The effects of cellulose and soybean hulls as sources of dietary fiber on the growth performance, organ growth, gut histomorphology, and nutrient digestibility of broiler chickens

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ABSTRACT This study evaluated the effects of dietary fiber provided as purified cellulose (Solka-Floc, SF) or soybean hulls (**SH**) on the growth performance, organ growth, intestinal histomorphology, and nutrient digestibility. A total of 420 one-day-old Cobb male broilers were randomly assigned to 7 dietary treatments and reared to 20 d of age in battery cages (n = 6 replicates per treatment). The control group consisted of a simple corn and soybean-meal–based diet. The 6 fiber treatments had increasing amounts of SF or SH to achieve 4, 6, and 8% crude fiber (**CF**). Chromium oxide was added as an indigestible marker at 0.3% in all treatment diets from 14 to 20 d for nutrient digestibility analyses. Weights for digestive organs were taken on day 20. Growth performance was measured weekly. Birds fed 4% SH diet had a higher day 20 body weight gain than those fed 8% CF regardless of fiber sources ($P = 0.0118$). Control and 4% SH groups had the best feed conversion ratio among the treatments at 7, 14, and 20 d ($P < 0.05$). SH-containing diets had heavier relative gizzard and intestine weights ($P < 0.001$). Birds fed 8% SH diets had the highest duodenal villi height among the treatments ($P < 0.001$). Birds fed control and 4% SH had the highest jejunal villi height among the treatments ($P < 0.001$). Birds fed 4% SF and 4% SH had the highest ileal villi height among the treatments ($P < 0.001$). Dry matter digestibility was higher in 6% SF than in 8% SH ($P = 0.0105$). In general, birds fed high-SH diets had higher amino acid digestibility ($P < 0.001$). In conclusion, the study suggests that fiber type and inclusion level are crucial factors regulating intestinal development, nutrient digestion, and growth performance.

Key words: broiler chicken, dietary fiber, digestibility, gut morphology, organ growth

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INTRODUCTION

Dietary fiber is an intrinsic component in plant feedstuffs and varies in amount, structure, digestibility, and solubility depending on the origin (Hetland et al., 2004). Previous studies have reported that components of dietary fiber are associated with changes in growth performance (Sadeghi et al., 2015) and general modulation of the gastrointestinal tract (Owusu-Asiedu et al., 2006). These changes include alterations in villi height and crypt depth (Sklan et al., 2003), enzymatic activity and digestive organ size (Mateos et al., 2012), and nutrient digestibility (Sigleo and Vahouny, 1984; Owusu-Asiedu et al., 2006). The different chemical structures of the fiber found in feedstuffs lead to differences in physicochemical properties that influence digestibility and solubility and, therefore, nutrient utilization (Hetland et al., 2004).

Soluble fiber sources have been indicated to contain hygroscopic compounds (i.e., pectins, gums, and mucilages) with the ability to trap water and increase viscosity of the digesta, leading to changes in passage rate and nutrient absorption (Langhout et al., 2000; Owusu-Asiedu et al., 2006; Tellez et al., 2014; Perera et al., 2019). Insoluble fiber (i.e., cellulose, hemicellulose, and lignin) is thought to be inert in the sense that it does not interfere with nutrient absorption, but it actually accumulates in the gizzard, increasing the retention time of smaller particles and the digestibility of starches, fats, and crude protein (Cao et al., 2003; Mateos et al., 2012). In general, it has been suggested that fibrous feedstuffs can be added to the diet at 3 to 5% without causing any negative effects in nutrient digestibility or growth performance of different poultry species (Cao et al., 2003; Sklan et al., 2003; Amerah et al., 2009; Jiménez-Moreno et al., 2009).

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The accumulation of fiber in the gizzard actually increases the retention time of smaller particles, increasing digestibility of nutrients (Hetland et al., 2004). Owing to the lack of consistency in results obtained when studying dietary fiber (Jiménez-Moreno et al., 2009; Sadeghi et al., 2015), understanding the functional role of dietary fiber in poultry nutrition grants further investigation regarding roles of fiber inclusion level and type. Therefore, the objective of this study was to evaluate the effects of purified cellulose (Solka-Floc; Skidmore, Schollcraft, MI) or soybean hulls (**SH**) as sources of dietary fiber on the growth performance, organ growth, gut morphology, and nutrient digestibility of broiler chickens.

MATERIAL AND METHODS

General Procedures

The experiment was approved by the Institutional Animal Care and Use Committee of the University of Georgia (Athens, Georgia). A total of 420 one-day-old Cobb500 broiler chicks (Cobb × Cobb) were distributed in a complete randomized design with 7 dietary treatments and 6 replicates of 12 birds each. The inclusion level of CF from 2 fiber sources (cellulose and SH) was considered the main factor. The chicks were allocated in 42 cages equipped with one drinker and one feeder, providing ad libitum access to water and mash feed from 1 to 20 d of age. Temperature and lighting program followed the recommendation of Cobb Broiler Management Guide (Cobb-Vantress, 2018a,b).

Dietary Treatments

The diets were corn and soybean meal-based and formulated to meet the nutrient requirements specified by Cobb500 performance and nutritional guide (Cobb-Vantress, 2018a,b). Diets were provided in mash form during the entire rearing period (0–20 d). All diets were isonitrogenous and isocaloric and are shown in Table 1. Control was a corn-soybean meal–based diet containing 2% CF. Control diet was used as a basal diet to which purified cellulose (**SF**: 99% cellulose, Solka-Floc) was added as a source of CF by replacing an inert filler (sand) to achieve 4, 6, and 8% CF (4% SF, 6% SF, and 8% SF) in the diets. The rest 3 diets were formulated using increasing amounts of SH to achieve 4, 6, and 8% CF (4% SH, 6% SH, and 8% SH). The nutrient matrix composition used for soy hull diets was taken from the study by Barros Dourado et al. (2011). For ileal nutrient digestibility determination, chromic oxide (Cr_2O_3; Sigma Aldrich, St. Louis, MO) was added at 0.3% as an indigestible marker to all diets from 14 to 20 d.

Table 1. Ingredient composition of diets fed to male Cobb × Cobb broilers from 1 to 20 d of age.

Ingredients	CTL	4% SF	6% SF	8% SF	4% SH[1]	6% SH[1]	8% SH[1]
Corn	49.59	49.59	49.59	49.59	52.26	43.79	35.03
Soybean meal	35.19	35.19	35.19	35.19	32.94	32.38	31.86
SF	–	2.02	4.04	6.06	–	–	–
Soybean hulls	–	–	–	–	6.12	12.72	19.33
Soybean oil	4.99	4.99	4.99	4.99	3.94	6.68	9.52
Defluorinated phosphate	1.04	1.04	1.04	1.04	0.26	0.53	0.83
Biofos 16/21P	0.51	0.51	0.51	0.51	1.17	0.98	0.76
Calcium carbonate	0.91	0.91	0.91	0.91	1.24	1.01	0.76
L-Thr	0.12	0.12	0.12	0.12	0.14	0.15	0.17
DL-Met	0.32	0.32	0.32	0.32	0.33	0.35	0.37
Lysine HCl	0.20	0.20	0.20	0.20	0.23	0.22	0.21
Vitamin premix[2]	0.25	0.25	0.25	0.25	0.25	0.25	0.25
Mineral premix[3]	0.15	0.15	0.15	0.15	0.15	0.15	0.15
Sodium Chloride	0.23	0.23	0.23	0.23	0.47	0.29	0.26
Filler (sand)	6.50	4.48	2.46	0.44	0.50	0.50	0.50
Calculated nutrient composition[4]							
Dry matter (%)	90	90	90	90	90	90	90
ME energy (Kcal/kg)	3,000	3,000	3,000	3,000	3,000	3,000	3,000
Protein (%)	21.0	21.0	21.0	21.0	21.0	21.0	21.0
Total crude fiber (%)	2.0	4.0	6.0	8.0	4.0	6.0	8.0
Calcium (%)	0.89	0.89	0.89	0.89	0.89	0.89	0.89
Dig. Phosphorus (%)	0.44	0.44	0.44	0.44	0.44	0.44	0.44
Dig. Met (%)	0.63	0.63	0.63	0.63	0.63	0.63	0.63
Dig. TSAA (%)	0.90	0.90	0.90	0.90	0.90	0.91	0.90
Dig. Lys (%)	1.22	1.22	1.22	1.22	1.22	1.22	1.22
Dig. Thr (%)	0.86	0.86	0.86	0.86	0.86	0.86	0.86

Abbreviations: CTL, control; ME, metabolizable energy; SF, Solka-Floc; SH, soybean hulls.

[1]Nutrient matrix used for soy hulls contained 871 kcal/kg of ME, 11.2% CP. Av-TSSA: 0.21 Av-lys: 0.59%; Av-Trp: 0.09%; Av-Thr: 0.25; Av-Arg: 0.64, as reported by (Barros Dourado et al., 2011).

[2]Vitamin premix provided the following per kilogram of DSM premix (Parsippany, NJ): Vit. A, 2,204,586 IU; vit. D_3, 200,000 ICU; vit. E, 2,000 IU; vit. B12, 2 mg; biotin, 20 mg; menadione, 200 mg; thiamine, 400 mg; riboflavin, 800 mg; D-pantothenic acid, 2,000 mg; vit. B6, 400 mg; niacin, 8,000 mg; folic acid, 100 mg; choline, 34,720 mg.

[3]Mineral premix includes per kg of premix: Ca, 0.72 g; Mn, 3.04 g; Zn, 2.43 g; Mg, 0.61 g; Fe, 0.59 g; Cu, 22.68 g; I, 22.68 g; Se, 9.07 g.

[4]Values reported as percentages unless noted otherwise.

Growth Performance and Organ Weights

The birds and feed were weighed weekly to determine mortality-corrected body weight gain (**BWG**), mortality-corrected feed intake (**FI**), and mortality-corrected feed conversion ratio (**FCR**). Mortality was recorded daily. On day 20, 2 average birds per cage were euthanized, and gizzard, pancreas, liver, duodenum, jejunum, ileum, and ceca were weighed to determine the relative organ weight.

Intestinal Morphology

On day 20, samples from the duodenum, jejunum, and ileum (~2-cm long) were collected from one average bird per replicate cage (n = 6 per treatment). Intestinal samples were collected and stored in 10% neutral-buffered formalin and left in solution for a minimum period of 48 h for tissue fixation. During slide preparation, the tissues were dehydrated in increasing amounts of ethanol, diaphonized in dimethylbenzene, and fixed in paraffin. Subsequently, tissue sections with a thickness of 4-μm on slides were stained using hematoxylin and eosin procedures. Pictures were taken using a light microscope (10x eyepiece and 1.6x magnification; Leica DC500 camera; Leica Mycrosystems Inc, Buffalo Groove, IL). Measurements for villi height and crypt depth were taken using ImageJ software (Image Processing and Analysis in JAVA–ImageJ 1.52r, National Instituted of Health).

Nutrient Digestibility

On day 20, five birds per replicate cage were euthanized, and ileal digesta were collected from two-third of the distal ileum (from Meckel's diverticulum to about 1 inch anterior to ileocecal junction). The digesta samples were pooled and dried for analyses of energy, crude protein, and amino acids (**AA**). The chromium oxide concentration was measured in duplicate according to Dansky and Hill (1952), and gross energy was evaluated in duplicate using a bomb calorimeter (IKA Calorimeter C1; IKA Works Inc, Wilmington, NC) at the University of Georgia. The crude protein (N × 6.25) and AA were analyzed at the Chemical Laboratories at the University of Missouri-Columbia. The apparent ileal digestibility of apparent metabolizable energy (**AME**), crude protein, AA, and dry matter were calculated using the following equation:

$$AID,\ \% = 100\left[1 - \left(\frac{Cr_{feed}}{Cr_{dig}}\right) \times \left(\frac{Nutrient_{dig}}{Nutrient_{feed}}\right)\right]$$

where Cr_{feed} and Cr_{dig} are the chromium dioxide in feed and ileal digesta, respectively, and $nutrient_{dig}$ and $nutrient_{feed}$ are the nutrient in ileal digesta and feed, respectively.

Statistical Analyses

Dietary fiber level was used as the fixed effect in the model. Pen was used as the experimental unit for growth performance and nutrient digestibility; bird was used as the experimental unit for organ growth and intestinal morphology. Data were analyzed using one-way ANOVA by the following model:

$$Y_{ij} = \mu + \alpha_i + \varepsilon_{ij}$$

where Y_{ij} represents the value for each random variable; μ is the overall mean; α_i are the fixed factor level effects corresponding to the ith treatment such that $\Sigma\alpha_i = 0$; and the random errors ε_{ij} are identically and independently normally distributed with a mean 0 and a variance σ. All statistical procedures were performed using the SAS University Edition (SAS Institute, 2020). In case of significant differences, means were separated using the Tukey's test Honestly Significant Difference option. For all hypothesis tests, statistical significance was considered at $P < 0.05$.

RESULTS

Growth Performance and Organ Weights

The results for growth performance are shown in Table 2. Birds fed 4% SH diet had a higher D20 BWG than those fed 8% CF regardless of fiber sources ($P = 0.012$). No statistical differences were observed in either BWG or FI on 7 and 14 d ($P > 0.05$) among the treatments; however, 4% SH group had the highest BWG and FI during the entire study. Moreover, FCR of birds fed 4% SH diet was the lowest among the treatment during the entire study. The group fed 4% SH had significantly lower FCR than 8% SF or 8% SH on 7, 14, or 20 d ($P < 0.05$). The group fed 4% SH was heavier than the group fed 4% SF; however, the contrary was true in groups fed 6% SH and SF, respectively. The FCR of 4% SH was lower than that of the group fed 4% SF. However, the FCR of 6 and 8% SH was lower than that of birds fed SF. There were no significant differences in BWG, FI, and FCR between control and 4% SH groups ($P > 0.05$).

The results for relative organ weights and organ relative weights are shown in Table 3. The livers from birds fed the control diet were heavier than those fed 6 and 8% SH diets ($P = 0.001$). However, relative weight of the liver was not statistically different among different dietary treatments ($P = 0.183$). The relative weight of the gizzard was higher in birds fed 6% SH diet than that in control, 4% SF, and 6% SF groups ($P < 0.001$), whereas birds fed 8% SH had significantly higher relative weight of the gizzard than those fed 4 and 6% SF. The relative weights of the jejunum and ileum were higher for birds fed 8% SH diet than those for the rest of treatments, except for 6% SH ($P < 0.001$). Birds fed 6% SH had significantly higher relative weights of the jejunum and ileum than control, 4% SF, or 6% SF.

Intestinal Histomorphology

The results for intestinal histomorphology are shown in Table 4. Birds fed 8% SH diet had the highest

Table 2. Effects of dietary fiber level on growth performance and of male broilers reared to 20 d of age[1].

Item[3]	Total crude fiber[2]							SEM[4]	P value
	CTL	4% SF	6% SF	8% SF	4% SH	6% SH	8% SH		
BWG (g), day 7	92	81	86	81	111	95	79	11	0.424
FI (g), day 7	122	111	125	121	141	132	131	13	0.771
FCR, day 7	1.34[a]	1.47[a,b]	1.49[a,b]	1.51[a,b]	1.27[a]	1.43[a,b]	1.73[b]	0.08	0.013
BWG (g), day 14	365	342	354	317	399	340	314	21	0.087
FI (g), day 14	526	539	553	513	571	562	539	32	0.864
FCR, day 14	1.45[a]	1.61[a,b]	1.58[a,b]	1.61[a,b]	1.43[a]	1.65[a,b]	1.73[b]	0.06	0.007
BWG (g), day 20	756[a,b]	729[a,b]	739[a,b]	625[b]	797[a]	670[a,b]	626[b]	37	0.012
FI (g), day 20	1,347	1,396	1,418	1,404	1,409	1,325	1,413	69	0.943
FCR, day 20	1.79[a]	1.94[a,b]	1.94[a,b]	2.25[b]	1.78[a]	1.98[a,b]	2.27[b]	0.10	0.004

[a,b]Means within a row not sharing a common superscript differ significantly ($P < 0.05$).

[1]Values are the least-square means of 6 replicate pens per treatment with 12 birds per cage. Where applicable, means were separated using Tukey's Honestly Significant Difference Test.

[2]Diets were formulated using increasing amounts of Solka-Floc (SF) or soy hulls (SH) to achieve a total of 4, 6, and 8% crude fiber (4% SF, 6% SF, 8% SF; and 4% SH, 6% SH, 8% SH, respectively), including the fiber from corn and soybean meal.

[3]Mortality-corrected body weight gain (BWG), feed intake (FI), and feed conversion ratio (FCR) per bird.

[4]SEM = largest pooled standard error of the pairwise mean comparison.

duodenal villi height among the treatments and significantly higher than those fed SF and SH ($P < 0.001$). The shortest duodenal villi height was observed in 6% SF-fed birds. No statistical differences were observed for duodenal crypt depth among the treatments ($P = 0.066$). Birds fed control and 4% SH diets had the highest jejunal villi height among treatments ($P < 0.001$). Birds fed 8% SH had significantly higher villi height than those fed 6% SH. The jejunal crypt depth of 4% SH–fed birds was significantly higher than that of 6% SF and 6% SH groups ($P = 0.008$). Birds fed 4% SF and 4% SH had significantly higher ileal villi height than those in the other treatments ($P < 0.001$). Ileal villi height of 6% SH group was significantly higher than that of 8% SF group. The ileal crypt depth of 4% SH group was significantly higher than that of 6% SF and 6% SH groups. No statistical differences were observed in duodenal or jejunal villi:crypt ratio ($P > 0.05$). Birds fed 6% SH diet had higher villi:crypt ratio than the control, 6% SF, and 8% SH groups ($P < 0.001$).

Nutrient Digestibility

Results for nutrient digestibility are shown in Table 5. Dry matter digestibility was higher in 6% SF than in 8% SH diets ($P = 0.0105$). No differences in crude protein or AME digestibility were observed among treatments ($P > 0.05$). Birds fed 8% SH had the highest methionine digestibility among treatments ($P < 0.001$), and those fed 6 and 8% SH had the highest threonine digestibility among the treatments ($P < 0.001$). No differences in

Table 3. Effects of dietary fiber level on weights and relative organ weights of male broilers reared to 20 d of age[1].

Item[3]	Total crude fiber[2]							SEM[4]	P value
	CTL	4% SF	6% SF	8% SF	4% SH	6% SH	8% SH		
Gizzard, g	24	21	21	21	24	23	22	0.9	0.113
Gizzard, %	2.8[b,c]	2.8[c]	2.8[c]	3.0[a,b,c]	3.0[a,b,c]	3.4[a]	3.2[a,b]	0.10	<0.001
Pancreas, g	3	3	3	2	3	3	2	0.16	0.366
Pancreas, %	0.3	0.3	0.3	0.3	0.3	0.4	0.3	0.02	0.702
Liver, g	26[a]	25[a,b]	25[a,b]	22[a,b]	25[a,b]	20[b]	20[b]	1.32	0.001
Liver, %	3.1	3.2	3.3	3.1	3.1	3.0	3.1	0.12	0.183
Duodenum, g	12	12	12	11	12	11	12	0.55	0.244
Duodenum, %	1.5	1.6	1.5	1.6	1.5	1.6	1.7	0.07	0.141
Jejunum, g	30	27	29	26	29	29	31	1.5	0.279
Jejunum, %	3.5[c]	3.5[c]	3.7[b,c]	3.7[b,c]	3.6[b,c]	4.2[a,b]	4.5[a]	0.16	<0.001
Ileum, g	26	24	24	25	28	27	28	1.51	0.214
Ileum, %	3.1[c]	3.1[c]	3[c]	3.5[b,c]	3.4[b,c]	3.9[a,b]	4.0[a]	0.12	<0.001
Ceca, g	5	6	5	5	7	5	5	0.6	0.136
Ceca, %	0.6	0.7	0.6	0.7	0.9	0.8	0.8	0.07	0.157

[a-c]Means within a row not sharing a common superscript differ significantly ($P < 0.05$).

[1]Values are the least-square means of 12 replicate birds per treatment. Where applicable, means were separated using Tukey's Honestly Significant Difference Test.

[2]Diets were formulated using increasing amounts of Solka-Floc (SF) or soy hulls (SH) to achieve a total of 4, 6, and 8% crude fiber (4% SF, 6% SF, 8% SF; and 4% SH, 6% SH, 8% SH, respectively), including the fiber from corn and soybean meal.

[3]Duodenum, jejunum, ileum, and ceca were weighed including their contents.

[4]SEM = largest pooled standard error of the pairwise mean comparison.

Table 4. Villi height, crypt depth, and villi:crypt ratio from the duodenum, jejunum, and ileum of male broilers reared to 20 d of age[1].

	Total crude fiber[2]								
Item	CTL	4% SF	6% SF	8% SF	4% SH	6% SH	8% SH	SEM[3]	*P* value
Duodenum									
Villi, µm	2,194^{a,b}	2,137^{b,c}	2,006^{d}	2,119^{b,c,d}	2,076^{b,c,d}	2,049^{c,d}	2,315^{a}	30	<0.001
Crypt, µm	262	271	259	248	249	269	285	12	0.066
Ratio, µm	9	8.4	8.3	9	8.8	8.3	8.6	0.3	0.144
Jejunum									
Villi, µm	1,320^{a}	1,181^{b,c}	1,146^{b,c}	1,160^{b,c}	1,312^{a}	1,117^{c}	1,222^{b}	22	<0.001
Crypt, µm	188^{a,b}	181^{a,b}	178^{b}	179^{a,b}	196^{a}	173^{b}	182^{a,b}	5	0.008
Ratio, µm	7.3	6.7	6.8	6.7	7.1	6.6	7.1	0.2	0.071
Ileum									
Villi, µm	641^{b,c}	754^{a}	650^{b,c}	621^{c}	769^{a}	679^{b}	631^{b,c}	15	<0.001
Crypt, µm	159^{c}	177^{a,b}	160^{b,c}	146^{c}	180^{a}	146^{c}	162^{b,c}	5	<0.001
Ratio, µm	4.2^{b}	4.5^{a,b}	4.3^{b}	4.5^{a,b}	4.5^{a,b}	5^{a}	4^{b}	0.16	<0.001

$^{a\text{-}d}$Means within a row not sharing a common superscript differ significantly ($P < 0.05$).

[1]Values are the least-square means of 6 replicate birds per treatment. Where applicable, means were separated using Tukey's Honestly Significant Difference Test.

[2]Diets were formulated using increasing amounts of Solka-Floc (SF) or soy hulls (SH) to achieve a total of 4, 6, and 8% crude fiber (4% SF, 6% SF, 8% SF; and 4% SH, 6% SH, 8% SH, respectively), including the fiber from corn and soybean meal.

[3]SEM = largest pooled standard error of the pairwise mean comparison.

lysine, serine, and tryptophan digestibility were observed among the treatments ($P > 0.05$). In general, feeding 6 and 8% SH resulted in better digestibility of dietary essential AA (EAA; except lysine and tryptophan) and dietary nonessential AA (NEAA; except serine) ($P < 0.05$). Birds fed 6% SH diet had significantly higher digestibility of valine, isoleucine, tyrosine, phenylaniline, histidine, arginine, aspartate, glutamate, proline, glycine, alanine, or cysteine than control, 6% SF, 8% SF, or 4% SH ($P < 0.05$). The digestibility of isoleucine, leucine, tyrosine, phenylaniline, or aspartate in birds fed 8% SH was significantly higher than that in control, 6%

Table 5. Effect of dietary fiber level on nutrient digestibility of male broilers reared to 20 d of age[1].

	Total crude fiber[2]								
Item	CTL	4% SF	6% SF	8% SF	4% SH	6% SH	8% SH	SEM[3]	*P* value
DM, %	68.4^{a,b}	70.3^{a,b}	71.1^{a}	70.0^{a,b}	69.2^{a,b}	62.8^{a,b}	62.0^{b}	2.0	0.0105
CP, %	82.0	83.7	83.6	82.9	80.7	79.9	80.3	1.3	0.2115
AME, Kcal/kg	2,735	2,835	2,892	2,853	2,835	2,632	2,788	79	0.3083
Met, %	93.9^{b}	94.3^{b}	93.6^{b}	94.0^{b}	94.6^{b}	94.2^{b}	96.1^{a}	0.3	<0.001
Lys, %	88.9	89.9	88.4	89.3	88.4	89.4	89.4	0.4	0.1566
Thr, %	77.6^{b,c}	78.7^{b,c}	77.1^{c}	77.4^{b,c}	79.8^{b}	83.4^{a}	85.5^{a}	0.6	<0.001
Val, %	79.8^{b,c}	80.8^{a,b,c}	79.5^{b,c}	79.9^{b,c}	78.7^{c}	82.6^{a}	81.7^{a,b}	0.6	0.0002
Ile, %	82.5^{c}	83.3^{a,b,c}	82.0^{c}	82.8^{b,c}	81.7^{c}	85.1^{a}	85.0^{a,b}	0.5	<0.001
Leu, %	84.1^{a,b}	84.8^{a,b}	83.3^{b}	84.5^{a,b}	83.6^{b}	86.0^{a}	86.1^{a}	0.5	0.0028
Tyr, %	82.6^{a,b}	83.9^{a}	82.3^{a,b}	83.3^{a,b}	80.9^{b}	84.0^{a}	83.7^{a}	0.5	0.0036
Phe, %	83.9^{b}	85.1^{a,b}	83.4^{b}	84.7^{a,b}	83.9^{b}	86.8^{a}	87.1^{a}	0.6	0.0001
His, %	86.6^{b,c,d}	88.7^{a}	86.0^{d}	87.1^{a,b,c,d}	86.2^{c,d}	88.5^{a,b}	88.2^{a,b,c}	0.7	0.0421
Arg, %	89.7^{b}	91.1^{a,b}	89.6^{b}	90.7^{a,b}	90.3^{a,b}	91.8^{a}	91.4^{a,b}	0.5	0.0073
Trp, %	90.6	92.3	89.9	90.8	91.3	92.2	92.6	1.0	0.3759
Sum EAA[4]	85.8	86.9	85.3	86.1	85.9	88.0	88.3	-	-
Cys, %	70.7^{a,b}	73.9^{a}	70.0^{a,b}	70.1^{a,b}	69.2^{b}	74.2^{a}	72.9^{a,b}	1.1	0.0055
Asp, %	80.4^{c}	81.7^{a,b,c}	80.1^{c}	80.7^{b,c}	80.0^{c}	84.0^{a}	83.0^{a,b}	0.6	<0.001
Ser, %	81.6	83.1	81.2	81.6	81.1	82.9	81.7	0.6	0.175
Glu, %	87.1^{a,b}	87.9^{a,b}	86.8^{b}	87.5^{a,b}	86.7^{b}	88.8^{a}	88.4^{a,b}	0.4	0.0078
Pro, %	81.4^{a,b}	82.6^{a,b}	80.9^{b}	81.5^{a,b}	80.5^{b}	83.4^{a}	81.9^{a,b}	0.5	0.0025
Gly, %	78.3^{a,b}	79.4^{a}	78.3^{a,b}	78.1^{a,b}	76.1^{b}	78.7^{a}	77.8^{a,b}	0.6	0.0084
Ala, %	82.7^{a,b}	83.7^{a,b}	82.0^{b}	83.0^{a,b}	82.0^{b}	84.7^{a}	84.4^{a,b}	0.6	0.0083
Sum NEAA[4]	80.6	82.0	80.2	80.7	79.6	82.6	81.7	-	-
Ratio EAA/NEAA[5]	1.06	1.06	1.06	1.07	1.08	1.07	1.08	-	-

$^{a\text{-}d}$Means within a row not sharing a common superscript differ significantly ($P < 0.05$).

[1]Values are the least-square means of 6 replicate pens per treatment. Where applicable, means were separated using Tukey's Honestly Significant Difference Test.

[2]Diets were formulated using increasing amounts of Solka-Floc (SF) or soy hulls (SH) to achieve a total of 4, 6, and 8% crude fiber (4% SF, 6% SF, 8% SF; and 4% SH, 6% SH, 8% SH, respectively), including the fiber from corn and soybean meal.

[3]SEM = largest pooled standard error of the pairwise mean comparison.

[4]Sum of essential amino acids (EAA) and nonessential amino acids (NEAA) was calculated as the sum of the percentage digestibility of all the amino acids in each group divided by the number of amino acids in each group.

[5]The ration of EAA:NEAA was calculated by dividing the sum EAA by NEAA.

SF, or 4% SH ($P < 0.05$). However, there was no significant difference in AA digestibility between 6 and 8% SH groups.

DISCUSSION

Growth Performance and Organ Weights

Despite the fact that the diets were formulated with the same nutrient content, there were differences in growth performance among the treatments. Control and 4% SH groups had better FCR at 7, 14, and 20 d than 8% SH–fed group. However, no differences were observed between the 4 and 6% SF groups which indicates that insoluble fibers are inert when given in small amounts. The FCR of 4% SH was lower than that of the group fed 4% SF. However, the FCR of 6 and 8% SH was similar to that of birds fed SF, respectively. The group fed 4% SH was heavier than the group fed 4% SF, and the contrary was true in groups fed 6% SH and SF, where SF had heavier weights. There was a 5% improvement in BWG in 4% SH–fed birds compared to the control group on day 20. These results indicate that minimum amounts (4%) of dietary fibers are necessary to maximize growth performance in young broilers as indicated by other reports (Jiménez-Moreno et al. 2009). In a study, Gonzalez-Alvarado et al. (2007) reported a 5% increase in BWG and 2% improvement in FCR of broilers fed either 3% oat hulls or soy hulls compared to the control group. In the present study, the results obtained from feeding 4% CF were different for SH and SF despite the fact that both diets were formulated to be isonitrogenous and isocaloric, indicating that fiber type is a determinant factor in growth performance of broilers. On day 20, the BWG of birds fed 4% SH was 9% higher and the FCR was 8% lower (better) than those of birds fed 4% SF diets. These results from the present study are in agreement with a study (Jiménez-Moreno et al., 2009) reporting that the inclusion of 3% oat hulls in rice-soy protein concentrate–based diets improved BWG and FCR in broilers. Finally, inclusion of 8% CF either with SF or SH had adverse effects in BWG and FCR on 20 d of age. These results from the current experiment are in agreement with those of González-Alvarado et al. (2008) who reported 3 to 4% crude fiber an adequate amount to be used in broilers. There are different reasons why inclusion of crude fiber higher than 4% may cause reduction in growth performance, especially when including soluble dietary fibers. The body weight and FCR were similar in groups fed 4 and 6% SF, which points out that insoluble fibers tend to have an inert role in the gastrointestinal tract when provided in small amounts as described by Hetland et al. (2004). However, when given in larger amounts (higher than 8%), they can interrupt nutrient absorption, resulting in decreased performance (Cao et al., 2003) as observed when feeding 8% SF in the current experiment. The presence of larger amounts of dietary fiber in the gastrointestinal tract increases organ size (i.e., gizzard, intestines) as a way to offset the increase of the volume (i.e., bulky diets) of feed moving through the intestines (Hetland et al., 2004; González-Alvarado et al., 2008; Svihus, 2011; Rezaei et al., 2018). These changes in organ growth may also increase maintenance requirements associated with increases in tissue synthesis and protein turnover, leading to more nutrients being directed toward maintenance of such tissues and less toward muscle protein accretion and growth performance (Nyachoti et al., 2000) even when adequate nutrient absorption is taking place in the gastrointestinal tract. In addition, because of the bulkiness of diets containing fibrous components (i.e., SH and SF), increasing FI to compensate for such changes in nutrient partitioning does not seem to be possible; that might be why we observed the same FI but differences in BW and FCR when feeding 8% CF in isonitrogenous and isocaloric diets.

In the present study, it was observed that, except for liver weights, gross organ weights did not differ among treatments. Control group had heavier gross liver weights than 6 and 8% SH groups. Generally, body conformation is associated with internal organ size, with some variations in genetic lines (Kokoszyński et al., 2017); therefore, as the control-fed group had heavier BW, it is logical to think that such BW is associated with heavier livers even though relative (%) weights decrease overtime. This may also be associated with the negative impact of dietary fiber on fat digestibility. The current results are in agreement with those of González-Alvarado et al. (2008) who reported that the gross organ weights of birds fed 3% soy hulls did not differ statistically from the control group. However, in the present study, it was observed that when body weight was considered, the relative organ weights differed among the treatments. Similarly, Sadeghi et al. (2015) reported that different fiber sources are effective in stimulating intestinal and organ growth. The addition of CF with SH had more remarkable effects on gizzard and small intestine relative weights. Birds fed 6 and 8% SH had heaver relative weight of the gizzard than control, 4% SF, and 6% SF diets. In general, 6 and 8% SH diets had heavier relative jejunum and ileum weights than the rest of treatments. The current results indicate how fiber type can play a crucial role in the development of digestive organs; compositions of different fiber sources may be attributed to changes in growth performance and organ development. Soybean hulls have hemicellulolytic (insoluble) and pectin (soluble) carbohydrates (Stein et al., 2008). The mixture of these soluble and insoluble carbohydrates in soy hulls might alter the gastrointestinal tract and digestive organs differently compared with purified cellulose which is a simple form of fiber. Finally, inclusion of dietary fiber in the form of soy hulls modulates organ growth, especially the gizzard and the different portions of the small intestine, differently than cellulose. Similar results were reported by Chiou et al. (1996) when supplementing fiber in the form of alfalfa, barley, rice hulls, cellulose, lignin, or pectin.

Intestinal Histomorphology

Duodenal villus height was higher for the 8% SH–fed group than for the rest of treatments, except for the control group. The groups fed 4 and 6% SH or SF had similar results. The major differences were observed between 8% SH and SF groups. This might be associated with the stimulation of intestinal development caused by the increase in intestinal reflux in the upper intestinal tract as observed in other experiments (Sacranie et al., 2012). In the present study, control and 4% SH groups had the highest jejunal villi height among the treatments. These results are in agreement with those of Praes et al. (2011) who observed that laying hens fed 7.5% soy hulls had an improvement in duodenal and jejunal villus height compared with other fiber sources; however, they did not observe differences in performance as seen in the present study. The ileal villus height and depth were higher for 4% SF and 4% SH groups than for the rest of treatments. Dietary fiber is a critical factor affecting intestinal morphology as observed in this experiment and as reported by other authors in different poultry species (Chiou et al., 1996; Hetland et al., 2003; Sklan et al., 2003; González-Alvarado et al., 2008; Sadeghi et al., 2015; Rezaei et al., 2018). In the present study, SH-containing diets had a more pronounced effect in intestinal morphology than SF diets. According to Stein et al. (2008), SH contains 50% hemicellulose, 30% pectin, and 20% cellulose. The mix of different types of fibers appears to have a marked effect on intestinal morphology. Finally, there is a clear drop in the ileal and jejunal villus height in the 6 and 8% SH groups, which indicates that 4% CF as SH is adequate for stimulating intestinal villus growth in young broilers. Similarly, Sadeghi et al. (2015) reported that broilers fed sugar beet pulp at 3% in the diet had shorter jejunal and ileal villus height than the control and rice hull–fed groups. The same authors reported that sugar beet pulp contains 47% soluble carbohydrates (nonfiber carbohydrates) which points out that the presence of soluble fibers reduces villus growth. As previously mentioned, SH contains 30% soluble carbohydrates (i.e., pectins); therefore, higher inclusions of such water-soluble carbohydrates reduce villus height in the jejunum and ileum which might be associated to the lack of "abrasive stimulus" that is generally seen in such fibers compared with insoluble fibers (Rezaei et al., 2018).

Nutrient Digestibility

Dry matter apparent digestibility was 9% lower for 8% SH–fed birds than for 6% SF–fed group. The SF (cellulose) is a source of insoluble fiber (cellulose), whereas SH contains both soluble and insoluble fiber components. Cellulose and other insoluble fibers such as rice hulls and wood shavings act as inert materials affecting the gut functions and modulation of nutrient digestion that are often associated with improvements in nutrient digestion (Hetland et al., 2003). On the other hand, the viscous components of soluble fibers have been reported to reduce the coefficients of apparent digestibility of dry matter. Silva et al. (2013) reported that broilers fed pectin in increasing amounts from 10 to 50 g/kg had a quadratic and a linear response in the starter and grower phases, respectively; increase in pectin resulted in lower digestibility of dry matter, which is similar to the results from the present study. Another study by Shakouri et al. (2009) reports that birds fed grains containing soluble and viscous nonstarch polysaccharide had a lower apparent digestibility of dry matter which can be attributed to the soluble portion of the fiber components. In the present study, despite the reduction in dry matter digestibility, the apparent digestibility of crude protein and ME did not differ among the treatments. Similarly, Hetland and Svihus (2001) observed no differences in AME_n in broilers fed 3% oat hulls as a fiber source; however, adding 10% oat hulls reduced AME_n. Unlike the results in the present study, Sklan et al. (2003) reported lower digestibility of crude protein, fat, and gross energy in turkeys fed 8 to 9% CF in diets where sunflower meal was used as the main source of dietary fiber. The lack of agreement can be associated to differences in fiber type, amounts, and specie-related differences.

Dietary fiber had significant effects in AA digestibility. The sum of EAA shows that groups fed 6% and 8% SH had higher total EAA digestibility. In general, inclusion of dietary fiber as 6 or 8% SH improved digestibility of all dietary essential (except lysine and tryptophan) and dietary NEAA (except serine). AA digestibility for 6 and 8% SF groups was relatively constant compared with that of the groups fed SH. The sum of NEAA was similar among the groups. Finally, the EAA:NEAA ratio was close to 1.06 for all the treatments. Interestingly, the 4% SH group had increased villi height but decreased AA digestibility and showed better BW and FCR than 8% SH group. On the other hand, 8% SH group had higher AA digestibility and worse BW and FCR. The relative weights of gizzard, jejunum, and ileum were higher for 8% SH group, which indicates the possibility that more nutrients are being directed toward maintenance of such organs (i.e., protein synthesis and turnover) and that the nutrient partitioning is different between 8 and 4% SH groups, resulting in changes in muscle protein accretion (i.e., growth performance). In addition, the lower dry matter digestibility in birds fed higher levels of SH (6 and 8%) seems to be compensated by an increase in AA digestibility. This indicates that birds have the ability to modulate the structure of the gastrointestinal system to compensate for differences in dietary fiber components. Sadeghi et al. (2015) reported that changes in intestinal structure when broilers are exposed to 30 g/kg sugar beet pulp as soluble fiber are part of an adaption mechanism to the lower diffusion rates of nutrients. Interestingly, the AA digestibility of 6 and 8% SH diets in the present study was different from that of SF diets (6 and 8%) which resulted in lower AA digestibility. Cao et al. (2003) reported that laying hens had a lower nitrogen digestibility and absorption when fed 10% cellulose. The inclusion of soy hulls in the diets of broilers had more profound effects in intestinal histomorphology and organ growth that could be linked with improvement in AA digestibility. Improvement in AA digestibility, however, appears to be associated with an increase in nutrient requirements for maintenance of heavier digestive organs (i.e., gizzard, jejunum, and ileum) because of the presence of dietary fiber. Such changes in nutrient partitioning can be able to reduce muscle protein accretion and subsequent growth performance (Nyachoti et al., 2000). Fiber components, especially those water soluble, that escape digestion and absorption can also serve as substrate to intestinal bacteria that can synthesize short-chain fatty acids (i.e., propionate, acetate, and butyrate) and have been shown to have functional roles such as antimicrobial, an energy source, and intestinal immunomodulators (Fernández-Rubio et al., 2009; Liu et al., 2018) which can help in the improvement of the gastrointestinal tract, sometimes resulting in increased digestibility of AA as reported by Kaczmarek et al. (2016). Finally, in the present study, there were no differences in glucose and AA transporters (data not shown); however, this does not limit the probability of differences in the transporter proteins. Other authors have indicated the potential for improvement of protease activity when fibrous materials are added to diets of broilers (Hetland et al., 2004), but it is important to establish a balance between enzymatic activity stimulation, organ growth, and protein synthesis and turnover that can be regulated by dietary fiber inclusion to broiler diets to optimize performance. Therefore, further research is granted to better understand the role of dietary fiber on nutrient absorption and utilization.

CONCLUSIONS

Different fiber types and inclusion levels are determining factors in growth performance and intestinal development and functionality. In the present study, 4% SH had 5% improvement in BWG compared with the control group and 9 and 8% improvement in BWG and FCR on day 20, respectively, compared with the 4% SF group. Based on the results from the present study, it is concluded that CF can be added into broiler diets with SH at a level of 4% without having adverse effects in performance of broiler chickens under isonitrogenous and isocaloric dietary conditions. And even though 6% fiber can improve AA digestibility, growth was not favored with such fiber levels, which might be associated with an increase of nutrient requirements for maintenance of a higher epithelial cell turnover. In summary, fiber type and inclusion level are crucial factors regulating growth performance, intestinal development, and nutrient digestion, and further research is granted to understand how different fiber components can affect broiler performance from a physiological and nutritional perspective. This will provide us a pathway by which we may be able to formulate cost-effective diets with inexpensive fibrous feedstuffs.

DISCLOSURES

The authors declare no conflicts of interest.

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