FIBER IN POULTRY NUTRITION: BONUS OR BURDEN?

S. de Vries
Ingredient Research Centre, Nutreco R&D, P.O. Box 220, 5830 AE Boxmeer, the Netherlands; sonja.de.vries@nutreco.com

Abbreviated title: Fiber in poultry nutrition

Summary

The generic term fiber encompasses a very diverse group of polymers, with varying physicochemical properties. It is well known that dietary fiber can contribute significantly to the nutritive value of poultry diets both directly, as energy source, and indirectly, through its effects on digestive and metabolic processes. 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. Traditional analytical methods to analyze fiber, as crude fiber (CF) and neutral detergent fiber (NDF), recover only a variable part of the fiber fraction and are hence unfit to evaluate fiber fractions in raw materials and poultry diets. 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. In the chicken, solubilization is a prerequisite for fermentation, but even if solubilized during the digestive processes, a substantial part of non-starch polysaccharides (NSP) may remain undegraded. 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 fiber in poultry nutrition is often associated with reduced energy availability due to its minor role in energy supply and interference with digestive processes, low to moderate amounts of fiber (up to 50 g/kg) might be beneficial for gastrointestinal development, function, and health, thereby enhancing nutrient digestibility and growth performance. A better understanding on the relation between specific fiber fractions and factors as GIT development, digesta retention time, and microbial colonization will help to develop nutritional strategies using specific fiber fractions to steer on GIT health and function to enhance performance, especially under suboptimal environmental conditions.

Key words: analytical methods, fermentation, fibre, gastrointestinal health, non-starch polysaccharides,

Introduction

Although abundantly present in many feed ingredients used for poultry diets, dietary fiber (DF) has received little attention poultry nutrition for many years. It is well known that dietary fiber can contribute significantly to the nutritive value of diets both directly, as energy source (JAMROZ et al., 2002, JØRGENSEN et al., 1996), and indirectly, through its effects on digestive and metabolic processes (CHOCT et al., 1996, JØRGENSEN et al., 1996, SMITS et al., 2000, SMITS et al., 1998, SMITS et al., 1997, ANNISON, 1993, MONTAGNE et al., 2003). The generic term fiber, however, encompasses a very diverse group of polymers, with varying physicochemical properties, which hampers prediction of the nutritive value of fiber fractions. Not only the quantity of fiber, but maybe even more importantly, the type of fiber will determine the digestive utilization of the diet and, hence, affect its energetic value, either positively or negatively. 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.

How to track and trace the dietary fiber fraction?

CHALLENGES IN THE ANALYSIS OF DIETARY FIBER

Albeit extensive debates on the appropriate definition and adequate analytical methods, DF is generally defined as the non-digestible fraction of plant cell walls in food and feed ingredients[1] and typically includes oligosaccharides, pectic polysaccharides, hemicellulose, cellulose, lignin, gums, and some minor associated plant cell wall substances

[1] The currently most widely accepted definition of DF includes Dietary fiber means carbohydrate polymers with three or more monomeric units, which are not hydrolyzed by the endogenous enzymes in the small intestine of humans (JONES, 2014, CODEX ALIMENTARIUS COMMISSION, 2013).

(DE VRIES, 2004). Although the chemical constitution of these cell wall fractions varies widely, they can be considered alike from a nutritional viewpoint, as they are not enzymatically digested and exert similar physiological properties. Resistant starch – which is by definition resistant to enzymatic digestion, but mostly not originating from the cell wall (ASP and BJÖRCK, 1992) – is often included based on its similar behavior in the gastrointestinal tract.

Several methods to analyze DF – or its specific components as non-digestible oligosaccharides non-starch polysaccharides (NSP), RS, or lignin – are available (DE VRIES, 2004). Historically in animal nutrition, the gravimetrically based crude fiber (CF), and later neutral (NDF) and acid detergent fiber (ADF) methods, have been used. Although these methods, based on chemical extraction with alkali and acid solutions, are robust to analytical variation and might correlate well with degradability of specific fiber fractions in the animal (MERTENS, 2003), they recover only part of the fiber fraction (Figure 1). Depending on the material, a variable, but considerable part of the fiber fraction – such as cereal β-glucans and some pectic polysaccharides – can be solubilized and hence excluded from the detergent and crude fiber methods, whereas some other pectic polysaccharides that precipitate in strong acid will be included in the ADF fraction (MERTENS, 2003). In addition, also the physical characteristics of the sample, such as particle size, are of importance, because particles can be lost during the filtration step of these gravimetric methods. For CF, for example, this means that depending on the fiber structure of the material, 80-85 % of the hemicellulose, 0 to 60 % of the cellulose, and 10 to 95 % of the lignin are not recovered in this fraction (MERTENS, 2003). It follows that comparison between diets or feed ingredients with distinct fiber structures and physicochemical properties based on these analytical methods is specious. Moreover, this hampers not only comparisons between fiber sources, but also evaluation of fiber degradation in the animal, as physicochemical properties of the ingested feed will be modified by digestive processes along the gastrointestinal tract (GIT).

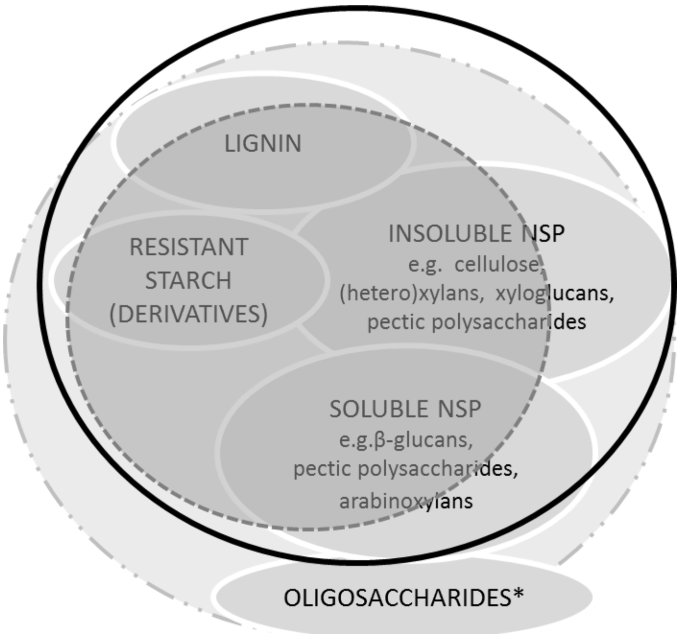

Figure 1. Indicative composition of total dietary fiber* (solid black line), fiber fractions analyzed by gravimetric methods† (dashed grey line), or calculated as residual fraction (calculated NSP)‡ (dashed-dotted grey line).*Analyzed by 'rational' methods as sum of non-starch polysaccharides (enzymatic-chemical methods) and lignin. Oligosaccharides can be separately quantified by liquid chromatography (MCCLEARY et al., 2011). †Empiric gravimetric methods, such as crude fiber or neutral detergent fiber (VAN SOEST et al., 1991). Recovery of various fractions depends on method and physical characteristics of sample (e.g. particle size). ‡Residual organic material after subtraction of ash, crude protein, crude fat, starch, and ethanol (40%)-soluble sugars from DM (CVB, 2011), including NSP, lignin, residual components not analyzed by the proximate system, and accumulated analytical error. Calculated NSP (dashed-dotted grey line) minus crude fiber (dashed grey line) approximates nitrogen-free extract minus digestible starch and sugars. Adapted from ZIELINSKI ET AL. (2013).

Alternatively, in feed formulation the fiber fraction is often calculated as the residual fraction remaining after subtraction of several components analyzed by the proximate or Weende analysis system (AOAC, 2009). In this system, the nitrogen-free extract (NFE) is defined as the organic material remaining after subtraction of ash, crude protein (CP), crude fat, and crude fiber from the dry matter (DM), representing the carbohydrate fraction that is potentially degraded in the animal without distinguishing between easily digestible starch and sugars and the (partly) fermentable fiber fraction. Due to the lack of specificity of the CF-method as described above, NFE also may contain considerable part of the lignin and poorly degradable NSP. The calculated NSP fractions as reported in the Dutch CVB tables (CVB, 2011, Figure 1), are obtained by subtraction of ash, CP, crude fat, starch, and ethanol-soluble sugars, and hence include NSP, lignin, and some low-molecular-weight carbohydrates that precipitate in 40%-ethanol. In both NFE and NSP fractions, components not analyzed by the proximate system – such as some nitrogenous components and vitamins – and analytical errors associated with the analyses accumulate in these residual fractions. Hence, the exact composition of these fractions depends on the raw material and its physicochemical properties.

For scientific purposes, a more appropriate alternative, is the use of enzymatic-chemical methods, as the Englyst or the Uppsala procedures (BACH KNUDSEN, 2001, ZIELINSKI et al., 2013). In these, so-called, "rational"[2] methods, NSP are measured as the sum of constituent monosaccharides released by acid hydrolysis of samples after removal of starch and small saccharides. Not only do these methods provide detailed information on the chemical composition of the fiber fraction, they also have the advantage that they are not sensitive to physical factors such as solubility and particle size of samples, which makes them more appropriate to evaluate fiber degradability in the animal. In addition, they are species-independent as opposed to the empirical DF methods that are typically optimized for their application in human. These sophisticated methods, are, however, not suitable for routine analysis as they are expensive, both in terms of labor and equipment, and are less robust to analytical errors due to the multiple subsequent analytical steps, as well as the small amount of sample material. Furthermore, the small amount of sample material hampers representative sampling in inhomogeneous feed materials. With the recent advances and consensus on optimization of analytical methods for DF in the human nutrition field (ZIELINSKI et al., 2013), the enzymatic-gravimetric methods for total, insoluble, and soluble DF recognized by AOAC (2009.01/2011.25) have evolved in robust methods that may be used for routine analyses of fiber fractions for day-to-day feed formulation practices. These methods could be further optimized in terms of filtration procedures, to avoid confounding effects of particle size. Additionally, near-infrared reflectance spectroscopy (NIRS) might be used to predict contents of DF and specific DF fractions (KAYS and BARTON, 2002, KAYS et al., 1996)).

MEASURING THE FATE OF DIETARY FIBER ALONG THE GASTROINTESTINAL TRACT

As discussed above, the nature of the gravimetric fiber methods makes them unfit to monitor degradation of fiber along the GIT, as changes in physicochemical properties of ingested fiber fractions during digestion confound the results. Hence, the use of "rational" methods is preferred for digestibility studies. When evaluating fiber degradation along the GIT, not only methods to correctly analyze the fiber constituents, but also obtaining a representative sample of the GIT-contents can be challenging. In chickens, soluble and solid digesta fractions are separated and retrograde digesta flows occur. Often, fiber-rich diets have pronounced effects on physical characteristics of the feed matrix, thereby affecting a.o. digesta flow and transit time (ROBERTSON, 1988). These processes may complicate digestion studies, particularly, but not exclusively, when fiber degradation is the matter of interest (DE VRIES et al., 2014a). Unrealistic high ileal and cecal digestibility values for NSP, sometimes exceeding total tract digestibility (PETTERSSON and ÅMAN, 1989, JAMROZ et al., 2002, BRENES et al., 2003, DE VRIES et al., 2014a), clearly indicate that that the marker method is unsuitable 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. When apparent total tract degradation of NSP is measured, 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. Ceca empty at irregular intervals; approximately 2 to 4 times a day, majorly in the morning, just after onset of light, and in the afternoon (HERRICK and EDGAR, 1947, GASAWAY and WHITE, 1975). Hence, short collection periods at single time points may promote selective recovery of excreta, resulting in considerable over- or underrepresentation of cecal contents and erroneous digestibility estimates for fermentable matter.

[2] Rational refers to methods in which an identifiable chemical or analyte is quantitated, as opposed to empirical, non-analyte specific, methods (ZIELINSKI et al., 2013).

Fate of fiber in the gastrointestinal tract

FIBER DEGRADATION IN THE CHICKEN

Degradation of NSP in the animal depends to a large degree on the original cell wall matrix in which the polysaccharides are embedded (DE VRIES et al., 2012). In chickens, ceca access is restricted to fluids and small particles (<0.2mm) and consequently solid digesta won't reach the major site of fiber degradation (JÓZEFIAK et al., 2004). It follows that NSP should be solubilized 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 (PUSTJENS et al., 2014) 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 (CATTD) 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 (Table 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 (MENG and SLOMINSKI, 2005, SLOMINSKI et al., 1994b, DE VRIES et al., 2014b), whereas higher CATTD 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 the wheat-soybean meal (SBM) diets, with and without inclusion of several fiber-rich byproducts, in the studies of BOROS et al. (2004) and MENG et al. (2005) are lower than expected based on NSP solubility. In these studies excreta were collected for a period of only 3 h, and selective recovery of ceca contents due the irregular emptying of the ceca may have resulted in erroneous CATTD estimates. Also the CATTD of NSP from diets containing pea fiber in the study of JØRGENSEN et al. (1994) 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.

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. 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 (PUSTJENS et al., 2014, PETTERSSON and ÅMAN, 1989, MENG and SLOMINSKI, 2005, MENG et al., 2006, BOROS et al., 2004, JIA and SLOMINSKI, 2010, MARSMAN et al., 1997), whereas the effect in adult birds can be even greater (MENG et al., 2006, LÁZARO et al., 2003, SLOMINSKI and CAMPBELL, 1990). Effects of common feed processing technologies are typically smaller, and generally mainly affect easily solubilizable NSP such as cereal β-glucans (DE VRIES et al., 2012).

FIBER AS NUTRIENT: DOES IT MAKE A DIFFERENCE?

Non-starch polysaccharides can be partly fermented by the microbiota residing in the gastrointestinal tract of the animal. The end products of NSP fermentation, short chain fatty acids (SCFA), can be absorbed and used as energy source (DIERICK et al., 1989, JØRGENSEN et al., 1997, JUST et al., 1983). Given that less than 40% of NSP are degraded, the lower efficiency of energy utilization obtained from microbial fermentation compared with enzymatic digestion, and the potential higher energy requirements for fiber-rich ingredients (DIERICK et al., 1989), it follows that, generally, the contribution of NSP to the energy supply in the bird is expected to be minor (JØRGENSEN et al., 1996). In addition, DF can interfere with digestive processes, thereby often reducing digestion and absorption of other nutrients from the diet (FENGLER and MARQUARDT, 1988, CHOCT and ANNISON, 1992b, CHOCT and ANNISON, 1992a, MONTAGNE et al., 2003, SMITS et al., 2000, SMITS et al., 1997, SMITS et al., 1998). Hence, DF is often considered as diluent or even anti-nutritional factor, in poultry nutrition. However, as reviewed by MATEOS et al. (2012), DF play an important role in GIT development and functioning and when fed at low to moderate levels (up to 50 g/kg) may enhance GIT health, nutrient digestibility, and bird performance. Especially insoluble, recalcitrant, fiber fractions that resist fermentation in the gut may be important from this perspective due to their effects on gizzard function and digesta retention time in the GIT (HETLAND et al., 2004). A better understanding on the relation between specific fiber fractions and factors as GIT development, digesta retention time, and microbial colonization will help to develop nutritional strategies using specific fiber fractions to steer on GIT health and function to enhance performance, especially under suboptimal environmental conditions.

Table 1. Coefficient of apparent total tract digestibility (CATTD) of non-starch polysaccharides (NSP) in chickens[1].

Diet characteristics				CATTD	Bird type	Reference[6]
Main NSP sources[2]	Adaptation[3]	NSP content[4]	NSP Solubility[5]			
Barley (100)	0 to 63 d[7]	45	0.29	0.31	Male broilers (2-13 wk)	1
Barley (73), oat bran (27)	0 to 63 d[7]	91	0.43	0.35	Male broilers (2-13 wk)	1
Barley (65), oat bran (35)	0 to 63 d[7]	127	0.39	0.25	Male broilers (2-13 wk)	1
Barley (47), SBM (31), wheat (22)	41 d	127	0.31	0.39	Male broilers (6 wk)	2
Wheat bran (51), barley (49)	0 to 63 d[7]	132	0.27	0.19	Male broilers (2-13 wk)	1
Wheat bran (61), barley (39)	0 to 63 d[7]	203	0.18	0.16	Male broilers (2-13 wk)	1
Wheat (70), SBM (30)	37 d	97[8]	0.24[9]	0.05	Male broilers (7 wk)	3
Wheat (45) SBM (27), canola meal (12), wheat screenings (10), peas (6)	12 d	101[8]	0.25[9]	0.06	Male broilers (2-3 wk)	4
Wheat (37) SBM (33), barley (16), canola meal (9), wheat screenings (5)	37 d	120[8]	0.31[9]	0.15	Male broilers (7 wk)	3
Rye (58), SBM (26), wheat (16)	20 d	121	0.26	0.40	Mixed sex broilers (5-6 wk)	5
Pea fiber (54), barley (36)	0 to 63 d[7]	149	0.40	0.06	Male broilers (2-13 wk)	1
Pea fiber (64), barley (46)	0 to 63 d[7]	251	0.40	0.12	Male broilers (2-13 wk)	1
Maize (54), peas (49)	12 d	88	0.07	0.05	Male broilers (2-3 wk)	6
Maize (100)	12 d	57	0.08	0.08	Male broilers (2-3 wk)	6
Maize (100)	11 d	68	0.10[9]	0.14	Female broilers (4-5 wk)	7
Maize (52), SBM (48)	12 d	100	0.09	0.09	Male broilers (2-3 wk)	6
SBM (51), maize (35), canola meal (14)	12 d	136[9]	0.16[9]	0.12	Male broilers (2-3 wk)	8
SBM (51), maize (35), canola seed (14)	12 d	136[9]	0.16[9]	0.11	Male broilers (2-3 wk)	8
Canola meal (75), maize (25)	11 d	176	0.25[9]	0.20	Female broilers (4-5 wk)	7
Canola meal (56), maize (44)	12 d	106	0.09	0.08	Male broilers (2-3 wk)	6
Canola meal, brown seeded (100)	7 d	91	0.10	0.03	Adult laying hens	9
Canola meal, yellow seeded (100)	7 d	113	0.09	0.09	Adult laying hens	9
Canola meal (100)	4 d	71	0.14	0.02	Adult laying hens	10

[1] Only studies that reported CATTD of total NSP in (semi-purified) complete diets were included. Studies in which CATTD measurements were preceded by fasting were excluded.
[2] Values between brackets indicate contribution of NSP from raw materials to total NSP content of diet (%) calculated using data from original publications or BACH KNUDSEN (1997).
[3] Time in days (d) birds were allowed to adapt to the diet before CATTD measurements.
[4] NSP content of diet (g/kg DM) as reported or calculated from analyzed NSP contents of raw materials, unless indicated otherwise. Dry matter contents diets were assumed to be 900 g/kg, if not provided.
[5] Fraction of soluble NSP in total NSP (g/g), calculated from analyzed NSP contents, unless indicated otherwise.
[6] Data from: 1. JØRGENSEN et al. (1996); 2. JAMROZ et al. (2002); 3. BOROS et al. (2004); 4. MENG et al. (2005); 5. PETTERSON and ÅMAN (1989); 6. MENG and SLOMINSKI (2005); 7. DE VRIES et al. (2014b); 8. MENG et al. (2006); 9. SLOMINSKI et al. (1994) ; and 10. SLOMINSKI and CAMPBELL (1990).
[7] CATTD was measured during two blocks of five and four weeks from 12 d of age onwards, without preceding adaptation.
[8] Calculated based on data from BACH KNUDSEN (1997) and SLOMINSKI et al. (2004).
[9] Calculated based on data from BACH KNUDSEN (1997).

Conclusion

Traditional analytical methods to analyze fiber, as crude fiber (CF) and neutral detergent fiber (NDF), recover only a variable part of the fiber fraction and are hence unfit to evaluate fiber fractions in raw materials and poultry diets. 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. 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 fiber in poultry nutrition is often associated with reduced energy availability due to its minor role in energy supply and interference with digestive processes, low to moderate amounts of fiber (up to 50 g/kg) might be beneficial for gastrointestinal development, function, and health, thereby enhancing nutrient digestibility and growth performance. A better understanding on the relation between specific fiber fractions and factors as GIT development, digesta retention time, and microbial colonization will help to develop nutritional strategies using specific fiber fractions to steer on GIT health and function to enhance performance, especially under suboptimal environmental conditions.

References

ANNISON, G. (1993) The role of wheat non-starch polysaccharides in broiler nutrition. *Australian Journal of Agricultural Research* **44:** 405-422.

AOAC (2009) Official methods of analyses (Arlington, VA, AOAC Int.).

ASP, N.-G. and BJÖRCK, I. (1992) Resistant starch. *Trends in Food Science & Technology* **3:** 111-114.

BACH KNUDSEN, K. E. (1997) Carbohydrate and lignin contents of plant materials used in animal feeding. *Animal Feed Science and Technology* **67:** 319-338.

BACH KNUDSEN, K. E. (2001) The nutritional significance of 'dietary fibre'analysis. *Animal Feed Science and Technology* **90:** 3-20.

BOROS, D., SLOMINSKI, B. A., GUENTER, W., CAMPBELL, L. D. and JONES, O. (2004) 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. *Canadian Journal of Animal Science* **84:** 429-435.

BRENES, A., SLOMINSKI, B. A., MARQUARDT, R. R., GUENTER, W. and VIVEROS, A. (2003) Effect of enzyme addition on the digestibilities of cell wall polysaccharides and oligosaccharides from whole, dehulled, and ethanol-extracted white lupins in chickens. *Poultry Science* **82:** 1716-1725.

CHOCT, M. and ANNISON, G. (1992a) Anti-nutritive effect of wheat pentosans in broiler chickens: Roles of viscosity and gut microflora. *British Poultry Science* **33:** 821-834.

CHOCT, M. and ANNISON, G. (1992b) The inhibition of nutrient digestion by wheat pentosans. *British Journal of Nutrition* **67:** 123-132.

CHOCT, M., HUGHES, R. J., WANG, J., BEDFORD, M. R., MORGAN, A. J. and ANNISON, G. (1996) Increased small intestinal fermentation is partly responsible for the anti-nutritive activity of non-starch polysaccharides in chickens. *British Poultry Science* **37:** 609-621.

CODEX ALIMENTARIUS COMMISSION (2013) Guidelines on nutritional labelling. **CAC/GL-2-1985** (Rome, FAO).

CVB (2011) Feed table (Lelystad, The Netherlands, Centraal Veevoederbureau).

DE VRIES, J. W. (2004) Dietary fiber: The influence of definition on analysis and regulation. *Journal of AOAC international* **87:** 682-706.

DE VRIES, S., KWAKKEL, R. P., PUSTJENS, A. M., KABEL, M. A., HENDRIKS, W. H. and GERRITS, W. J. J. (2014a) Separation of digesta fractions complicates estimation of ileal digestibility using marker methods with cr_2o_3 and co-edta in broiler chickens. *Poultry Science* **93:** 1-8.

DE VRIES, S., PUSTJENS, A. M., KABEL, M. A., KWAKKEL, R. P. and GERRITS, W. J. J. (2014b) Effects of processing technologies and pectolytic enzymes on degradability of non-starch polysaccharides from rapeseed meal in broilers. *Poultry Science* **93:** 589-598.

DE VRIES, S., PUSTJENS, A. M., SCHOLS, H. A., HENDRIKS, W. H. and GERRITS, W. J. J. (2012) Improving digestive utilization of fiber-rich feedstuffs in pigs and poultry by processing and enzyme technologies: A review. *Animal Feed Science and Technology* **178:** 123-138.

DIERICK, N. A., VERVAEKE, I. J., DEMEYER, D. I. and DECUYPERE, J. A. (1989) Approach to the energetic importance of fibre digestion in pigs. I. Importance of fermentation in the overall energy supply. *Animal Feed Science and Technology* **23:** 141-167.

FENGLER, A. I. and MARQUARDT, R. R. (1988) Water-soluble pentosans from rye: Ii. Effects on rate of dialysis and on the retention of nutrients by the chick. *Cereal Chem* **65:** 298-302.

GASAWAY, W. C. and WHITE, R. G. (1975) Flow of digesta in the intestine and cecum of the rock ptarmigan. *The Condor* **77:** 467-474.

HERRICK, C. A. and EDGAR, S. A. (1947) Some relationships between cecal function and coccidiosis of chickens. *Poultry Science* **26:** 105-107.

HETLAND, H., CHOCT, M. and SVIHUS, B. (2004) Role of insoluble non-starch polysaccharides in poultry nutrition. *World's Poultry Science Journal* **60:** 415-422.

JAMROZ, D., JAKOBSEN, K., BACH KNUDSEN, K. E., WILICZKIEWICZ, A. and ORDA, J. (2002) Digestibility and energy value of non-starch polysaccharides in young chickens, ducks and geese, fed diets containing high amounts of barley. *Comparative Biochemistry and Physiology, Part A* **131:** 657-668.

JIA, W. and SLOMINSKI, B. A. (2010) Means to improve the nutritive value of flaxseed for broiler chickens: The effect of particle size, enzyme addition, and feed pelleting. *Poultry Science* **89:** 261-269.

JONES, J. M. (2014) Codex-aligned dietary fiber definitions help to bridge the 'fiber gap'. *Nutrition Journal* **13:** 1-10.

JØRGENSEN, H., LARSEN, T., ZHAO, X. Q. and EGGUM, B. O. (1997) The energy value of short-chain fatty acids infused into the caecum of pigs. *British Journal of Nutrition* **77:** 745-756.

JØRGENSEN, H., ZHAO, X. Q., BACH KNUDSEN, K. E. and EGGUM, B. O. (1996) The influence of dietary fibre source and level on the development of the gastrointestinal tract, digestibility and energy metabolism in broiler chickens. *British Journal of Nutrition* **75:** 379-395.

JÓZEFIAK, D., RUTKOWSKI, A. and MARTIN, S. A. (2004) Carbohydrate fermentation in the avian ceca: A review. *Animal Feed Science and Technology* **113:** 1-15.

JUST, A., FERNÁNDEZ, J. A. and JØRGENSEN, H. (1983) The net energy value of diets for growth in pigs in relation to the fermentative processes in the digestive tract and the site of absorption of the nutrients. *Livestock Production Science* **10:** 171-186.

KAYS, S. E. and BARTON, F. E. (2002) Near-infrared analysis of soluble and insoluble dietary fiber fractions of cereal food products. *Journal of Agricultural and Food Chemistry* **50:** 3024-3029.

KAYS, S. E., WINDHAM, W. R. and BARTON, F. E. (1996) Prediction of total dietary fiber in cereal products using near-infrared reflectance spectroscopy. *Journal of Agricultural and Food Chemistry* **44:** 2266-2271.

LÁZARO, R., GARCIA, M., ARANIBAR, M. J. and MATEOS, G. G. (2003) Effect of enzyme addition to wheat-, barley-and rye-based diets on nutrient digestibility and performance of laying hens. *British Poultry Science* **44:** 256-265.

MARSMAN, G. J., GRUPPEN, H., VAN DER POEL, A. F. B., KWAKKEL, R. P., VERSTEGEN, M. W. A. and VORAGEN, A. G. J. (1997) The effect of thermal processing and enzyme treatments of soybean meal on growth performance, ileal nutrient digestibilities, and chyme characteristics in broiler chicks. *Poultry Science* **76:** 864-872.

MATEOS, G. G., JIMÉNEZ-MORENO, E., SERRANO, M. P. and LÁZARO, R. P. (2012) Poultry response to high levels of dietary fiber sources varying in physical and chemical characteristics. *The Journal of Applied Poultry Research* **21:** 156-174.

MCCLEARY, B. V., DE VRIES, J. W., RADER, J. I., COHEN, G., PROSKY, L., MUGFORD, D. C., CHAMP, M. and OKUMA, K. (2011) Collaborative study report: Determination of insoluble, soluble, and total dietary fiber (codex definition) by an enzymatic-gravimetric method and liquid chromatography. *Cereal foods world* **56:** 238-247.

MENG, X. and SLOMINSKI, B. A. (2005) Nutritive values of corn, soybean meal, canola meal, and peas for broiler chickens as affected by a multicarbohydrase preparation of cell wall degrading enzymes. *Poultry Science* **84:** 1242-1251.

MENG, X., SLOMINSKI, B. A., CAMPBELL, L. D., GUENTER, W. and JONES, O. (2006) The use of enzyme technology for improved energy utilization from full-fat oilseeds. Part i: Canola seed. *Poultry Science* **85:** 1025-1030.

MENG, X., SLOMINSKI, B. A., NYACHOTI, C. M., CAMPBELL, L. D. and GUENTER, W. (2005) Degradation of cell wall polysaccharides by combinations of carbohydrase enzymes and their effect on nutrient utilization and broiler chicken performance. *Poultry Science* **84:** 37-47.

MERTENS, D. R. (2003) Challenges in insoluble dietary fiber. *Journal of Animal Science* **81:** 3233-3249.

MONTAGNE, L., PLUSKE, J. R. and HAMPSON, D. J. (2003) A review of interactions between dietary fibre and the intestinal mucosa, and their consequences on digestive health in young non-ruminant animals. *Animal Feed Science and Technology* **108:** 95-117.

PETTERSSON, D. and ÅMAN, P. (1989) Enzyme supplementation of a poultry diet containing rye and wheat. *British Journal of Nutrition* **62:** 139-149.

PUSTJENS, A. M., DE VRIES, S., SCHOLS, H. A., GRUPPEN, H., GERRITS, W. J. J. and KABEL, M. A. (2014) 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. *Poultry Science* **93:** 926-934.

ROBERTSON, J. A. (1988) Physicochemical characteristics of food and the digestion of starch and dietary fibre during gut transit. *Proceedings of the Nutrition Society* **47:** 143-152.

SLOMINSKI, B. A., BOROS, D., CAMPBELL, L. D., GUENTER, W. and JONES, O. (2004) Wheat by-products in poultry nutrition. Part i. Chemical and nutritive composition of wheat screenings, bakery by-products and wheat mill run. *Canadian Journal of Animal Science* **84:** 422-428.

SLOMINSKI, B. A. and CAMPBELL, L. D. (1990) Non-starch polysaccharides of canola meal: Quantification, digestibility in poultry and potential benefit of dietary enzyme supplementation. *Journal of the Science of Food and Agriculture* **53:** 175-184.

SLOMINSKI, B. A., CAMPBELL, L. D. and GUENTER, W. (1994a) Carbohydrates and dietary fiber components of yellow- and brown seeded canola. *Journal of Agricultural and Food Chemistry* **42:** 704-707.

SLOMINSKI, B. A., CAMPBELL, L. D. and GUENTER, W. (1994b) Oligosaccharides in canola meal and their effect on nonstarch polysaccharide digestibility and true metabolizable energy in poultry. *Poultry Science* **73**.

SMITS, C. H. M., TE MAARSSEN, C. A. A., MOUWEN, J., KONINKX, J. and BEYNEN, A. C. (2000) The antinutritive effect of a carboxymethylcellulose with high viscosity on lipid digestibility in broiler chickens is not associated with mucosal damage. *Journal of Animal Physiology and Animal Nutrition* **83:** 239-245.

SMITS, C. H. M., VELDMAN, A., VERKADE, H. J. and BEYNEN, A. C. (1998) 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. *Poultry Science* **77:** 1534-1539.

SMITS, C. H. M., VELDMAN, A., VERSTEGEN, M. W. A. and BEYNEN, A. C. (1997) Dietary carboxymethylcellulose with high instead of low viscosity reduces macronutrient digestion in broiler chickens. *The Journal of Nutrition* **127:** 483-487.

VAN SOEST, P. J., ROBERTSON, J. B. and LEWIS, B. A. (1991) Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. *Journal of Dairy Science* **74:** 3583.

ZIELINSKI, G., DE VRIES, J. W., CRAIG, S. A. and BRIDGES, A. R. (2013) Dietary fiber methods in codex alimentarius: Current status and ongoing discussions. *Cereal foods world* **58:** 1-5.