

Dietary fiber in poultry nutrition: dispensable diluent or pivotal for digesta transit regulation?

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Abstract

Although the importance of dietary fibers to contribute to the nutrient supply in chickens is rather limited, fibers may interfere with the digestion of other nutrients through their effects on physicochemical properties of the digesta, thereby influencing nutrient accessibility, bulking properties, microbial activity, gut physiology and function, endogenous secretions, and flow of digesta through the GIT. Recent literature highlights the importance of dietary fibers for the regulation of digesta flow in the upper digestive tract, mainly through a prolonged retention of digesta in the gizzard. Furthermore, fiber may also be important for the regulation of digesta transit in other GIT segments. High fiber diets promote the separation of solid and liquid digesta and the amount of fiber directed to the ceca, seems to be influenced by fiber properties, as particle size and solubility.

Introduction

Nutrient digestion and absorption throughout the gastrointestinal tract (GIT) is a complex, dynamic process dependent on many factors, such as enzymatic hydrolysis, secretion of digestive juices, grinding, mixing and transit of digesta, microbial colonization, and fermentation including the formation of fermentation end-products. Hence, eventual fate of nutrients in the GIT of the animal is the result of many processes influenced by several animal-, environmental-, and diet-related factors.

The true nutritional value of diets results from complex, chemical and physical interactions between dietary components occurring inside the digestive tract, rather than being the simple sum of the assumed feeding values based on of the individual ingredients. Particularly fibers may considerably interfere with the digestion of other nutrients through their effects on physicochemical properties of the digesta, thereby influencing nutrient accessibility, bulking properties, microbial activity, gut physiology and function, endogenous secretions, and flow of digesta through the GIT^[1-7]. It is generally believed that fiber degradation in poultry is low and that role of fiber in energy supply to the bird is minor^[9], whereas the indirect effects on the nutritional value due to interactions with other nutrients may be considerable. For example, various soluble fiber sources have been found to reduce digestion of protein, starch, and fat in the upper GIT^[10-12], whereas insoluble fiber sources as oat hulls, may improve nutrient digestibility^[9, 14]. The adverse effects of soluble fibers are mainly explained by their viscous nature and fiber-degrading enzymes (as β -glucanases and xylanases) are generally added to poultry diets to reduce these effects. The beneficial effects of insoluble fibers likely result from improved development of the muscular gizzard and are generally ascribed to the physical structure of the fibrous ingredients. Hence, fibers or coarse particles are often added to the feed to improve gastrointestinal functioning and nutrient use^[reviewed by 18, 19].

Digesta transit in chickens: From beak to cloaca AND reverse

The digestive system of chickens differs considerably from that of other monogastric animals. Soluble and insoluble fractions of the digesta are diverged into different sections of the digestive tract by

distinctive intestinal contractions and filtering mechanisms^[22, 23]. Reverse peristalsis of the intestine, causes digesta to flow in reverse direction (reflux). In this way, digesta retention time can be adapted to the type of feed^[25], presumably to optimize nutrient digestion or gut health.

Three major sites of reverse peristalsis in the digestive tract of birds are identified^[23]. First, reflux of contents from the gizzard (the muscular stomach) to the proventriculus (glandular stomach) facilitates grinding and compensates for the bird's lack of teeth. Second, reflux from the small intestine into the gizzard and proventriculus enhances mixing of digesta and exposure to digestive juices^[reviewed by 18, 19]. Third, reflux from the cloaca through the colon selectively delivers soluble contents, such as soluble fibers, to the ceca^[21, 26-28]. This so-called hindgut reflux plays a crucial role in the degradation of nutrients that cannot be digested by the bird itself and have to be fermented by the microbes residing in the ceca^[reviewed by 29, 30]. Also, reflux of urine from the cloaca to the ceca, represents a mechanism for recycling of urinary nitrogen (N) in a way analogous to urea recycling in mammals^[31]. Microbes in the ceca can degrade this urinary-N and use the generated ammonia for protein synthesis^[a.o.32, 33, 34]. The resulting microbial biomass can potentially become available to the host as N-source^[reviewed by 30, 31]. In this way, birds are capable of using non-protein nitrogen as source for amino acid synthesis when dietary protein supply is limited^[32, 35], although the contribution of urinary nitrogen to the total nitrogen supply in the bird has never been quantified.

Recent literature highlights the importance of dietary fibers for the regulation of digesta flow in the upper digestive tract^[14, 18, 19], but fiber may also be important for the regulation of digesta transit in other GIT segments. The meshwork of ridges and villi at the opening of the ceca, prevents coarse particles from entering and hindgut reflux seems restricted to fluids and small particles (<0.2mm)^[22]. Thus, physical properties of the feed, such as particle size, solubility, and viscosity likely influence also hindgut reflux^[36, 37]. High fiber diets exacerbate the separation of solid and soluble GIT contents, possibly because of increased reverse flow of gut contents^[26]. In addition, the amount of fiber directed to the ceca, seemed to be influenced by fiber content and fiber properties^[21].

Analyses of dietary fiber and its degradation

The generic term fiber encompasses a very diverse group of polymers, with varying physicochemical properties. Traditional analytical methods to analyze fiber, as crude fiber (CF) and neutral detergent fiber (NDF), recover only a variable part of the fiber fraction which hampers prediction of the nutritive value of fiber fractions from raw materials in poultry diets^[9]. In order to more accurately predict the nutritive effect of fiber from raw materials, a better characterization of fiber fractions, their degradation in the chicken, and their physiological effects are required. For scientific purposes, the enzymatic-chemical (Englyst or Uppsala) methods are more appropriate, whereas for routine analyses the AOAC (2009.01/2011.25) method for total, insoluble, and soluble dietary fiber can be used.

The separation of solid and soluble digesta fractions in the chicken GIT, may complicate digestion studies, particularly, but not exclusively, when fiber degradation is the matter of interest^[26]. Unrealistic high ileal and cecal digestibility values for NSP, sometimes exceeding total tract digestibility^[8, 16, 26, 38], clearly indicate that the traditional marker method maybe inadequate to measure fiber degradation along the GIT in chicken. In future research, a dual phase marker system combined with mathematical modelling of digesta flow pathways, quantitative digesta collection, and stable isotope methods can be helpful to keep track of fiber fractions along the GIT^[39]. For the measurement of total tract degradation of NSP, separation of digesta fractions does not have to be an issue provided that the collection time is sufficiently long and a representative sample of the excreta is collected. Short collection periods at single time points may promote selective recovery of excreta due to irregular evacuation of the ceca^[40, 41], resulting in considerable over- or underrepresentation of cecal contents and erroneous digestibility estimates^[reviewed by 9].

Fiber degradation in chickens

Degradation of NSP in the animal depends to a large degree on the original cell wall matrix in which the polysaccharides are embedded^[42]). Although it has been suggested that considerable NSP may be degraded in the upper GIT, presumably by microbial degradation in the crop^[16], quantitative information on degradation of NSP in the crop is lacking. Considering the limited retention time in the crop under practical feeding regimes^[43-47], substantial NSP degradation in the crop seems unlikely. Hence, it is generally assumed that fiber is majorly fermented in the ceca^[30], where digesta may be retained for up to 24h or longer, with a mean retention time of 7 to 15h (Figure 2)^[24, 48]. As ceca access is restricted to fluids and small particles in chickens, it follows that NSP should be solubilized or finely ground in order to be fermented. However, a substantial fraction of canola meal NSP that were solubilized during transit through the GIT, remained undegraded in broilers^[49] indicating that also the time available for fermentation or the lack of appropriate enzyme activities are possible limiting factors in NSP degradation.

Coefficients of apparent total tract digestibility (CATTDD) of NSP in chicken, as reported in literature range between 0 and 0.4 and generally reflect differences in solubility of the NSP fractions of the various feed ingredients (Figure 1). Degradation of NSP is particularly low (0-0.1) in diets containing poorly solubilizable NSP from ingredients as maize or some sources of canola meal^[15, 17, 20, 21], whereas higher CATTDD of NSP (0.2-0.4) are found for diets that contain more soluble NSP, originating mainly from cereal grains as barley, oats, wheat, and rye. Degradability of NSP from diets containing pea fiber in the study of Jørgensen et al. (1994)^[3] are lower than expected based on the NSP solubility. Apparently, the soluble NSP of this product, which is produced by water extraction of peas and has a high water-binding capacity, were poorly degraded and likely pea fiber even impeded degradation of barley NSP.

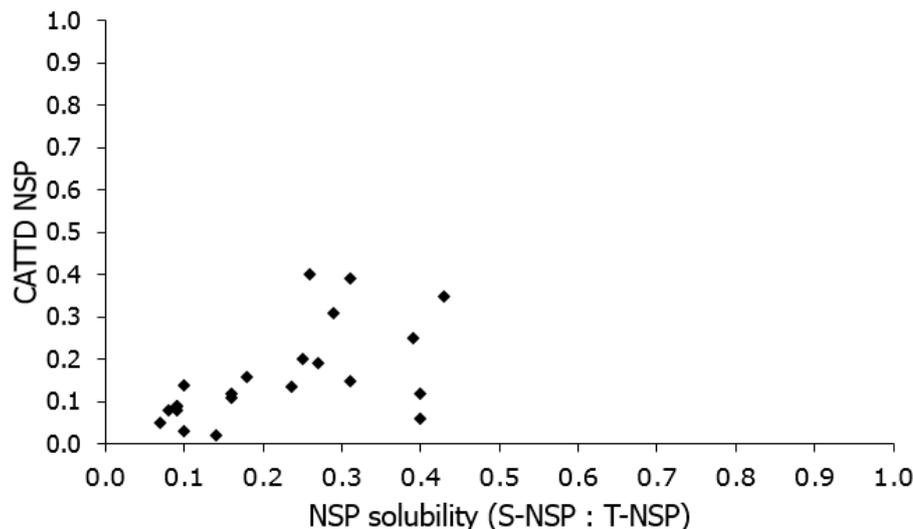


Figure 1. Coefficients of apparent total tract digestibility (CATTDD) of non-starch polysaccharides (NSP) in chickens for diets with varying in NSP solubility (soluble to total NSP ratio). Data from: Jamroz et al., 2002^[8]; Jørgensen et al., 1996^[3]; Meng et al. 2006^[13]; Meng and Slominski, 2005^[15]; Petterson and Åman, 1989^[16]; Slominski et al., 1994^[17]; and Slominski and Campbell, 1990^[20]; de Vries et al., 2014^[21]; and de Vries et al., unpublished^[24].

The degradation of certain fibers, may also depend on the presence of other fibers in the diet, presumably due to effects on digesta flow and retention time or microbial colonization in the GIT^[24, 50]. In common feed practices, NSP-degrading enzymes are usually added to broiler and laying hen diets. The use of such enzymes can facilitate degradation of specific NSP structures, when either appropriate enzyme activities are lacking or when time is limiting their full operation. Although such enzymes are traditionally added to reduce the viscosity of the digesta matrix for cereal-based diets, also the

fermentability of the fiber fraction can be affected. Depending on e.g. the NSP source and the type of enzymes used, CATTD of NSP can be improved over 0.2 units in broilers^[13, 21, 51-54], whereas the effect in adult birds can be even greater^[13, 20, 55]. Effects of common feed processing technologies on fiber degradation are typically smaller, and generally mainly affect easily solubilizable NSP such as cereal β -glucans^[42].

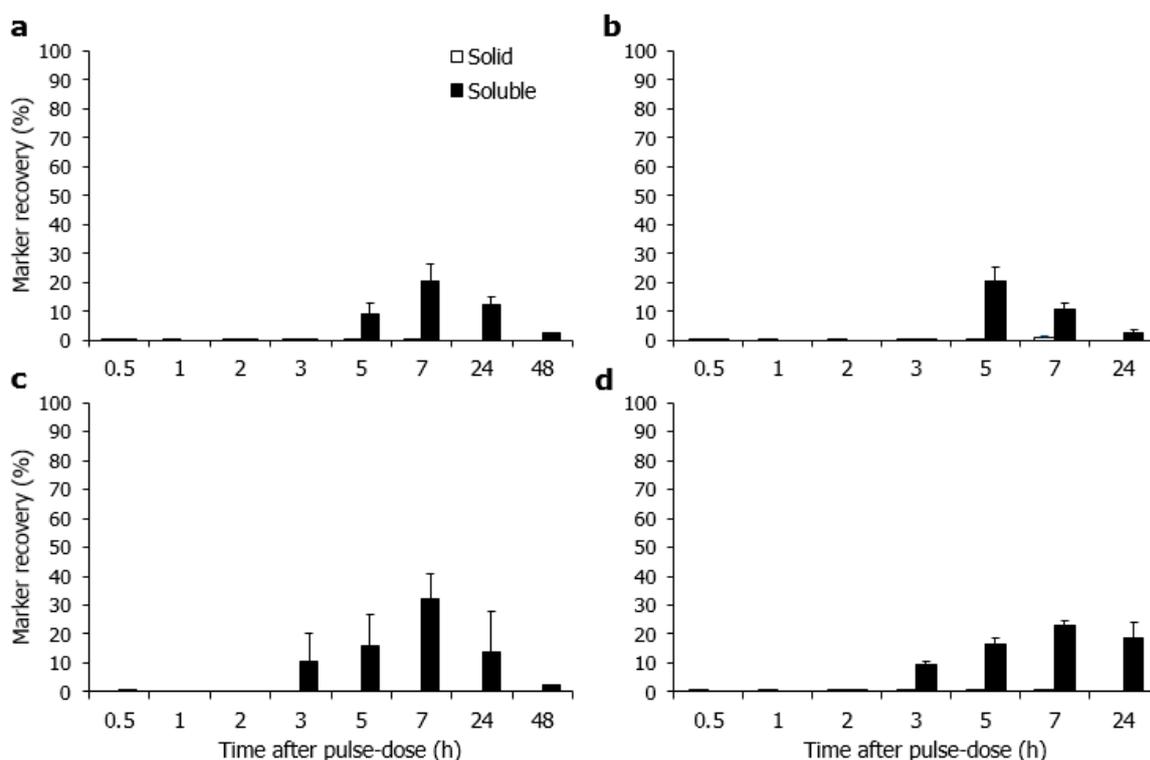


Figure 2. Recovery of chromium and cobalt in ceca of 35d broiler chickens after feeding a pulse dose of solid (Cr_2O_3) and soluble (Co-EDTA) markers. Birds were fed a wheat-soybean meal-maize based control diet (a), or the control diet diluted with 3% sugar beet pulp (b), oat hulls (c), or rice hulls (d). Data are presented as means. Error bars represent SEM.

Conclusion

The generic term fiber encompasses a very diverse group of polymers, with varying physicochemical properties. Not only the quantity of fiber, but also the type of fiber will determine the digestive utilization of the diet and, hence, affect its nutritional value, either positively or negatively. Coefficients of apparent total tract digestibility of NSP in chicken range between 0 and 0.4 and generally reflect differences in solubility of the fiber fraction. Besides, physical entanglement of polysaccharides in the cell wall matrix also time available for fermentation and the absence of appropriate enzyme activities as determined by the microbial colonization in the gastrointestinal tract are possible limiting factors for NSP degradation. Although the importance of dietary fibers to contribute to the nutrient supply in chickens is rather limited when compared with other species^[56], recent literature highlights the importance of dietary fibers for the regulation of digesta flow in the upper digestive tract^[14, 18, 19], mainly through a prolonged retention of digesta in the gizzard. Furthermore, high fiber diets promote the separation of solid and liquid digesta and the amount of fiber directed to the ceca, seems to be influenced by fiber properties, as particle size

and solubility^[21, 26].

References

1. Potkins ZV, Lawrence TLJ, Thomlinson JR. Effects of structural and non-structural polysaccharides in the diet of the growing pig on gastric emptying rate and rate of passage of digesta to the terminal ileum and through the total gastrointestinal tract. *Br J Nutr.* 2007;65:391-413.
2. Bach Knudsen KE, Jensen BB, Hansen I. Digestion of polysaccharides and other major components in the small and large intestine of pigs fed on diets consisting of oat fractions rich in β -glucan. *Br J Nutr.* 1993;70:537-56.
3. Jørgensen H, Zhao XQ, Bach Knudsen KE, Eggum BO. The influence of dietary fibre source and level on the development of the gastrointestinal tract, digestibility and energy metabolism in broiler chickens. *Br J Nutr.* 1996;75:379-95.
4. Johnson IT, Gee JM. Effect of gel-forming gums on the intestinal unstirred layer and sugar transport in vitro. *Gut.* 1981;22:398-403.
5. Smits CHM, Te Maarssen CAA, Mouwen J, Koninkx J, Beynen AC. The antinutritive effect of a carboxymethylcellulose with high viscosity on lipid digestibility in broiler chickens is not associated with mucosal damage. *J Anim Physiol Anim Nutr.* 2000;83:239-45.
6. Smits CHM, Veldman A, Verkade HJ, Beynen AC. The inhibitory effect of carboxymethylcellulose with high viscosity on lipid absorption in broiler chickens coincides with reduced bile salt concentration and raised microbial numbers in the small intestine. *Poult Sci.* 1998;77:1534-9.
7. Grala W, Verstegen MW, Jansman AJ, Huisman J, van Leeusen P. Ileal apparent protein and amino acid digestibilities and endogenous nitrogen losses in pigs fed soybean and rapeseed products. *J Anim Sci.* 1998 February 1, 1998;76:557-68.
8. Jamroz D, Jakobsen K, Bach Knudsen KE, Wiliczekiewicz A, Orda J. Digestibility and energy value of non-starch polysaccharides in young chickens, ducks and geese, fed diets containing high amounts of barley. *Comp Biochem Physiol A.* 2002;131:657-68.
9. de Vries S. Fiber in poultry nutrition: Bonus or burden? European Symposium on Poultry Nutrition; 2015 24-27 August 2015; Prague, Czech Republic; 2015. p. 40-7.
10. Smits CHM, Veldman A, Verstegen MWA, Beynen AC. Dietary carboxymethylcellulose with high instead of low viscosity reduces macronutrient digestion in broiler chickens. *J Nutr.* 1997;127:483-7.
11. Smits CHM, Annison G. Non-starch plant polysaccharides in broiler nutrition—towards a physiologically valid approach to their determination. *World Poult Sci J.* 1996;52:203-21.
12. Choct M, Annison G. The inhibition of nutrient digestion by wheat pentosans. *Br J Nutr.* 1992;67:123-32.
13. Meng X, Slominski BA, Campbell LD, Guenter W, Jones O. The use of enzyme technology for improved energy utilization from full-fat oilseeds. Part I: canola seed. *Poult Sci.* 2006;85:1025-30.
14. Sacranie A, Svihus B, Denstadli V, Moen B, Iji PA, Choct M. The effect of insoluble fiber and intermittent feeding on gizzard development, gut motility, and performance of broiler chickens. *Poult Sci.* 2012;91:693-700.
15. Meng X, Slominski BA. Nutritive values of corn, soybean meal, canola meal, and peas for broiler chickens as affected by a multicarbohydrase preparation of cell wall degrading enzymes. *Poult Sci.* 2005;84:1242-51.
16. Pettersson D, Åman P. Enzyme supplementation of a poultry diet containing rye and wheat. *Br J Nutr.* 1989;62:139-49.
17. Slominski BA, Campbell LD, Guenter W. Oligosaccharides in canola meal and their effect on nonstarch polysaccharide digestibility and true metabolizable energy in poultry. *Poult Sci.* 1994;73.
18. Svihus B. The gizzard: function, influence of diet structure and effects on nutrient availability. *World Poult Sci J.* 2011;67:207-23.
19. Hetland H, Choct M, Svihus B. Role of insoluble non-starch polysaccharides in poultry nutrition. *World Poult Sci J.* 2004;60:415-22.
20. Slominski BA, Campbell LD. Non-starch polysaccharides of canola meal: Quantification, digestibility in poultry and potential benefit of dietary enzyme supplementation. *J Sci Food Agric.* 1990;53:175-84.
21. de Vries S, Pustjens AM, Kabel MA, Kwakkel RP, Gerrits WJJ. Effects of processing technologies and pectolytic enzymes on degradability of non-starch polysaccharides from rapeseed meal in broilers. *Poult Sci.* 2014;93:589-98.
22. Fenna C, Boag DA. Filling and emptying of the galliform caecum. *Can J Zool.* 1974;52:537-40.
23. Duke GE. Gastrointestinal motility and its regulation. *Poult Sci.* 1982 July 1, 1982;61:1245-56.
24. de Vries S, Ellis JL, de Los Mozos Garcia J, Navarro Villa A. Addition of oat hulls, rice hulls, and beet pulp alters digestion, fermentation, and digesta transit in broilers. Unpublished.
25. Clench MH, Mathias JRC. Intestinal transit: How can it be delayed long enough for birds to act as long-distance dispersal agents? *Auk.* 1992;109:933-6.
26. de Vries S, Kwakkel RP, Pustjens AM, Kabel MA, Hendriks WH, Gerrits WJJ. Separation of digesta fractions complicates estimation of ileal digestibility using marker methods with Cr₂O₃ and Co-EDTA in broiler chickens. *Poult Sci.* 2014;93:2010 - 7.
27. Björnhag G, Sperber I. Transport of various food components through the digestive tract of turkeys, geese, and guinea fowl. *Swedish Journal of Agricultural Research.* 1977;7:57-66.
28. Björnhag G. Transport of water and food particles through the avian ceca and colon. *J Exp Zool Suppl.* 1989;3:32-7.
29. Denbow D. Gastrointestinal anatomy and physiology. In: Whittow G, (ed). *Sturkie's avian physiology.* Toronto, Canada: Academic Press; 2000. p. 299-325.

30. Józefiak D, Rutkowski A, Martin SA. Carbohydrate fermentation in the avian ceca: a review. *Anim Feed Sci Technol.* 2004;113:1-15.
31. Singer MA. Do mammals, birds, reptiles and fish have similar nitrogen conserving systems? *Comp Biochem Physiol B.* 2003;134:543-58.
32. Karasawa Y, Maeda M. Role of caeca in the nitrogen nutrition of the chicken fed on a moderate protein diet or a low protein diet plus urea. *Br Poult Sci.* 1994;35:383-91.
33. Karasawa Y, Son JH, Koh K. Ligation of caeca improves nitrogen utilisation and decreases urinary uric acid excretion in chickens fed on a low protein diet plus urea. *Br Poult Sci.* 1997;38:439-41.
34. Son J, Karasawa Y, Nahm K. Effects of cecectomy on nitrogen utilization and nitrogen excretion in chickens fed a low protein diet supplied with urea. *Asian-Australas J Anim Sci.* 1997;10:274-6.
35. Karasawa Y, Maeda M. In situ degradation and absorption of [15 N] urea in chicken ceca. *Comp Biochem Physiol A.* 1995;111:223-7.
36. Sacranie A, Svihus B, Iji P. The effect of digesta viscosity on transit time and gut motility in broiler chickens. 23rd Annu Austral Poult Symp; 2012; 2012. p. 60.
37. Duke GE. Alimentary Canal: Anatomy, Regulation of Feeding, and Motility. In: Sturkie PD, (ed). *Avian Physiology.* New York, NY, USA: Springer New York; 1986. p. 269-88.
38. Brenes A, Slominski BA, Marquardt RR, Guenter W, Viveros A. Effect of enzyme addition on the digestibilities of cell wall polysaccharides and oligosaccharides from whole, dehulled, and ethanol-extracted white lupins in chickens. *Poult Sci.* 2003;82:1716-25.
39. de Vries S, Gerrits WJJ. The use of tracers or markers in digestion studies. In: Moughan PJ, Hendriks WH, (eds). *Feed evaluation science.* Wageningen, The Netherlands: Wageningen Academic Publishers; 2018. p. 271-91.
40. Herrick CA, Edgar SA. Some Relationships between Cecal Function and Coccidiosis of Chickens. *Poult Sci.* 1947 March 1, 1947;26:105-7.
41. Gasaway WC, White RG. Flow of digesta in the intestine and cecum of the rock ptarmigan. *Condor.* 1975;77:467-74.
42. de Vries S, Pustjens AM, Schols HA, Hendriks WH, Gerrits WJJ. Improving digestive utilization of fiber-rich feedstuffs in pigs and poultry by processing and enzyme technologies: A review. *Anim Feed Sci Technol.* 2012;178:123-38.
43. Svihus B. Function of the digestive system. *J Appl Poult Res.* 2014;23:306-14.
44. Van Krimpen M, Kwakkel R, Van Der Peet-Schwering C, Den Hartog L, Verstegen M. Effects of dietary energy concentration, nonstarch polysaccharide concentration, and particle sizes of nonstarch polysaccharides on digesta mean retention time and gut development in laying hens. *Br Poult Sci.* 2011;52:730-41.
45. Moquet PCA, Salami SA, Onrust L, Hendriks WH, Kwakkel RP. Butyrate presence in distinct gastrointestinal tract segments modifies differentially digestive processes and amino acid bioavailability in young broiler chickens. *Poult Sci.* 2018;97:167-76.
46. Van der Klis J, Verstegen M, De Wit W. Absorption of minerals and retention time of dry matter in the gastrointestinal tract of broilers. *Poult Sci.* 1990;69:2185-94.
47. Shires A, Thompson JR, Turner BV, Kennedy PM, Goh YK. Rate of passage of corn-canola meal and corn-soybean meal diets through the gastrointestinal tract of broiler and white leghorn chickens. *Poult Sci.* 1987 February 1, 1987;66:289-98.
48. Vergara P, Jimenez M, Ferrando C, Fernandez E, Goñalons E. Age Influence on Digestive Transit Time of Particulate and Soluble Markers in Broiler Chickens. *Poult Sci.* 1989;68:185-9.
49. Pustjens AM, de Vries S, Schols HA, Gruppen H, Gerrits WJJ, Kabel MA. Understanding carbohydrate structures fermented or resistant to fermentation in broilers fed rapeseed (*Brassica napus*) meal to evaluate the effect of acid-treatment and enzyme-addition. *Poult Sci.* 2014;93:926-34.
50. de Vries S, Gerrits WJJ, Kabel MA, Vasanthan T, Zijlstra RT. β -Glucans and resistant starch alter the fermentation of recalcitrant fibers in growing pigs. *PLoS ONE.* 2016;11:e0167624.
51. Boros D, Slominski BA, Guenter W, Campbell LD, Jones O. Wheat by-products in poultry nutrition. Part II. Nutritive value of wheat screenings, bakery by-products and wheat mill run and their improved utilization by enzyme supplementation. *Can J Anim Sci.* 2004;84:429-35.
52. Marsman GJ, Gruppen H, Van der Poel AFB, Kwakkel RP, Verstegen MWA, Voragen AGJ. The effect of thermal processing and enzyme treatments of soybean meal on growth performance, ileal nutrient digestibilities, and chyme characteristics in broiler chicks. *Poult Sci.* 1997;76:864-72.
53. Jia W, Slominski BA. Means to improve the nutritive value of flaxseed for broiler chickens: The effect of particle size, enzyme addition, and feed pelleting. *Poult Sci.* 2010;89:261-9.
54. Meng X, Slominski BA, Nyachoti CM, Campbell LD, Guenter W. Degradation of cell wall polysaccharides by combinations of carbohydrase enzymes and their effect on nutrient utilization and broiler chicken performance. *Poult Sci.* 2005;84:37-47.
55. Lázaro R, Garcia M, Aranibar MJ, Mateos GG. Effect of enzyme addition to wheat-, barley- and rye-based diets on nutrient digestibility and performance of laying hens. *Br Poult Sci.* 2003;44:256-65.
56. CVB. Feed Table. Lelystad, The Netherlands: Centraal Veevoederbureau; 2011.

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