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Original Research Article

Starch digestion rates in multiple samples of commonly used feed grains in diets for broiler chickens

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ABSTRACT

In this study the starch digestion rates in broiler chickens from 18 samples of 5 commonly used feed grains (sorghum, wheat, maize, barley, triticale) were determined. The methodology to determine starch digestion rates in poultry is detailed herein. Starch digestion rates were not significantly different ($P = 0.128$) across the 18 feed grains, which reflects the wide variations that were observed within a given feedstuff. Nevertheless, starch digestion rates in broiler chickens offered wheat-based diets were significantly more rapid by 56.0% (0.117 versus 0.075 min^{-1}; $P = 0.012$) than their sorghum-based counterparts on the basis of a pair-wise comparison. In descending order, the following starch digestion rates were observed: wheat (0.117 min^{-1}), barley (0.104 min^{-1}), triticale (0.093 min^{-1}), maize (0.086 min^{-1}), sorghum (0.075 min^{-1}). The implications of these findings are discussed as they almost certainly have implications for poultry nutrition and the development of reduced crude protein diets for broiler chickens.

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1. Introduction

The relevance of starch and protein digestive dynamics to chicken-meat production has been reviewed by Liu and Selle (2015) and Selle and Liu (2019). The fundamental tenet is that an appropriate balance of glucose and amino acids should be made available at sites of skeletal protein synthesis to drive efficient growth performance. Glucose is derived from dietary starch and amino acids from dietary protein; thus, the digestive dynamics of both macronutrients are pivotal. While amino acids are the “building-blocks” of protein, the energy cost of whole-body protein synthesis equates to 5.35 MJ/g of protein in poultry (Aoyagi et al., 1988). Essentially, this energy input is derived from glucose, which emphasises the importance of starch digestion rates to ensure adequate energy is available at sites of protein deposition.

Even in isolation, the digestion rate of starch in broiler chickens is an intriguing subject because there are differences across feedstuffs in starch digestion rates along the small intestine (Weurding et al., 2001a). Also, sites of starch digestion have been shown to influence broiler growth performance (Weurding et al., 2003). Starch digestion rates of 5 wheat samples ranged from 1.80 to 2.56 h^{-1} and broiler diets based on these wheats quadratically influenced weight gain and FCR from 1 to 34 d as reported by Gutierrez del Alamo et al. (2009). Moreover, there are some indications that some slowly digestible starch may be advantageous. Herwig et al. (2019) compared semi-purified starch derived from wheat or peas as rapidly or slowly digestible starch sources, respectively. There was a quadratic response ($r^2 = 0.49$; $P < 0.001$) in gain-to-feed ratio to 31 d post–hatch in birds offered a range of 6 diets with these 2 starch sources. The quadratic regression predicted that

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the maximum gain-to-feed ratio would be generated by a diet containing a 75:25 blend of rapid (wheat) to slow (pea) starch, or some slowly digestible starch.

The advantages of slowly digestible starch have yet to be firmly established as are the underlying mechanisms. One interesting possibility is that slowly digestible starch may be sparing amino acids from catabolism in the gut mucosa (Enting et al., 2005). Both glucose and amino acids, especially glutamate and glutamine, are catabolised in avian enterocytes for energy provision (Watford et al., 1979). If this proposition is valid, energy would be more efficiently derived from glucose (Fleming et al., 1997) and post-enteral availability of amino acids would be enhanced.

The likelihood is that starch and protein digestive dynamics and the post-enteral availability of glucose and amino acids should be considered in tandem. The relevance of this was unequivocally demonstrated by Sydenham et al. (2017), who found that distal jejunal starch-to-protein digestibility ratios of 3.59 and 3.88 supported the maximum weight gain and minimum FCR, respectively in broiler chickens from 15 to 28 d post–hatch. Also, with diets formulated on the basis of pre-determined starch and protein digestion rates, Liu et al. (2020) found that broiler diets with a starch-to-protein digestion rate ratio of 1.66 generated the optimal FCR of 1.450 from 7 to 35 d post–hatch. Nevertheless, if practical nutritionists are to harness digestive dynamics into their formulation of broiler diets, starch and protein digestion rates of relevant feedstuffs need to be established. Thus, the purpose of this study was to determine the starch digestion rate constants in broiler chickens of multiple samples of commonly used feed grains including sorghum, wheat, maize, barley and triticale.

2. Materials and methods

All experimental procedures were approved by the Animal Ethics Committee of the University of Sydney (Project number 2016/1016).

2.1. Experimental design

The present study consisted of 18 dietary treatments, with 6 replicates per treatment (6 birds per cage). A total of 648 male Ross 308 broiler chicks were offered experimental diets from 21 to 28 d post–hatch. Nineteen cereal grains and cassava, including sorghum, wheat, maize, barley, triticale, oats and cassava were analysed for their respective chemical compositions (Tables 1–4).

2.2. Diet preparation

The 18 dietary treatments were formulated to standard 2014 Ross 308 broiler nutrient specifications such that they were iso-energetic and iso-nitrogenous to allow the comparison of the cereal grains. Each diet contained 650 g/kg of the respective cereal grain (Tables 5 and 6). Diets did not contain synthetic amino acids to limit any possible influence on digestive rate. All cereal grains were hammer-milled through a 4.0-mm screen before mixing and the diets were cold-pelleted through a 4.0-mm die. A dietary marker (Celite World Minerals, Lompoc, CA, USA) was included at 20 g/kg in diets as an inert acid insoluble ash marker in order to determine nutrient digestibility coefficients in 4 small intestinal sites. A commercial starter diet based on wheat with 2,900 kcal/kg energy and 220 g/kg crude protein (CP), was offered to broiler chickens from 1 to 21 d post–hatch.

2.3. Bird management

A proprietary starter diet was offered to birds from 0 to 21 d post–hatch. At 21 d post–hatch, a total of 720 male Ross 308 broilers were individually identified (wing-tags), weighed and allocated into bioassay cages (6 birds per cage) on the basis of body weights. Bird allocation was such that cage means and variations were almost identical. Each dietary treatment was offered to 6 replicate cages from 21 to 28 d post–hatch or a total of 108 cages (750 mm in width, 750 mm in length and 510 mm in height). Birds had unlimited access to feed and water under an “18-h-on-6-h-off” lighting regime in an environmentally controlled facility. An initial room temperature of 32 ± 1 °C was maintained for the first week, which was gradually decreased to 22 ± 1 °C by the end of the third week and maintained at this temperature for the duration of the feeding study.

2.4. Sample collection and chemical analysis

Initial and final body weights were determined and feed intakes (FI) recorded, from which FCR were calculated. Any dead or culled birds were removed on a daily basis and their body weights recorded and used to correct FCR calculations. Total excreta were collected from 25 to 27 d post–hatch from each cage to determine parameters of nutrient utilisation which included apparent metabolisable energy (AME), metabolisable energy-to-gross energy ratios (AME:GE), N retention and N-corrected apparent

Table 1
Feed grain identification.

Treatment	Code	Description	Supplier
1	Sorghum-1	Waxy sorghum White	Gatton, University of Queensland
2	Sorghum-2	Waxy sorghum Red	Gatton, University of Queensland
3	Sorghum-3	Pullulanase sorghum A	Gatton, University of Queensland
4	Sorghum-4	Pullulanase sorghum B	Gatton, University of Queensland
5	Sorghum-5	Red sorghum - Tiger	Murrumbidgee Irrigation Area, NSW
6	Sorghum-6	White sorghum - Liberty	Darling Downs, QLD
7	Sorghum-7	Sorghum 7895	Narrabri, University of Sydney
8	Wheat-1	Wheat high viscosity	Commercial feed mill - NSW
9	Wheat-2	Wheat low viscosity	Commercial feed mill - NSW
10	Wheat-3	Wheat Spitfire	Narrabri, University of Sydney
11	Wheat-4	Wheat JM	Camden, feedstock supplier
12	Maize-1	Maize 8108	Narrabri, University of Sydney
13	Maize-2	Maize JM	Camden, feedstock supplier
14	Barley-1	Barley 3765	Narrabri, University of Sydney
15	Barley-2	Barley JM	Camden, feedstock supplier
16	Barley-3	Barley	Commercial feed mill - Victoria
17	Triticale-1	Triticale 6871	Narrabri, University of Sydney
18	Triticale-2	Triticale	Commercial feed mill - NSW

Table 2
Analysed chemical compositions in 7 sorghum samples (as-is basis, g/kg)[1].

Item	Sorghum-1	Sorghum-2	Sorghum-3	Sorghum-4	Sorghum-5	Sorghum-6	Sorghum-7	Mean	CV, %	Min	Max
Histidine	2.76	2.73	2.51	2.51	2.37	2.42	2.59	2.56	6	2.37	2.76
Serine	5.00	4.68	4.16	4.36	4.06	4.14	4.21	4.37	8	4.06	5.00
Arginine	3.6	3.71	3.54	3.9	3.4	3.01	3.41	3.51	8	3.01	3.90
Glycine	2.74	2.83	2.68	2.69	2.68	2.56	2.66	2.69	3	2.56	2.83
Aspartic acid	7.78	7.37	6.49	6.83	7	5.95	6.55	6.85	9	5.95	7.78
Glutamic acid	26.73	23.81	20.46	22.1	20.07	20.47	21.33	22.14	11	20.07	26.73
Threonine	3.64	4.87	3.08	3.17	2.95	3.01	3.04	3.39	20	2.95	4.87
Alanine	10.21	9.15	7.87	8.48	7.88	7.93	8.1	8.52	10	7.87	10.21
Proline	9.83	8.9	7.65	8.13	7.35	7.94	7.99	8.26	10	7.35	9.83
Lysine	1.96	2.13	2.2	2.19	2.2	1.84	2.01	2.08	7	1.84	2.20
Tyrosine	2.8	2.96	1.55	2.31	1.73	1.32	1.81	2.07	31	1.32	2.96
Methionine	1.41	1.49	1.16	1.34	1.1	1.21	1.43	1.31	11	1.10	1.49
Valine	5.81	5.42	4.89	5.12	4.82	4.68	4.88	5.09	8	4.68	5.81
Isoleucine	5.17	4.69	4.06	4.28	3.93	3.99	4.06	4.31	11	3.93	5.17
Leucine	17.46	15.45	13.11	14.07	12.67	13.38	13.51	14.24	12	12.67	17.46
Phenylalanine	6.94	6.16	5.29	5.62	5.03	5.36	5.35	5.68	12	5.03	6.94
Total protein	139	134	117	125	120	111	121	124	8	111	139
Ca	0.13	0.26	0.2	0.17	0.31	0.09	0.12	0.18	43	0.09	0.31
K	3.33	3.74	3.43	3.18	3.71	2.52	3.03	3.28	13	2.52	3.74
Na	0.03	0.04	0.02	0.02	0.01	0.01	0	0.02	72	0.00	0.04
P	3.28	3.81	3.71	3.65	3.16	2.07	2.48	3.17	21	2.07	3.81
Protein solubility index	29.3	28.9	20.9	19	45.1	36.1	31.8	30.2	29	19.0	45.1
Pepsin digestibility, %	91.8	91.6	85.7	89.9	90.4	90.4	91.4	90.2	2	85.7	91.8
Starch	523	538	557	531	517	515	617	543	7	515	617
NIR estimates											
Ether extract	40	28	29	36	30	27	29	31	15	27	40
Crude fibre	20	24	24	21	20	27	23	23	11	20	27
Acid detergent fibre	28	55	55	46	40	59	56	48	23	28	59
Neutral detergent fibre	101	109	111	124	109	112	114	111	6	101	124

CV = coefficient of variation; NIR = near-infrared spectroscopy.
[1] Chemical analyses were conducted in duplicate.

Table 3
Analysed chemical compositions of wheat and maize samples (as-is basis, g/kg)[1].

Item	Wheat								Maize			
	Wheat-1	Wheat-2	Wheat-3	Wheat-4	Mean	CV	Min	Max	Maize-1	Maize-2	Mean	CV
Histidine	3.06	3.04	3.35	2.88	3.08	6	2.88	3.35	2.58	3.01	2.80	11
Serine	5.01	5.05	5.67	4.95	5.17	6	4.95	5.67	3.45	3.64	3.55	4
Arginine	4.88	4.97	5.8	4.46	5.03	11	4.46	5.80	3.31	3.62	3.47	6
Glycine	4.15	4.17	4.56	4.06	4.24	5	4.06	4.56	2.42	2.75	2.59	9
Aspartic acid	5.28	5.31	5.97	5.09	5.41	7	5.09	5.97	4.79	5.32	5.06	7
Glutamic acid	34.96	34.75	39.56	35.03	36.08	6	34.75	39.56	14.38	15.07	14.73	3
Threonine	3.25	3.27	3.55	3.11	3.30	6	3.11	3.55	2.55	2.78	2.67	6
Alanine	3.48	3.5	3.81	3.34	3.53	6	3.34	3.81	5.01	5.19	5.10	2
Proline	11.17	11.15	12.76	11.38	11.62	7	11.15	12.76	6.58	6.96	6.77	4
Lysine	3.06	3.08	3.27	2.88	3.07	5	2.88	3.27	2.02	2.44	2.23	13
Tyrosine	1.57	1.61	2.16	1.35	1.67	21	1.35	2.16	1.51	1.32	1.42	9
Methionine	1.39	1.48	1.76	1.26	1.47	14	1.26	1.76	1.11	1.08	1.10	2
Valine	4.83	4.81	5.4	4.65	4.92	7	4.65	5.40	3.5	3.92	3.71	8
Isoleucine	4.07	4.03	4.48	3.86	4.11	6	3.86	4.48	2.69	2.87	2.78	5
Leucine	7.51	7.51	8.48	7.45	7.74	6	7.45	8.48	9.41	9.73	9.57	2
Phenylalanine	5.35	5.35	5.97	5.28	5.49	6	5.28	5.97	3.78	3.92	3.85	3
Total protein	144	141	161	140	147	7	140	161	90	100	95	7
Ca	0.3	0.3	0.44	0.36	0.35	19	0.30	0.44	0.02	0.05	0.04	61
K	3.07	3.06	3.17	4.09	3.35	15	3.06	4.09	2.9	3.55	3.23	14
Na	0.02	0.02	0.02	0.01	0.02	29	0.01	0.02	–	–	0.00	
P	1.98	1.94	2.83	2.49	2.31	19	1.94	2.83	2.4	2.99	2.70	15
Protein solubility index	87	71.9	73.9	71.1	76.0	10	71.1	87.0	–	–	–	–
Pepsin digestibility, %	96.9	97.5	98.1	97.7	97.6	1	96.9	98.1	–	–	–	–
Starch	516	484	604	630	559	12	484	630	549	513	531	5
NIR estimates												
Ether extract	18	18	19	19	19	3	18	19	34	56	45	35
Crude fibre	52	21	22	22	29	52	21	52	19	109	64	99
Acid detergent fibre	69	24	27	27	37	59	24	69	32	136	84	88
Neutral detergent fibre	114	96	99	103	103	8	96	114	110	274	192	60

CV = coefficient of variation; NIR = near-infrared spectroscopy.
[1] Chemical analyses were conducted in duplicate.

Table 4
Analysed chemical compositions of barley and triticale samples (as-is basis, g/kg)[1].

Item	Barley							Triticale				Soybean meal
	Barley S1	Barley S2	Barley S3	Mean	CV	Min	Max	Triticale S1	Triticale S2	Mean	CV	
Histidine	2.4	2.18	2.6	2.39	9	2.18	2.60	3.08	2.27	2.68	21	11.13
Serine	3.83	3.17	3.9	3.63	11	3.17	3.90	4.89	4.06	4.48	13	19.99
Arginine	4.15	3.78	4.7	4.21	11	3.78	4.70	5.39	4.15	4.77	18	29.52
Glycine	3.26	2.96	3.5	3.24	8	2.96	3.50	4.16	3.39	3.78	14	15.23
Aspartic acid	5.43	4.77	5.9	5.37	11	4.77	5.90	6.76	5.33	6.05	17	42.38
Glutamic acid	24.08	17.99	24.3	22.12	16	17.99	24.30	30.01	25.1	27.56	13	71.71
Threonine	3	2.67	3.2	2.96	9	2.67	3.20	3.45	2.74	3.10	16	15.93
Alanine	3.38	2.85	3.5	3.24	11	2.85	3.50	3.96	3.17	3.57	16	15.51
Proline	10.7	7.84	10.8	9.78	17	7.84	10.80	10.28	8.31	9.30	15	20.08
Lysine	3.39	3.06	3.8	3.42	11	3.06	3.80	3.72	3.02	3.37	15	24.30
Tyrosine	1.16	1.3	1.6	1.35	17	1.16	1.60	1.57	1.28	1.43	14	11.86
Methionine	1.03	0.98	1.1	1.04	6	0.98	1.10	1.39	1.05	1.22	20	2.73
Valine	4.71	3.92	4.7	4.44	10	3.92	4.71	5.04	3.98	4.51	17	19.53
Isoleucine	3.52	2.85	3.6	3.32	12	2.85	3.60	4.01	3.13	3.57	17	19.21
Leucine	6.67	5.55	6.8	6.34	11	5.55	6.80	7.4	5.95	6.68	15	32.03
Phenylalanine	5.22	4	5.5	4.91	16	4.00	5.50	5.24	4.3	4.77	14	21.81
Total protein	122	92	118	111	15	92	122	139	111	125	16	488
Ca	0.39	0.43	0.25	0.36	26	0.25	0.43	0.23	0.31	0.27	21	3.22
K	5.38	3.62	4.84	4.61	20	3.62	5.38	4.54	4.83	4.69	4	23.2
Na	0.06	0.04	0.2	0.10	87	0.04	0.20	0.01	0.08	0.05	110	0.01
P	2.86	2.61	3.66	3.04	18	2.61	3.66	2.54	3.43	2.99	21	6.90
Protein solubility index		85.6	70.5	78.05	14	70.5	85.6	84.4	68.1	76.25	15	–
Pepsin digestibility, %		89.3	92.9	91.10	3	89.3	92.9	96.7	96.1	96.40	0	–
Starch	508	626	507	547	13	507	626	594	505	550	11	–
NIR estimates												
Ether extract	25	25	13	21.00	33	13	25	–	25			24
Crude fibre	39	45	–	42.00	10	39	45	–	49			102
Acid detergent fibre	47	51	–	49	6	47	51	–	54			147
Neutral detergent fibre	163	170	–	167	3	163	170	–	185			210

CV = coefficient of variation; NIR = near-infrared spectroscopy.
[1] Chemical analyses were conducted in duplicate.

metabolisable energy (AMEn). They were expressed on a dry matter basis. Feed and water intakes during this period were recorded. Excreta were air-forced oven dried for 24 h until no further loss of moisture at 80 °C. The gross energy of diets and excreta were determined via bomb calorimetry using an adiabatic calorimeter (Parr 1281 bomb calorimeter, Parr Instruments Co., Moline, IL). The AME was calculated by the following equation:

$$\text{AME}_{\text{diet}} = \frac{(\text{FI} \times \text{GE}_{\text{diet}}) - (\text{Excreta output} \times \text{GE}_{\text{excreta}})}{\text{FI}}$$

N-corrected AME values were calculated by correcting to zero N retention, using the factor of 36.54 kJ/g (Hill and Anderson, 1958).

N retention was calculated by the following equation:

$$\text{Retention }(\%) = \frac{(\text{FI} \times \text{Nitrogen}_{\text{diet}}) - (\text{Excreta output} \times \text{Nitrogen}_{\text{excreta}})}{(\text{FI} \times \text{Nitrogen}_{\text{diet}})} \times 100$$

At day 28, birds were euthanized by an intravenous injection of sodium pentobarbitone 3 h after the chicken house was illuminated. Feed intake over the 24 h immediately prior to sampling was recorded. The pH of digesta within the gizzard was determined in situ with a pH probe (EZ Do model 7011, Pakistan). Gizzard and pancreas were removed and weighed to determine their relative weights. The small intestine was removed and divided into the 4 segments: proximal jejunum (PJ), distal jejunum (DJ), proximal ileum (PI), distal ileum (DI). The 4 segments were demarcated by the end of the duodenal loop, Meckel's diverticulum and the ileo-caecal junction and their mid-points. Digesta was collected in its entirety from each segment. Digesta samples were gently expressed from each segment, pooled by cage, homogenized, freeze dried and weighed to determine the mean retention time (MRT) and the apparent digestibility of starch and N.

Mean retention time (min) was calculated using the following equation (Wilson and Leibholz, 1981; Weurding et al., 2001a):

$$\text{MRT} = (1{,}440 \times \text{AIA}_{\text{digesta}} \times \text{W})/(\text{FI}_{24\text{hr}} \times \text{AIA}_{\text{feed}}),$$

where $\text{AIA}_{\text{digesta}}$ is the acid insoluble ash (AIA) concentration in the digesta (mg/g), W is the weight of dry gut content (g), $\text{FI}_{24\text{hr}}$ is the FI over 24 h before sampling (g), AIA_{feed} is the AIA concentration in the feed (mg/g) and 1,440 equals minutes per day.

Starch concentration in diets and digesta was determined by a procedure based on dimethyl sulphoxide, α-amylase and amyloglucosidase as described by Mahasukhonthachat et al. (2010). Nitrogen and AIA concentrations were determined as outlined in Siriwan et al. (1993). Apparent digestibility coefficients of starch and N were calculated by the following equation:

$$\text{Digestibility coefficient} = \frac{(\text{Nutrient/AIA})_{\text{diet}} - (\text{Nutrient/AIA})_{\text{digesta}}}{(\text{Nutrient/AIA})_{\text{diet}}}$$

Starch and protein (N) disappearance rates (g/d per bird) were deduced from the following equation:

Nutrient disappearance rate (g/d per bird) = Average daily FI (21 to 28 d) × Dietary nutrient × Apparent digestibility coefficient

The pattern of fractional digestibility coefficients was calculated as previously described in (Liu et al., 2013). Briefly, it is derived by relating the digestion coefficient at each site with the digestion time (t). The digestion time (t) was calculated from the sum of the MRT determined in each intestinal segment. The curve of digestion is often described by the exponential model developed by Orskov and McDonald (1979): $D_t = D_\infty(1 - e^{-kt})$, where D_t (g/g starch or N) is the starch or N digested at time t (min); the fraction D_∞ is the amount of potential digestible starch or N (asymptote) (g/g); and k (per unit time, min^{-1}) is defined as digestion rate constant. This mathematical model is applied with the assumptions that glucose and amino acid absorption do not take place proximal to the small intestine.

2.5. Statistical analysis

Experimental data were analysed as one-way ANOVA and pairwise comparisons were drawn by Student's t-test via JMP Pro 13 (SAS, 2016 Institute Inc, JMP Software, Cary, NC, USA). The experimental units for growth performance, nutrient utilisation and apparent digestibilities were cage means and differences were considered significant at the 5% level of probability by Tukey test.

3. Results

The effects of diets based on multiple samples of commonly used feed grains on a collective basis on predicted potential digestible starch, starch digestion rate and growth performance are shown in Table 7. There were no treatment effects on potential digestible starch ($P > 0.95$); however, there was a trend to towards treatment effects on starch digestion rates ($P < 0.15$). Sorghum-based diets generated slower starch digestion rates than wheat-based diets by 35.9% (0.075 versus 0.117 min^{-1}; $P = 0.012$) and this difference was significant from a pair-wise comparison. The mean and standard deviation of starch digestion rates for sorghum-based diets was 0.075 ± 0.0435 min^{-1} which is indicative of a wide variation within a given feed grain. There were significant effects ($P < 0.005$) on weight gain from 21 to 28 d post–hatch where birds

Table 5
Ingredients and nutrient specifications of dietary treatments 1 to 11 (as-is basis, g/kg).

Item	Diet 1	Diet 2	Diet 3	Diet 4	Diet 5	Diet 6	Diet 7	Diet 8	Diet 9	Diet 10	Diet 11
	Sorghum-1	Sorghum-2	Sorghum-3	Sorghum-4	Sorghum-5	Sorghum-6	Sorghum-7	Wheat-1	Wheat-2	Wheat-3	Wheat-4
Ingredients											
Grain	650	650	650	650	650	650	650	650	650	650	650
Soybean meal	198	194	177	185	181	172	181	181	177	162	178
Soy oil	44.2	43.6	40.8	42.1	41.3	39.9	41.5	57.9	57.3	54.5	57.1
Limestone	11.3	11.1	11.8	11.5	11.5	12.1	11.8	14	14.1	14.4	13.9
Di-calcium phosphate	15.5	15.3	14.7	15	14.9	14.5	14.9	10.9	10.8	10.2	10.7
Salt	1.1	1	0.6	0.7	0.7	0.4	0.7	1.8	1.8	1.4	1.7
Sodium bicarbonate	2.6	2.5	2.4	2.4	2.4	2.3	2.4	1.3	1.2	1.1	1.2
Choline chloride 60%[1]	4.5	4.5	4.5	4.5	4.5	4.5	4.5	4.5	4.5	4.5	4.5
Isolated soy protein	50.3	55.5	75.4	66.3	71.2	82.1	70.7	55	58.9	77.9	59.9
Premix[2]	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5
Celite	20	20	20	20	20	20	20	20	20	20	20
Sand	0	0	0	0	0	0	0	1	2	2	1
Calculated nutrients											
Crude protein	220	220	220	220	220	220	220	220	220	220	220
AMEn, kcal/kg	3,150	3,150	3,150	3,150	3,150	3,150	3,150	3,150	3,150	3,150	3,150
Lysine[3]	9.2	9.5	10.4	10.0	10.2	10.5	10.1	9.8	10.0	10.9	9.9
Methionine[3]	2.1	2.2	2.2	2.2	2.1	2.3	2.3	2.1	2.2	2.6	2.1
Threonine[3]	7.3	8.3	7.6	7.4	7.4	7.7	7.4	7.0	7.1	7.7	7.0
Valine[3]	10.0	9.9	10.2	10.1	10.0	10.3	10.0	9.3	9.4	10.3	9.3
Isoleucine[3]	9.6	9.4	9.7	9.5	9.4	9.8	9.5	8.8	8.8	9.8	8.8
Ca	8.7	8.7	8.7	8.7	8.7	8.7	8.7	8.7	8.7	8.7	8.7
Total P	7.1	7.4	7.2	7.3	6.9	6.1	6.5	5.2	5.1	5.6	5.5
Available P	3.9	3.9	3.9	3.9	3.9	3.9	3.9	3.9	3.9	3.9	3.9
Ether extract	31	23	23	28	24	22	23	16	16	16	17
Crude fibre	33	35	34	33	31	35	33	52	32	31	32
Acid detergent fibre	47	64	62	57	53	64	63	71	42	41	44
Neutral detergent fibre	107	112	110	119	109	109	112	112	100	98	104
Choline	2	2	2	2	2	2	2	2	2	2	2
Na	1.6	1.6	1.6	1.6	1.6	1.6	1.6	1.6	1.6	1.6	1.6
Cl	2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.3
K	6.8	7	6.4	6.4	6.7	5.7	6.2	6.3	6.2	5.9	6.8
DEB[4], mEq/kg	179	183	168	169	176	150	164	165	163	156	179
Analysed concentrations											
Starch	333	346	344	337	333	324	361	327	299	323	363
Protein (N × 6.25)	234	227	232	228	237	228	232	213	230	248	227

[1] Contains 447.6 g/kg choline.

[2] The vitamin-mineral premix supplied per tonne of feed: [MIU] retinol 12, cholecalciferol 5, [g] tocopherol 50, menadione 3, thiamine 3, riboflavin 9, pyridoxine 5, cobalamin 0.025, niacin 50, pantothenate 18, folate 2, biotin 0.2, copper 20, iron 40, manganese 110, cobalt 0.25, iodine 1, molybdenum 2, zinc 90, selenium 0.3.

[3] All amino acids are on total basis.

[4] $\text{DEB} = \text{Na}^+ + \text{K}^+ - \text{Cl}^-$.

Table 6
Ingredients and nutrient composition and nutrient of dietary treatments 12 to 18 (as-is basis, g/kg).

Item	Diet 12	Diet 13	Diet 14	Diet 15	Diet 16	Diet 17	Diet 18
	Maize-1	Maize-2	Barley-1	Barley-2	Barley-3	Triticale-1	Triticale-2
Ingredients							
Grain	650	650	650	650	650	650	650
Soybean meal	173	183	150	152	146	159	159
Soy oil	23.2	24.9	59.8	56.3	59.1	61.7	61.7
Limestone	13	12.7	14.1	12.1	14.4	12.7	12.7
Di-calcium phosphate	13.2	13.6	10.7	9.9	10.6	13.4	13.4
Salt	1.3	1.5	0.4	0	0.3	2	2
Sodium bicarbonate	0.6	0.7	2.1	2.1	1.8	0.5	0.5
Choline chloride 60%[1]	4.5	4.5	4.5	4.5	4.5	4.5	4.5
Isolated soy protein	96	84.4	86	91	89.8	68.7	68.7
Premix[2]	2.5	2.5	2.5	2.5	2.5	2.5	2.5
Celite	20	20	20	20	20	20	20
Sand	3	2	0	0	1	5	5
Calculated nutrients							
Crude protein	220	220	220	220	220	220	220
AMEn, kcal/kg	3150	3150	3150	3150	3150	3150	3150
Lysine[3]	11.5	11.3	11.2	11.3	11.6	10.5	10.1
Methionine[3]	2.4	2.3	2.2	2.2	2.3	2.2	2.0
Threonine[3]	7.9	7.8	7.4	7.4	7.6	7.2	6.8
Valine[3]	10.2	10.1	10.0	9.8	10.1	9.6	8.9
Isoleucine[3]	9.7	9.4	9.3	9.1	9.5	9.0	8.4
Ca	8.7	8.7	8.7	8.7	7.8	8.7	8.7
Total P	5.5	6.2	6.6	5.8	5.5	6.3	6
Available P	3.9	3.9	3.9	3.9	3.9	3.9	3.9
Ether extract	26	41	20	20	12	4	20
Crude fibre	30	90	41	44	15	16	48
Acid detergent fibre	46	115	53	55	21	23	58
Neutral detergent fibre	108	217	137	140	31	33	154
Choline	2	2	2	2	2	2	2
Na	1.6	1.6	1.6	1.6	1.6	1.6	1.6
Cl	2.3	2.3	2.3	2.3	2.3	2.3	2.3
K	6.8	6	6.6	7.1	5.9	6.6	6.7
DEB[4], mEq/kg	179	158	173	185	155	173	176
Analysed concentrations							
Starch	355	336	329	367	332	347	320
Protein (N × 6.25)	227	225	228	222	232	229	215

[1] Contains 447.6 g/kg choline.
[2] The vitamin-mineral premix supplied per tonne of feed: [MIU] retinol 12, cholecalciferol 5, [g] tocopherol 50, menadione 3, thiamine 3, riboflavin 9, pyridoxine 5, cobalamin 0.025, niacin 50, pantothenate 18, folate 2, biotin 0.2, copper 20, iron 40, manganese 110, cobalt 0.25, iodine 1, molybdenum 2, zinc 90, selenium 0.3.
[3] All amino acids are on total basis.
[4] DEB = $Na^+ + K^+ - Cl^-$.

Table 7
Effects of diets based on commonly used feed grains on predicted PDS and SDR and growth performance from 21 to 28 d post–hatch.

Feed grain[1]	Starch parameters		Growth performance		
	PDS, g/g	SDR, min^{-1}	Weight gain, g/bird	Feed intake, g/bird	FCR, g/g
Sorghum (7)	0.850	0.075	$631^{a,b}$	1,023	1.649
Wheat (4)	0.849	0.117	669^{c}	1,032	1.549
Maize (2)	0.854	0.086	681^{c}	1,031	1.518
Barley (3)	0.861	0.104	607^{a}	1,006	1.667
Triticale (2)	0.951	0.093	$650^{b,c}$	1,035	1.601
SEM	0.0152	0.0136	13.37	10.89	0.0385
Significance (*P*-value)	0.988	0.128	0.004	0.440	0.052
LSD ($P < 0.05$)	–	–	37.5	–	–

PDS = potential digestible starch; SDR = starch digestion rate; LSD = Least Significant Difference.
[a, b, c] Means within a column not sharing a common superscript are significantly different at the 5% level of probability.
[1] Number in parentheses are the number of samples.

offered maize-based diets outperformed their barley counterparts by 12.2% (681 versus 607 g/bird). Treatment effects for FCR closely approached significance ($P = 0.052$). For example, broiler chickens offered maize-based were more efficient converters than birds offered sorghum-based diets by 7.94% (1.518 versus 1.649; $P = 0.028$) on the basis of a pair-wise comparison.

The influence of dietary treatments on growth performance and nutrient utilisation in broiler chickens from 21 to 28 d post–hatch on an individual basis is shown in Table 8. When the feed grains with multiple samples are considered, the overall performance was a weight gain of 647 g/d, FI of 1,025 g/d with an FCR of 1.597. There were highly significant differences between feed grains and, on average, maize was numerically superior supporting a weight gain of 681 g/d, FI of 1,031 g/d with an FCR of 1.518. Highly significant differences for parameters of nutrient utilisation were also observed and overall mean outcomes were an

Table 8
The influence of dietary treatments on growth performance and nutrient utilisation in broiler chickens from 21 to 28 d post–hatch.

Treatment		Growth performance			Nutrient utilisation			
Diet	Grain	Weight gain, g/bird	Feed intake, g/bird	FCR, g/g	AME, MJ/kg	AME:GE, MJ/MJ	N retention, %	AMEn,MJ/kg
1	Sorghum-1	603^{cd}	973^{fg}	1.622^{bcd}	14.96^{abcd}	0.790^{ab}	54.99^{abcd}	13.60^{abc}
2	Sorghum-2	539^{e}	985^{efg}	1.938^{a}	15.14^{abc}	0.791^{ab}	55.99^{abc}	13.72^{abc}
3	Sorghum-3	630^{bc}	$1,024^{bcdef}$	1.633^{bcd}	14.70^{bcde}	0.766^{bcd}	53.95^{abcd}	13.30^{cdef}
4	Sorghum-4	645^{abc}	$1,056^{abc}$	1.637^{bcd}	13.83^{fgh}	0.719^{fg}	43.87^{e}	12.67^{f}
5	Sorghum-5	645^{abc}	$1,049^{abcd}$	1.628^{bcd}	14.61^{cdef}	0.764^{bcd}	52.54^{abcd}	13.21^{cdef}
6	Sorghum-6	646^{abc}	$1,013^{cdefg}$	1.572^{bcde}	15.01^{abcd}	0.788^{ab}	56.77^{abc}	13.55^{abcd}
7	Sorghum-7	706^{a}	$1,064^{ab}$	1.509^{cde}	14.90^{bcd}	0.776^{abc}	54.05^{abcd}	13.49^{bcde}
8	Wheat-1	628^{bc}	$1,034^{abcde}$	1.647^{bcd}	14.99^{abcd}	0.762^{bcde}	58.58^{ab}	13.53^{bcd}
9	Wheat-2	677^{ab}	$1,009^{cdefg}$	1.493^{de}	14.26^{def}	0.741^{cdef}	56.20^{abc}	12.82^{ef}
10	Wheat-3	703^{a}	$1,005^{defg}$	1.432^{e}	14.29^{def}	0.740^{cdef}	54.17^{abcd}	12.89^{def}
11	Wheat-4	667^{ab}	$1,081^{a}$	1.624^{bcd}	13.08^{h}	0.688^{gh}	47.28^{de}	11.82^{g}
12	Maize-1	680^{ab}	$1,023^{bcdef}$	1.507^{cde}	15.53^{ab}	0.814^{a}	58.72^{ab}	14.02^{ab}
13	Maize-2	681^{ab}	$1,038^{abcd}$	1.528^{cde}	15.78^{a}	0.815^{a}	60.33^{a}	14.25^{a}
14	Barley-1	602^{cd}	$1,028^{bcde}$	1.714^{b}	13.19^{gh}	0.679^{h}	53.14^{abcd}	11.79^{g}
15	Barley-2	563^{de}	965^{g}	1.724^{b}	15.01^{abcd}	0.765^{bcd}	57.44^{abcd}	12.73^{f}
16	Barley-3	656^{abc}	$1,024^{bcdef}$	1.564^{bcde}	13.97^{efg}	0.732^{def}	52.30^{bcd}	12.63^{f}
17	Triticale-1	666^{ab}	$1,012^{cdefg}$	1.521^{cde}	14.40^{cdef}	0.745^{cdef}	54.82^{abcd}	13.03^{cdef}
18	Triticale-2	634^{bc}	$1,058^{abc}$	1.680^{bc}	13.93^{efg}	0.724^{efg}	50.47^{cde}	12.64^{f}
SEM		21.84	1,7.97	0.0653	0.299	0.0138	2.847	0.250
Significance (*P*-value)		<0.0001	<0.001	<0.001	<0.0001	<0.0001	0.018	<0.0001

$^{a–h}$ Means within a column not sharing a common superscript are significantly different at the 5% level of probability.

Table 9
The influence of dietary treatments on apparent starch digestibility coefficients and apparent starch disappearance rates in the proximal jejunum (PJ), distal jejunum (DJ), proximal ileum (PI) and distal ileum (DI) in broiler chickens at 28 d post–hatch.

Treatment		Apparent starch digestibility coefficients				Apparent starch disappearance rates, g/d per bird			
Diet	Grain	PJ	DJ	PI	DI	PJ	DJ	PI	DI
1	Sorghum-1	0.623	0.821^{bcd}	0.909^{abc}	0.942^{ab}	32.76^{cdefg}	43.06^{cde}	47.67^{bcde}	49.35^{bcd}
2	Sorghum-2	0.610	0.784^{bcde}	0.876^{bcde}	0.889^{bcde}	31.22^{defg}	40.21^{defg}	45.06^{def}	45.72^{defgh}
3	Sorghum-3	0.654	0.753^{cdef}	0.830^{efgh}	0.850^{defg}	37.30^{abcd}	42.67^{cde}	47.01^{cde}	48.20^{cdef}
4	Sorghum-4	0.637	0.767^{bcde}	0.841^{defgh}	0.842^{efg}	38.97^{abc}	46.96^{bcd}	51.54^{ab}	51.60^{bc}
5	Sorghum-5	0.634	0.796^{bcde}	0.874^{bcdef}	0.906^{abcd}	35.46^{bcdef}	44.46^{bcd}	48.82^{bcd}	50.59^{bc}
6	Sorghum-6	0.584	0.737^{efg}	0.829^{efgh}	0.866^{cdef}	33.25^{bcdefg}	41.87^{def}	47.04^{cde}	49.19^{bcde}
7	Sorghum-7	0.534	0.682^{fg}	0.833^{efgh}	0.831^{fg}	30.20^{efg}	38.51^{efg}	47.04^{cde}	46.92^{defg}
8	Wheat-1	0.657	0.745^{def}	0.799^{h}	0.831^{fg}	36.01^{abcde}	40.87^{defg}	43.89^{ef}	45.67^{efgh}
9	Wheat-2	0.603	0.755^{bcdef}	0.810^{fgh}	0.820^{fg}	32.44^{cdefg}	40.64^{defg}	43.61^{ef}	44.16^{ghi}
10	Wheat-3	0.640	0.759^{bcdef}	0.859^{cdefgh}	0.806^{g}	34.24^{bcdef}	40.48^{defg}	45.51^{def}	42.69^{hij}
11	Wheat-4	0.603	0.662^{g}	0.669^{i}	0.736^{h}	32.87^{cdefg}	36.20^{g}	36.56^{h}	40.19^{j}
12	Maize-1	0.717	0.834^{ab}	0.928^{ab}	0.955^{a}	42.73^{a}	49.69^{a}	55.27^{a}	56.88^{a}
13	Maize-2	0.735	0.906^{a}	0.948^{a}	0.959^{a}	40.09^{ab}	49.40^{a}	51.68^{ab}	52.28^{b}
14	Barley-1	0.610	0.780^{bcde}	0.805^{gh}	0.851^{defg}	28.67^{fg}	36.42^{g}	37.63^{gh}	39.73^{j}
15	Barley-2	0.706	0.813^{bcde}	0.903^{abcd}	0.915^{abc}	34.83^{bcdef}	40.08^{defg}	44.53^{ef}	45.12^{fgh}
16	Barley-3	0.568	0.770^{bcde}	$0.863^{bcdefgh}$	0.861^{cdefg}	27.22^{g}	37.02^{fg}	41.50^{fg}	41.40^{ij}
17	Triticale-1	0.634	0.790^{bcde}	0.831^{efgh}	0.846^{efg}	29.37^{efg}	36.49^{g}	38.40^{gh}	39.06^{j}
18	Triticale-2	0.679	0.832^{abc}	0.870^{bcdefg}	0.867^{cdef}	39.93^{ab}	48.72^{ab}	51.01^{bc}	50.81^{bc}
	SEM	0.0422	0.0289	0.0232	0.0202	2.466	1.736	1.452	1.299
	P-value	0.119	<0.0001	<0.0001	<0.0001	<0.001	<0.0001	<0.0001	<0.0001

$^{a–j}$ Means within a column not sharing a common superscript are significantly different at the 5% level of probability.

AME of 14.55 MJ/kg, an ME:GE ratio of 0.755, N retention of 54.76% and an AMEn of 13.10 MJ/kg when the same comparison is drawn. Again, maize was numerically superior supporting an AME of 15.16 MJ/kg, an ME:GE ratio of 0.815, N retention of 59.53% and an AMEn of 14.14 MJ/kg.

The effects of feed grains on apparent digestibility coefficients and disappearance rates of starch in 4 intestinal segments at 28 d post–hatch are shown in Table 9. There were highly significant differences in starch digestibility coefficients across all dietary treatments; however, on an overall basis, digestibility coefficients progressively increased from 0.651 in PJ, 0.788 in DJ, 0.862 in PI to 0.876 in DI. The highest distal ileal digestibility coefficient in each of the starch sources ranged from 0.831 in wheat, 0.867 in triticale, 0.915 in barley, 0.942 in sorghum, 0.952 in cassava, 0.959 in maize to 0.987 in oats. Similarly, there were highly significant differences in starch disappearance rates, which progressively increased from 33.98 g/d per bird in PJ, 41.19 g/d per bird in DJ, 45.00 g/d per bird in PI to 45.90 g/d per in DI across all 18 treatments. The highest distal ileal starch disappearance rate ranged from 27.11 g/d per bird in oats, 45.12 g/d per bird in barley, 45.67 g/d per bird in wheat, 50.81 g/d per bird in triticale, 51.34 g/d per bird in cassava, 51.60 g/d per bird in sorghum to 56.88 g/d per bird in maize.

The influence of dietary treatments on mean digesta retention times in 4 small intestinal segments in broiler chickens at 28 d post–hatch is shown in Table 10. There was no significant treatment effect on the retention of digesta in the distal jejunum; otherwise, significant effects were observed. Overall retention times ranged from 17.9 min in PJ to 36.3 min in DJ, 51.1 min in PI and to 47.1 min in DI. Thus, digesta was retained in the small intestine for an average of 152 min or about 2.5 h. Results for predicted

Table 10
The influence of dietary treatments on mean retention time of digesta in the proximal jejunum (PJ), distal jejunum (DJ), proximal ileum (PI) and distal ileum (DI) of broiler chickens from at 28 d post–hatch and predicted potential digestible starch (PDS) and starch digestion rate (SDR).

Treatment		Retention times, min					Starch parameters	
Diet	Grain	PJ	DJ	PI	DI	Total	PDS, g/g	SDR, min^{-1}
1	Sorghum-1	15.0	37.6	58.6^{ab}	59.9^{a}	171^{abc}	0.906^{ab}	0.102
2	Sorghum-2	17.5	30.7	54.6^{abcd}	48.1^{cde}	151^{abcde}	0.869^{bcde}	0.086
3	Sorghum-3	24.9	39.1	59.4^{ab}	57.7^{abc}	181^{a}	0.831^{defg}	0.060
4	Sorghum-4	24.1	39.0	57.7^{abc}	48.4^{bcde}	169^{abcd}	0.828^{defg}	0.067
5	Sorghum-5	17.1	30.9	47.5^{cde}	44.4^{cde}	140^{bcde}	0.890^{bc}	0.088
6	Sorghum-6	22.5	35.4	62.0^{a}	59.0^{ab}	179^{ab}	0.836^{cdefg}	0.055
7	Sorghum-7	16.0	38.4	53.5^{abcde}	57.9^{abc}	166^{abcde}	0.813^{fg}	0.067
8	Wheat-1	17.5	38.3	46.9^{cde}	41.1^{de}	144^{cde}	0.798^{g}	0.153
9	Wheat-2	17.7	34.3	47.2^{cde}	38.0^{e}	137^{cde}	0.804^{g}	0.094
10	Wheat-3	19.9	38.9	53.9^{abcde}	41.4^{de}	154^{abcde}	0.831^{defg}	0.137
11	Wheat-4	22.2	42.1	49.2^{bcde}	43.9^{de}	157^{abcde}	0.702^{h}	0.086
12	Maize-1	19.3	34.1	59.3^{ab}	47.9^{cde}	161^{abcde}	0.917^{ab}	0.090
13	Maize-2	16.1	53.0	47.5^{cde}	42.4^{de}	159^{abcde}	0.951^{a}	0.083
14	Barley-1	10.2	31.9	45.3^{de}	41.8^{de}	129^{e}	0.816^{efg}	0.132
15	Barley-2	15.3	33.6	44.6^{de}	40.1^{e}	134^{de}	0.882^{bcd}	0.110
16	Barley-3	17.7	42.0	51.6^{abcde}	51.1^{abcd}	162^{abcde}	0.844^{cdefg}	0.071
17	Triticale-1	20.3	37.4	43.3^{e}	39.5^{e}	141^{cde}	0.834^{defg}	0.087
18	Triticale-2	18.6	33.2	46.8^{cde}	41.3^{de}	140^{cde}	0.863^{bcdef}	0.098
	SEM	273	7.57	3.88	3.84	13.28	0.0194	0.0269
	P-value	0.056	0.955	0.006	<0.0001	0.030	<0.0001	0.489

$^{a-g}$ Means within a column not sharing a common superscript are significantly different at the 5% level of probability.

potential digestible starch and starch digestion rate are also included in Table 10. The effects of starch source had highly significant impacts ($P < 0.0001$) on potential digestible starch, which ranged from 0.702 to 0.979 about a mean value of 0.855 ± 0.0611. Collectively, starch source did not impact on starch digestion rates.

4. Discussion

Wheat and sorghum are the 2 commonly used feed grains in Australian broiler diets, while maize is dominant on a global basis. Given that growth performance was monitored for only 7 d in this study the outcomes should be treated with caution. However, not surprisingly, maize-based diets supported the best growth performance. Also, wheat-based dies supported significantly greater weight gains than sorghum-based diets by 6.02% (669 versus 631 g/d) from 21 to 28 d post–hatch. In the present study, starch in wheat-based diets was more rapidly digested by broiler chickens than sorghum by 56.0% (0.117 versus 0.075 min^{-1}; $P = 0.012$) and tended to be more rapidly digested than maize by 36.0% (0.117 versus 0.086 min^{-1}; $P = 0.175$), where the significance of pair-wise comparisons is stated in parentheses. These in vivo outcomes are similar, but less pronounced, than the in vitro data generated by Giuberti et al. (2012) where wheat starch was more rapidly digested than starch from maize or sorghum by about a 2-fold factor. Nevertheless, the variations in in vivo starch digestion rates are noteworthy. The average for starch-based diets was 0.075 min^{-1}, but the range of observations was from 0.055 to 0.102 min^{-1} across 7 samples. The corresponding values for wheat-based diets were a mean of 0.117 min^{-1} with a range from 0.086 to 0.153 min^{-1} across 4 samples. These variations represent a real challenge, but it is possible that rapid visco-analyses of feed grains to determine their starch pasting profiles will provide an indication of starch digestion rates (Truong et al., 2017).

In the present study, the following in vivo starch digestion rates were observed in a descending order: wheat (0.117 min^{-1}), barley (0.104 min^{-1}), triticale (0.093 min^{-1}), maize (0.086 min^{-1}), sorghum (0.075 min^{-1}). In comparison, in vitro starch digestion rates reported by Giuberti et al. (2012) were as follows: wheat (0.035 min^{-1}), barley (0.024 min^{-1}), triticale (0.036 min^{-1}), maize (0.017 min^{-1}), sorghum (0.018 min^{-1}). Thus, while in vitro differences in starch digestion rates were more pronounced, the patterns of outcomes were quite similar. This is consistent with Weurding et al. (2001b), who concluded that starch digestion rates in broiler chickens may be predicted by in vitro methodology.

The merits of including some slowly digestible starch in broiler diets was demonstrated by Herwig et al. (2019); however, the likelihood is that protein digestion rates hold more importance (Liu et al., 2014) in respect of broiler growth performance. Nevertheless, starch digestive dynamics assume increasing importance in reduced CP diets because feed grain inclusions are increased at the expense of soybean meal in reduced CP diets resulting in greater concentrations of dietary starch. Interestingly, broiler chickens are better able to accommodate CP reductions in maize-based diets than wheat-based diets (Chrystal et al., 2021). Moreover, restricting starch concentration increases in wheat-based, reduced CP diets appears advantageous (Greenhalgh et al., 2020). The reasons for the superiority for maize over wheat in this context need to be identified. One probable factor is that the higher protein content of wheat results in higher inclusions of non-bound (crystalline, synthetic) amino acids and lesser quantities of “intact” soy protein in reduced CP diets, which may result in more amino acid imbalances and the “costs of deamination” (Selle et al., 2020). Another probable factor is the likelihood that wheat starch is more rapidly digested than maize starch as was the trend in this study with a differential of 36.0% (0.117 versus 0.086 min^{-1}) in starch digestion rates.

Greater quantities of rapidly digestible starch in reduced CP diets may well have negative consequences. Rapidly digestible starch will yield more glucose in the anterior small intestine which can lead to competition between glucose and amino acids, particularly non-bound amino acids, for intestinal uptakes through co-absorption with sodium via their respective Na^{+}-dependent transport systems (Moss et al., 2018). Reciprocally, there will be less glucose yielded from rapidly digestible starch in the posterior small intestine which may increase catabolism of amino acids in the gut mucosa to provide energy to drive digestive processes (Wu, 1998). As mentioned, glucose, glutamate, glutamine (Watford et al., 1979), and probably aspartate and asparagine (Porteous, 1980) are the major energy substrates catabolised in avian enterocytes for energy provision. Therefore, slowly digestible starch may enhance intestinal uptakes of amino acids and, perhaps more importantly, increase their post-enteral availability by sparing them from catabolism in gut mucosa in favour of glucose.

In addition, digestion rates of starch and the post-enteral availabilities of glucose will almost certainly have an impact on pancreatic secretions of insulin. However, in respect of insulin, there are recognised differences between avian and mammalian species. Poultry have high circulating glucose levels and are resistant to insulin (Tesseraud et al., 2011) and, arguably, the broiler chicken is almost a Type II diabetic animal. Poultry appear to lack the insulin-responsive glucose transporter insulin-sensitive glucose transporter (GLUT-4); nevertheless, insulin has been shown to increase glucose uptakes in skeletal muscle in broiler chickens (Tokushima et al., 2005). Interestingly, exogenous insulin had similar hypoglycaemic effects in chickens selected for high and low fasting glycaemia (Simon et al., 2000) and it has been argued that studies with poultry could expand our overall comprehension of the action of insulin (Simon, 1989). Thus, the role of insulin in the metabolism of poultry has yet to be fully clarified. However, it has been suggested that slowly digestible starch may trigger a more sustained insulin response and this gradual response may result in more efficient protein deposition (Weurding et al., 2003). Therefore, an enhanced comprehension of the fundamentals of the starch–glucose–insulin axis in poultry is required to interpret the full importance of starch digestion rates.

5. Conclusions

It is our contention that harnessing starch-protein digestive dynamics into the formulation of broiler diets will enhance efficiency of feed conversion. Clearly, more research is needed to clarify the impacts of starch digestive dynamics on broiler performance, and the starch digestion rates of many more feed grains need to be determined. However, given the variation in starch digestion rates in a given feed grain, a rapid, in vitro method of assessment would be highly desirable and it is possible that rapid visco-analyses of starch pasting profiles is one such method. The determination of starch digestion rates of various feed grains in poultry, allied to their starch pasting profiles, merits further investigation as this could greatly facilitate the consideration of starch digestion rates in the formulation of broiler diets.

Author contributions

Dr Sonia Yun Liu was the principal investigator of the relevant project. All co-authors were variously involved in completion of this paper. **Dr Amy F. Moss** supervised the feeding study. **Dr Ali Khoddami** completed the starch analyses. **Mr Peter V. Chrystal** formulated the diets. **Dr Peter H. Selle**, **Dr Amy F. Moss** and **Dr Sonia Yun Liu** completed the statistical analyses, writing and editing of the manuscript.

Conflict of interest

We declare that we have no financial and personal relationships with other people or organizations that might inappropriately influence our work, and there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the content of this paper.

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References

Aoyagi Y, Tasaki I, Okumura J-I, Muramatsu T. Energy cost of whole-body protein synthesis measured in vivo in chicks. Comp Biochem Physiol 1988;91A:765–8.

Chrystal PV, Greenhalgh S, McInerney BV, McQuade LR, Akter Y, De Paula Dorigam JC, Selle PH, Liu SY. Maize-based diets are more conducive to crude protein reductions than wheat-based diets for broiler chickens. Anim Feed Sci Technol 2021;275:114867.

Enting H, Pos J, Weurding RE, Veldman A. Starch digestion rates affect broiler performance. Proc Aust Poult Sci Symp 2005;17:17–20.

Fleming SE, Zambell KL, Fitch MD. Glucose and glutamine provide similar proportions of energy to mucosal cells of rat small intestine. Amer J Physiol (Gastro Liver Physiol) 1997;273:G968–78.

Giuberti G, Gallo A, Cerioli C, Masoero F. In vitro starch digestion and predicted glycemic index of cereal grains commonly utilized in pig nutrition. Anim Feed Sci Technol 2012;174:163–73.

Greenhalgh S, McInerney BV, McQuade LR, Chrystal PV, Khoddami A, Zhuang MAM, Liu SY, Selle PH. Capping dietary starch:protein ratios in 197.5 g/kg crude protein, wheat-based diets showed promise but further crude protein reductions generated inferior growth performance and feathering issues in broiler chickens. Anim Nutr 2020;6:168–78.

Gutierrez del Alamo AG, Verstegen MWA, den Hartog LA, de Ayala PP, Villamide MJ. Wheat starch digestion rate affects broiler performance. Poultry Sci 2009;88:1666–75.

Herwig E, Abbott D, Schwean-Lardner KV, Classen HL. Effect of rate and extent of starch digestion on broiler chicken performance. Poultry Sci 2019;98:3676–84.

Hill FW, Anderson DL. Comparison of metabolizable energy and productive energy determinations with growing chicks. J Nutr 1958;64:587–603.

Liu SY, Selle PH. A consideration of starch and protein digestive dynamics in chicken-meat production. World's Poult Sci J 2015;71:297–310.

Liu SY, Cadogan DJ, Péron A, Truong HH, Selle PH. Effects of phytase supplementation on growth performance, nutrient utilisation and digestive dynamics of starch and protein in broiler chickens offered maize-, sorghum- and wheat-based diets. Anim Feed Sci Technol 2014;197:164–75.

Liu SY, Chrystal PV, Selle PH. Pre-determined starch and protein digestion rates attain optimal feed conversion ratios in broiler chickens. Proc Aust Poult Sci Symp 2020;31:90–3.

Mahasukhonthachat K, Sopade PA, Gidley MJ. Kinetics of starch digestion and functional properties of twin-screw extruded sorghum. J Cereal Sci 2010;51:392–401.

Moss AF, Sydenham CJ, Khoddami A, Naranjo VD, Liu SY, Selle PH. Dietary starch influences growth performance, nutrient utilisation and digestive dynamics of protein and amino acids in broiler chickens offered low-protein diets. Anim Feed Sci Technol 2018;237:55–67.

Orskov ER, McDonald I. The estimation of protein degradability in the rumen from incubation measurements weighted according to rate of passage. J Agric Sci 1979;92:499–503.

Porteous JW. Glutamate, glutamine, aspartate, asparagine, and glucose ketone-body metabolism in chick intestinal brush-border cells. Biochem J 1980;188:619–32.

Selle PH, Liu SY. The relevance of starch and protein digestive dynamics in poultry. J Appl Poultry Res 2019;28:531–45.

Selle PH, Chrystal PV, Liu SY. The cost of deamination in reduced-crude protein broiler diets. Proc Aust Poult Sci Symp 2020;31:63–6.

Simon J. Chicken as a useful species for the comprehension of insulin action. Crit Rev Poult Biol 1989;2:121–48.

Simon J, Guillaumin S, Chevalier B, Derouet M, Guy G, Marche G, Ricard FH, Leclercq B. Plasma glucose-insulin relationship in chicken lines selected for high or low fasting glycaemia. Br Poultry Sci 2000;41:424–9.

Siriwan P, Bryden WL, Mollah Y, Annison EF. Measurement of endogenous amino-acid losses in poultry. Br Poultry Sci 1993;34:939–49.

Sydenham CJ, Truong HH, Moss AF, Selle PH, Liu SY. The differing impacts of fish-meal and corn starch inclusions in sorghum-soybean meal diets on growth performance, nutrient utilisation, starch and protein digestive dynamics of broiler chickens. Anim Feed Sci Technol 2017;227:32–41.

Tesseraud S, Everaert N, Ezzine SB-O, Collin A, Métayer-Coustard S, Berri C. Manipulating tissue metabolism by amino acids. World's Poult Sci J 2011;67:243–51.

Tokushima Y, Takahashi K, Sato K, Akiba Y. Glucose uptake in vivo in skeletal muscles of insulin-injected chicks. Comp Biochem Physiol B Biochem Mol Biol 2005;141:43–8.

Truong HH, Khoddami A, Moss AF, Liu SY, Selle PH. The potential of rapid visco-analysis starch pasting profiles to gauge the quality of sorghum as a feed grain for chicken-meat production. Anim Nutr 2017;3:11–8.

Watford M, Lund P, Krebs KA. Isolation and metabolic characteristics of rat and chicken enterocytes. Biochem J 1979;178:589–96.

Weurding RE, Veldman A, Veen WAG, van der Aar PJ, Verstegen MWA. Starch digestion rate in the small intestine of broiler chickens differs among feedstuffs. J Nutr 2001a;131:2329–35.

Weurding RE, Veldman A, Veen WA, van der Aar PJ, Verstegen MWA. In vitro starch digestion correlates well with rate of starch digestion in broiler chickens. J Nutr 2001b;131:2336–42.

Weurding RE, Enting H, Verstegen MWA. The effect of site of starch digestion on performance of broiler chickens. Anim Feed Sci Technol 2003;110:175–84.

Wilson RH, Leibholz J. Digestion in the pig between 7 and 35 d of age: 5. The incorporation of amino acids absorbed in the small intestines into the empty-body gain of pigs given milk or soya-bean proteins. Br J Nutr 1981;45:359–66.

Wu G. Intestinal mucosal amino acid catabolism. J Nutr 1998;128:1249–52.