	Se	k	Se
All	170	0.581	0.086	1.57	0.138
A	5	0.702	0.071	2.26	0.206
B	5	0.717	0.032	1.74	0.135
C	5	0.579	0.090	1.25	0.035
D	5	0.625	0.069	1.93	0.186
E	5	0.525	0.095	1.44	0.069
F	5	0.650	0.070	1.75	0.346
G	5	0.510	0.125	1.44	0.097
H	5	0.598	0.121	1.24	0.040
I	5	0.480	0.127	1.30	0.047
J	5	0.633	0.080	1.18	0.037
K	5	0.390	0.091	2.22	0.195
L	5	0.556	0.082	1.40	0.121
M	5	0.474	0.150	1.10	0.072
N	5	0.566	0.061	1.63	0.068
O	5	0.558	0.157	1.46	0.041
P	5	0.551	0.068	1.62	0.042
Q	5	0.603	0.066	1.88	0.035
R	5	0.550	0.075	1.49	0.210
S	5	0.550	0.083	1.76	0.292
T	5	0.522	0.054	1.53	0.209
U	5	0.495	0.098	1.71	0.269
V	5	0.599	0.060	2.31	0.365
W	5	0.583	0.062	1.57	0.072
X	5	0.610	0.077	1.60	0.170
Y	5	0.494	0.075	1.62	0.114
Z	5	0.663	0.041	1.60	0.055
AA	5	0.537	0.105	1.80	0.530
AB	5	0.736	0.093	1.61	0.175
AC	5	0.696	0.076	1.57	0.056
AD	5	0.659	0.073	1.15	0.141
AE	5	0.627	0.102	1.53	0.040
AF	5	0.597	0.111	1.24	0.132
AG	5	0.570	0.103	1.16	0.068
AH	5	0.565	0.093	1.20	0.027

Abbreviation: k, Digestion rate constant.

relative physiological time points for the sites were 0, 1.4, and 2 for diet, jejunum, and ileum, for N and starch decay functions.

The rate of N disappearance ranged from 0.390 to 0.796 h^{-1} and rate of starch disappearance ranged from 1.10 to 2.31 h^{-1}. Disappearance rate constants are presented in Table 5.

Effect of Feed Ingredients on the Disappearance Rate Constant

Dietary treatments were divided into 4 previously described groups, and the influence of the different feed ingredients on N and starch disappearance rates in the complex diets were tested.

Variations relating to the cereal source showed that N disappearance rate was decreased by sorghum and the combinations of corn*wheat (diet D) and corn*sorghum (diet E). Disappearance rate for the combination of corn*wheat (diet D) was numerically lower than for each single ingredient. The disappearance rate for the combination was decreased by 11 and 14% compared with corn (diet A) and wheat (diet B) alone, respectively.

Variations relating to the protein source showed that N disappearance rate was decreased by canola meal, PKM, and the combinations of soybean meal*FFSB (diet M) and canola meal* FFSB*PKM (diet U). Disappearance rate for the combination of soybean meal*FFSB (diet M) was significantly lower ($P < 0.002$) than for each single ingredient. Disappearance rate for this combination decreased by 22 and 25% compared with soybean meal (diet H) and FFSB (diet J) alone, respectively. Combination of FFSB*PKM (diet Q) and canola meal*PKM (diet P) increased disappearance rate of N. A numerical increase in the rate was observed for the combination of canola meal*PKM (diet P) compared with each single ingredient. Disappearance rate for the combination compared with single ingredients increased by 13 and 29% for canola meal (diet I) and PKM (diet K), respectively.

Variations relating to the by-product source showed that the combination of DDGS*MBM (diet Y) decreased N disappearance rate and MBM*wheat bran (diet Z) increased N disappearance rate. Disappearance rate for the combination of MBM*wheat bran (diet Z) was numerically higher than for each single ingredient. Disappearance rate for the combination compared with single ingredients increased with 8 and 9% for wheat bran (diet X) and MBM (diet V), respectively. Disappearance rate for the combination of DDGS*MBM (diet Y) was significantly lower ($P < 0.03$) than for each single ingredient. Disappearance rate for the combination compared with single ingredients decreased by 16

Table 6. Parameters important for N disappearance rate.

Diet	n	Parameters	Estimate	Se
Cereal source	35	Sorghum	$-2.48*10^{-3}$	$8.73*10^{-4}$
		Corn*sorghum	$-1.91*10^{-4}$	$5.78*10^{-5}$
		Corn*wheat	$-1.47*10^{-4}$	$6.15*10^{-5}$
Protein source	70	Canola meal	$-4.69*10^{-3}$	$1.37*10^{-3}$
		PKM[1]	$-7.24*10^{-3}$	$1.37*10^{-3}$
		FFSB[2]*PKM[1]	$3.55*10^{-4}$	$1.68*10^{-4}$
		Canola meal * PKM[1]	$4.42*10^{-4}$	$1.76*10^{-4}$
		Soybean meal*FFSB[2]	$-6.36*10^{-4}$	$1.68*10^{-4}$
		Canola meal* FFSB[2]*PKM[1]	$-9.43*10^{-5}$	$4.12*10^{-5}$
By-product source	30	MBM[3]*DDGS[4]	$-4.35*10^{-3}$	$1.54*10^{-3}$
		MBM[3]*wheat bran	$3.99*10^{-3}$	$1.54*10^{-3}$
Standard	35	Corn*sorghum	$-1.01*10^{-4}$	$4.89*10^{-5}$
		Wheat*sorghum	$-1.32*10^{-4}$	$4.89*10^{-5}$

[1]Palm kernel meal.
[2]Full-fat soybean meal.
[3]Meat and bone meal.
[4]Wheat distillers grain with solubles.

and 18% for DDGS (diet W) and MBM (diet V), respectively.

Variations relating to the cereal source and keeping a constant level of soybean meal as the only protein source showed that the combination of corn*sorghum (diet AF) and wheat*sorghum (diet AG) decreased the N disappearance rate. The combination of corn*sorghums (diet AF) disappearance rate was numerically lower than for each single ingredient. Disappearance rate for the combination decreased by 9 and 19% compared with the single ingredient sorghum (diet AD) and corn (diet AB), respectively. Disappearance rate for the combination of wheat*sorghum (diet AG) was numerically lower than for each single ingredient. Disappearance rate for the combination decreased by 14 and 19% compared with the single ingredients sorghum (diet AD) and wheat (diet AC), respectively. All parameters are shown in Table 6.

Variations relating to the cereal source showed that starch disappearance rate was decreased by sorghum. Varying the protein source showed that starch disappearance increased with the presence of PKM or the combination of either canola meal*FFSB (diet O) or canola*soybean meal (diet L) in the diet. Disappearance rate of starch for the combination of canola meal*FFSB (diet O) was increased with 11 and 19% compared with the single ingredients canola meal (diet I) and FFSB (diet J), respectively. Disappearance rate of starch for the combination of canola meal*soybean meal (diet L) was increased with 7 and 11% compared with the single ingredient canola meal (diet I) and soybean meal (diet H), respectively. Variations relating to the by-product source showed that starch disappearance was increased by the addition of MBM. Variations relating to the cereal source and keeping a constant level of soybean meal as the only protein source showed that starch disappearance rate was decreased by sorghum. All parameters are shown in Table 7.

DISCUSSION

The present study examined the in vivo N and starch small intestinal disappearance rate constant for 34 complex diets. Because all starch in digesta originates from feed and no endogenous starch is affecting the starch measurement, starch disappearance was chosen for the determination of the relative jejunal timepoint.

Starch disappeared faster than N in the present study in accordance with previous reports (Selle and Liu, 2018). Starch is digested more proximal in the digestive tract than protein, resulting in a faster disappearance rate (Selle et al., 2013). The digestion rates for different protein sources performed by Bryan et al. (2019) showed that canola meal was digested numerically faster than soybean meal. We found that the N disappearance rate for canola meal was significantly lower than for soybean meal. The discrepancy of ranking of diets as per digestion rate between that reported by Bryan et al. (2019) and the current study might be explained by a difference in specific source of canola and soybean meal, as pointed out by Khajali and Slominski (2012), who also pointed out that both variety and processing method influence the feedstuff quality. Diets consisting of 54% wheat or 54% corn had a significant higher starch disappearance rate constant compared with the diet with 54% sorghum. Weurding et al. (2001) observed the same relation among wheat, corn, and sorghum, where corn and wheat had a significantly faster starch digestion than sorghum.

In the present study, diet K with PKM had the lowest rate of digestion indicating that the protein is difficult to hydrolyze, but at the same time, specific endogenous N secession might be high from excessive release of enzyme, mucus, and cellular shedding. Appearance of basal and specific endogenous N into the intestinal lumen influences the measurement of apparent protein digestion. Basal loss is independent of the diet and relates to proteins that are secreted in the lumen of the digestive tract and not reabsorbed, including endogenous enzymes, mucin proteins, serum albumin, microbial protein from the hindgut, and sloughed epithelial cells from the intestine (Nyachoti et al., 1997). The specific endogenous loss is feed ingredient dependent and relates to the diet's protein, fiber, and antinutritional factor content (Adeola et al., 2016). The N disappearance rates calculated are thus influenced by both basal and specific endogenous loss of N. Angkanaporn et al. (1994) showed that the

Table 7. Parameters important for starch disappearance rate.

Diet	n	Parameters	Estimates	Se
Cereal source	35	Sorghum	$-1.35*10^{-2}$	$4.54*10^{-3}$
Protein source	70	Canola meal*FFSB[1]	$1.25*10^{-3}$	$4.47*10^{-4}$
		PKM[2]	$3.43*10^{-2}$	$3.39*10^{-3}$
		Soybean meal*canola meal	$1.14*10^{-3}$	$4.47*10^{-4}$
By-product source	30	MBM[3]	$5.54*10^{-2}$	$2.31*10^{-2}$
Standard	35	Sorghum	$-8.13*10^{-3}$	$1.96*10^{-3}$

[1]Full-fat soybean meal.
[2]Palm kernel meal.
[3]Meat and bone meal.

antinutritional effect of wheat pentosans decreased apparent protein digestion by increasing the endogenous AA secretion, supporting that antinutritional factors of 1 feedstuff can interact negatively with the apparent digestion of other nutrients. Using the rate of disappearance takes the endogenous loss into account and models the net protein available for the host. As the specific endogenous loss of N increases, the rate of disappearance will decrease, thus, a high rate of disappearance is preferred because it indicates a high rate of hydrolysis together with a low endogenous loss of N.

The present study showed that a specific feed ingredient such as sorghum can affect the overall disappearance rate of starch and protein both positive and negative, for example sorghum did decrease both protein and starch disappearance rate constants. Current result is supported by previous report showing that the digestion of starch and protein in sorghum is slow owing to an indigestible protein matrix surrounding the starch granules and protein bodies (Black et al., 2005). However, we observed an interaction between dietary inclusion of sorghum with corn or wheat that reduced N disappearance rate. The effect of the interaction between wheat and sorghum (diet AG) was beyond what could be ascribed to a lower rate of digestion in the sorghum (diet AD) itself in the standard diets. Diets with only corn, wheat, or sorghum (diet AB-AD) as cereal source in the standard diets had a faster N disappearance rate than the diets with a combination of sorghum with wheat (diet AG) or corn (diet AF) as cereal source. The N disappearance rates for the combinations of cereal sources decreased with as much as 19% compared with diets with only 1 cereal source. This indicates that the interactions between sorghum and wheat or corn influence kinetics of digestion in a nonadditive way. Tannins, polyphenols, and phytate are antinutritional factors found in sorghum, which could decrease the overall digestibility of protein (Black et al., 2005; Selle et al., 2012). In contrast to N disappearance, the effects of sorghum on starch disappearance were only additive. Hence, sorghum affects starch disappearance rate by decreasing true digestibility of starch opposite to N disappearance rate which affects both by the true digestibility and endogenous losses of N. Sorghum influence the N disappearance rate of both wheat and corn in a nonadditive way, indicating that 1 feed ingredient can affect an entire diet.

A slow but thorough digestion of starch have been proposed as superior to rapid digestible starch because it is synchronized with the protein digestion. Sorghum as a cereal source belongs to the group of slowly digestible starch. Numerous studies have indicated improved feed conversion efficiency owing to it slow starch digestion rate (Weurding et al., 2003; Herwig et al., 2019). For the present study, it was observed that sorghum influenced protein digestion nonadditively, which will lead to a decrease in the synchronization between protein and starch digestion. An asynchronization can result in impaired protein deposition and growth performance (Liu and Selle, 2015). To optimize the digestion dynamics, considerations must therefore be given, when feed ingredients are combined with sorghum.

Addition of PKM to diets increased starch disappearance rate and decreased N disappearance rate. A high content of insoluble NSP containing mannose is present in PKM, which leads to a decrease in viscosity when added to broiler diets (Sundu et al., 2005). Palm kernel consists of only 1.1% starch (Knudsen, 1997), and it is therefore not the starch fraction in the PKM itself, which can account for the increased starch disappearance rate of the complex diets. High viscosity in digesta is known to reduce the mixing of digesta with endogenous enzymes, which is associated with reduced digestibility (Choct et al., 1996). It could be speculated that the positive effect of PKM on starch disappearance rate could be owing to the decreased viscosity of digesta when PKM is added to diets. The PKM decreased N disappearance rate but the ileal digestibility of PKM was greater than average N ileal digestibility. Sundu et al. (2005) showed that PKM decreased digesta viscosity and that might decrease the retention time thus affecting protein digestion negatively in line with the slower digestion rate in the proximal intestine. Ezieshi and Olomu (2008) showed that a replacement of 50% of corn in the diet with 30% and 32.5% PKM resulted in a decrease in BW and a deteriorated FCR. The availability of some essential amino acids in PKM does not meet the requirements of the birds (Sundu et al., 2005). Whether it is the rate of digestion or a poor amino acids composition that relates to the impaired performance when increased amounts of PKM is included in the diet is unknown. The dynamics between protein and starch digestion are important for an efficient broiler meat production (Liu and Selle, 2015), and current

study points to PKM as a tool to modulate the starch rate of digestion.

Combining PKM with canola meal (diet P) increased the N disappearance rate as much as 29% compared with diets with only PKM (diet K) or canola meal (diet I). The increased rate could not be ascribed to a higher rate of digestion in the canola meal itself compared with PKM. The interaction of the 2 ingredients increased the digestion rate by 13 and 29% compared with diets with only canola meal or PKM, respectively. We suggest that combining the 2 protein sources will bring the level of their individual antinutritional components under a critical limit, and thereby, N disappearance rate is indirectly increased. High amount of NSP increases the secretion of endogenous proteins, this could influence the rate of N disappearance indirectly not by decreasing the N digestion per se but through increased contents of endogenous loss of N in digesta in both the jejunum and ileum (Low, 1989). Canola meal has a high content of antinutritional lignin with associated polyphenols. Canola meal might be unfavorable, when it comes to protein digestion rate, but Khajali and Slominski (2012) reviewed its favorable amino acid content compared with soybean meal. Canola meal as a single protein source also decreased N disappearance rate. As mentioned previously, canola meals antinutritional effects can be reduced both by the processing of the meal and type of canola, which would be favorable for the digestion kinetics.

Meat and bone meal and combinations of canola meal*soybean meal and canola meal*FFSB are all feed ingredients with a starch content lower than 2%, and they increased starch disappearance rate. Combining canola meal with FFSB or soybean meal increased starch digestion rate as much as 19% compared with diets based on the single protein sources. Truong et al. (2017) showed that an increase in the rate of N disappearance resulted in an increase of starch disappearance, which suggest that it might be the high N disappearance rate for MBM, FFSB, and soybean meal that increases starch disappearance rate. Contradicting to these findings, PKM also increased starch digestion but had an impaired digestion of N. It suggested that the effect of PKM does not relate to the N digestion rate but the hypothesized effect of viscosity.

Feed ingredients with a relative high content of NSP wheat and DDGS were observed to decrease N disappearance rates. A decrease of N disappearance rate was observed when combinations of corn*-wheat (diet D) and MBM*DDGS (diet Y) were part of the diets. These combinations of feed ingredients had as much as 19% lower disappearance rates compared with diets with the single ingredients, which indicates that the interaction between ingredients are nonadditive. Insoluble NSP can encapsulate potential degradable nutrients within cereal cell wall components (Knudsen, 2014), and soluble NSP have a high water-holding capacity, which increases the digesta viscosity. Higher viscosity in digesta reduces the mixing of feed with endogenous enzymes, which decrease nutrient digestibility (Choct et al., 1996). Matthiesen et al. (in press) showed that supplementation of a xylanase to normal and high viscous wheat-based diets for broilers increased the nutrient disappearance rate of N and starch. Xylanases solubilize insoluble NSP and thereby enhance the digestibility of encapsulated nutrients and reduce the viscosity of digesta (Pettersson and Åman, 1989; Choct et al., 1996, 1999). Conflicting to the previously described results, the combination of MBM*wheat bran (diet Z) proved to influence N disappearance rate positively by as much as 9% compared with diets based on single ingredients. The effect of the different feed ingredients in the present study supports that that digesta viscosity is an important parameter, when it comes to digestion kinetics (Choct et al., 1996; Matthiesen et al., in press).

The combination of soybean meal*FFSB (diet M) decreased the N disappearance rate. Full-fat soybean meal in combination with soybean meal had a significantly lower intestinal disappearance rate than diets with only soybean meal (diet H) or FFSB (diet J), again demonstrating that effects of feed ingredients are nonadditive. Rada et al. (2017) showed that an inclusion level of raw FFSB until 8% had no effect on the **FCR** of broilers, whereas an inclusion greater than 12% of raw FFSB resulted in negative effect on FCR. Trypsin inhibitors are known to reduce protein digestion, but with the right processing of soybean products, they are eliminated (Ravindran et al., 2014). The present study included commercial feed ingredients, and the method for processing of FFSB was unknown. It is therefore difficult to conclude, whether trypsin inhibitors may have influenced the digestion rate on diets containing FFSB or not. Contradictory to these observations both soybean meal and FFSB as single protein source had a positive effect on the N disappearance rate. Both soybean meal and FFSB are known to have high digestibility (CVB, 2016), and it is therefore puzzling that the combination of them would decreases N disappearance rate.

The present study showed that feed ingredients can have opposite effects on starch and N digestion highlighting the complexity relating to synchronization of starch and N digestion. Gutiérrez Del Alamo et al. (2009) showed that starch digestion rate influenced FCR in a quadratic manner, which suggest that an ideal balance between slow and rapidly digestible starch is needed to optimize FCR. This ideal balance is also influenced by protein digestion kinetics. The present article suggests that the disappearance rates of nutrients are affected by the composition of feed ingredients in the diet in both an additive and nonadditive way. The interaction between feed ingredients are affecting the N digestion kinetics more compared with starch digestion kinetics, where most of the effects of feed ingredients were found to be additive. These interactions are important to take into considerations when designing diets in the future if a more dynamic digestion of N and starch is desired to optimize FCR.

DISCLOSURES

The authors declare no conflicts of interest.

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