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Review article

Improving fiber utilization from rapeseed and sunflower seed meals to substitute soybean meal in pig and chicken diets: A review

C. Lannuzel [a,*], A. Smith [b], A.L. Mary [b], E.A. Della Pia [c], M.A. Kabel [d], S. de Vries [a]

[a] Wageningen University & Research, Animal Nutrition Group, De Elst 1, 6708 WD Wageningen, The Netherlands
[b] DSM Nutritional Products Europe AG, Wurmisweg 576, 4303 Kaiseraugst, Switzerland
[c] Novozymes A/S, Biologiens Vej 2, 2800 Kgs. Lyngby, Denmark
[d] Wageningen University & Research, Laboratory of Food Chemistry, Bornse Weilanden 9, 6708 WG Wageningen, The Netherlands

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ABSTRACT

Locally produced rapeseed meal (RSM) and sunflower seed meal (SFM) are preeminent alternatives in monogastric feed to reduce the reliance of the European Union (EU) on soy imports. However, RSM and SFM have greater fiber contents compared with soybean meal (SBM). Currently, the lack of information on the composition of RSM and SFM fibers, their degradation and influence on digestive processes hampers accurate prediction of their nutritional value when included in pig and poultry diets, and limits the development of strategies to enhance RSM and SFM fiber degradation. This review emphasizes the diversity of fibers, found in RSM, SFM and SBM, identifies recalcitrant non-starch polysaccharides (NSP) of these meals in monogastric animals, and indicates opportunities to improve degradation of these fibers. In pigs, undegraded NSP from RSM represent ~65 g/kg dry matter (DM), due to the limited degradation of uronyl-rich polysaccharides (0.50) and cellulose (0.66). SFM has the highest recalcitrant NSP content (~147 g/kg DM), because of poor degradation of xylosyl-rich polysaccharides (0.25) and cellulose (0.38). SBM has the lowest recalcitrant NSP content (~39 g/kg DM), mainly limited by degradation of cellulose (0.57), non-cellulosic glucosyl (0.53) and xylosyl-rich polysaccharides (0.61–0.65). In chickens, undegraded NSP represent ~165 g/kg DM for SBM and ~197 g/kg DM for RSM. Even the degradation of soluble fiber is often not complete. Substantial improvements in fiber degradation can be achieved using technologies targeting ingredient-specific recalcitrant fibers, potentially increasing energy yield from the meals by fermentation, and releasing encapsulated nutrients. For example, multi-carbohydrase addition improved degradation of RSM fibers in chickens by 113%, and in an in vitro pig model by 122%. In another study, cellulases improved RSM fiber degradation in an *in sacco* pig model by ~35%. Typically, synergistic effects between pectinases and (hemi)cellulases are seen, as expected from the complex cell-wall structures found in RSM and SFM. Modifying fibers from RSM and SBM using mechanical, (hydro)thermal, or chemical treatments is less successful (0–20%), due the recalcitrant nature of

Abbreviations: ADL, acid detergent lignin; ADF, acid detergent fiber; CAID, coefficient of apparent ileal degradation; CATTD, coefficient of apparent total tract degradation; CF, crude fiber; CM, canola meal; CP, crude protein; DM, dry matter; EU, European Union; GOS, galacto-oligosaccharides; NDF, neutral detergent fiber; NGP, non-glucosyl polysaccharides; NSP, non-starch polysaccharides; RSM, rapeseed meal; SBM, soybean meal; SFM, sunflower seed meal.

* Corresponding author.
E-mail address: corentin.lannuzel@wur.nl (C. Lannuzel).

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the fibers and the drastic conditions required. So far, only alkali treatment substantially improved degradation of RSM fibers (~48%) in an *in sacco* pig model. In conclusion, RSM and particularly SFM have a greater recalcitrant fiber content than SBM. To improve degradation of their fibers, technologies targeting cellulose from RSM and SFM, uronyl-rich polysaccharides from RSM, and xylosyl-rich polysaccharides from SFM seem essential. To that end, multi-carbohydrases including esterase activity, alkali-, or ligninolytic treatments, should be considered.

Table 1
Minimum and maximum content of fibers and their constituents (in g/kg dry matter) in rapeseed, sunflower seed, and soybean meals[a], and hulls as reported in literature[b].

	Rapeseed		Sunflower seed[j]		Soybean	
	Meal	Hull	Meal	Hull	Meal	Hull
Dietary fiber[c]	180–354	615	358–510	801	159–233	666
Total NSP[d]	150–276	353	264–350	562	141–221	513–645
Soluble-NSP	11–55	42	9–62	57	12–63	12–73
Insoluble-NSP	152–203	311	207–294	505	118–191	440–523
Cellulose[e]	46–60	108	87–136	245	29–62	322
NCP[f]	129–178	245	172–222	317	131–155	320
Arabinosyl	43–76	71	31–34	34	22–31	38–44
Galactosyl[g]	13–29	27	13–14	11	41–53	18–25
Uronyl	41–192	95	58–74	79	24–48	60–107
Mannosyl	3–29	7	11–12	12	5–14	26–50
Xylosyl	16–32	18	46–65	145	10–19	75–80
Glucosyl	21	15	11–19	29	4–7	10
Lignin[h]	28–134	262	95–160	239	2–18	21
GOS[i]	16–33		19–21		53–73	9
Reference	(Bach Knudsen, 1997; de Vries et al., 2016; Meng and Slominski, 2005; Navarro et al., 2019; Pustjens et al., 2014a, 2014b, 2013, 2012; Simbaya et al., 1995; Slominski and Campbell, 1990; Slominski et al., 1994a, 1994b)		(Bach Knudsen, 1997; Centraal Veevoederbureau, 2018;Düsterhöft et al., 1992;Irish and Balnave, 1993; Jankowski et al., 2011)		(Bach Knudsen, 2014, 1997; Graham and Åman, 2014; Grieshop et al., 2003; Huisman et al., 1998; Irish and Balnave, 1993; Jankowski et al., 2011, 2009; Meng and Slominski, 2005; Navarro et al., 2019)	

[a] Meals originating from hulled or (partially) de-hulled seeds.

[b] Concentrations reported in fresh material were converted into dry matter concentrations using data from Centraal Veevoederbureau (2018).

[c] Dietary fiber was calculated as the sum of non-starch polysaccharides + lignin for Bach Knudsen (2014, 1997), Düsterhöft et al. (1992), Graham and Åman (2014), Simbaya et al. (1995) and Slominski et al. (1994a), (1994b), analyzed using the Prosky et al. (1985) procedure for Grieshop et al. (2003), analyzed using the AOAC 991.43 (AOAC International, 2007) procedure for Navarro et al. (2019), and calculated the sum of neutral detergent insoluble polysaccharides + neutral detergent soluble polysaccharides + lignin for Slominski and Campbell (1990). For Jankowski et al. (2011), the procedure was not reported.

[d] Non-starch polysaccharides (NSP) were analyzed using the modified Uppsala (Theander and Aaman, 1979; Theander and Westerlund, 1986) and Englyst et al. (1982) procedures for Bach Knudsen (2014, 1997), using the Englyst and Cummings (1984) procedure for de Vries et al. (2016), Düsterhöft et al. (1992), Huisman et al. (1998), Irish and Balnave (1993) and Pustjens et al., (2014a, 2014b, 2013, 2012), using the Englyst and Cummings (1984) procedure with modifications from Slominski and Campbell (1990) for Jankowski et al., (2011, 2009), Meng and Slominski (2005), Simbaya Slominski and Campbell et al., (1995, 1990) and Slominski et al. (1994a), (1994b), and calculated as total dietary fiber-lignin for Navarro et al. (2019).

[e] Cellulose was calculated as NSPglucose (12 mol/l) – NSPglucose (1 mol/l) for Bach Knudsen (1997), calculated as the difference between glucose with and without starch pre-hydrolysis for Huisman et al. (1998), calculated as the difference between NSP and non-cellulosic polysaccharides for Irish and Balnave (1993), and analyzed using the Englyst et al. (1982) procedure for Slominski and Campbell (1990).

[f] Non-cellulosic polysaccharides (NCP). Monosaccharides represent anhydrous sugar moieties.

[g] For de Vries et al. (2016) and Pustjens et al., (2014a, 2014b, 2013, 2012), total galactosyl content was corrected for galactosyl residues originating from raffinose and stachyose using data from Putsjens et al. (2012).

[h] Lignin was analyzed using the Klason lignin (Dence, 1992) procedure for Bach Knudsen (2014, 1997) and Pustjens et al. (2012), analyzed using the acid detergent lignin (Kaar and Brink, 1991) procedure for Centraal Veevoederbureau (2018) and Navarro et al. (2019), calculated as NDF-(NSP + protein in NDF+ ash in NDF) for Simbaya et al. (1995) and Slominski et al. (1994a), and calculated as the difference between NDF and NSP for Slominski and Campbell (1990). For Jankowski et al. (2011), the method was not reported.

[i] Galacto-oligosaccharides (GOS), with a degree of polymerization (DP) $3 \leq DP \leq 10$, were analyzed using the Bach Knudsen and Li (1991) procedure for Bach Knudsen (1997), using the Smiricky et al. (2002) procedure for Grieshop et al. (2003), using the Muzquiz et al. (1992) procedure for Jankowski et al. (2009), using the Slominski et al. (1994a) for Simbaya et al. (2005), for Slominski et al. (1994a), the procedure was described in the study, using the Slominski and Campbell (1991) procedure for Slominski et al. (1994b).

[j] Data on sunflower cake and partly dehulled sunflower cake from Bach Knudsen (1997) were corrected for fat content using data from Centraal Veevoederbureau (2018).

1. Introduction

In 2019–2020, soybean meal (SBM) was the primary plant protein meal used to feed livestock in the European Union (EU) (30 million tons), followed by rapeseed meal (RSM; 13 million tons), and sunflower seed meal (SFM; 8 million tons). Most of this SBM was imported, either as such or obtained from crushing of non-EU soybeans, whereas 72% of RSM and 53% of SFM used originated from crops produced in the EU (European Commission, 2020). During the past decades, this considerable reliance of the European feed industry on non-EU protein-rich feed ingredients, has raised concerns (e.g. the EU's dependency, genetically modified origin, deforestation) (Häusling, 2011). Meanwhile, the competitive price of RSM and SFM has reinforced their attractiveness for the feed industry (Florou-Paneri et al., 2014). Therefore, the share of RSM and SFM in the EU livestock feed is expected to increase in the coming years (de Boer et al., 2014; de Visser et al., 2014; Häusling, 2011; Pérez De Nanclares et al., 2019). RSM and SFM, however, typically have lower digestible protein and lysine contents (Heuzé et al., 2020a, 2020b), and greater fiber contents (RSM: 180–354 g/kg and SFM: 358–510 g/kg dry matter (DM)) compared with SBM (159–233 g/kg DM; Table 1), limiting their inclusion in pig and chicken diets (Khajali and Slominski, 2012).

Fibers – in these meals mainly composed of non-starch polysaccharides (NSP), lignin and non-digestible oligosaccharides - resist auto-enzymatic digestion but can be partly degraded by the enzymes produced by the microbiota residing in the digestive tract (Bach Knudsen et al., 2008; de Vries, 2004). This degradation by microbial enzymes and, if applicable, exogenous enzymes or physical and/or chemical feed pretreatments, corresponds to the disappearance of (poly)saccharides from the gastrointestinal tract by hydrolysis into smaller molecules (e.g. sugar- and uronic monomers deriving from NSP), assuming they are absorbed as such or metabolized by microorganisms forming for example short-chain fatty acids. Short-chain fatty acids are absorbed through the intestinal epithelium, and contribute to the energy supply of the animal (Jørgensen et al., 1997). The extent of degradation and the resulting energy derived from these fibers depends on (1) (in-) accessibility of the polysaccharides due to physical entanglement in the cell-wall matrix, (2) the presence of appropriate microbial enzymes, (3) the digesta matrix in which the fibers are present, and, (4) the time available for fermentation, and thus digesta retention time (Bach Knudsen, 2001; de Vries et al., 2014; Le Goff et al., 2002). In addition, fibers affect digesta physicochemical and rheological properties, thereby affecting digesta mixing, retention time and solute diffusion, which impacts accessibility, hydrolysis, and absorption of other nutrients (Le Goff et al., 2002; Lentle and Janssen, 2010, 2008; Smits and Annison, 1996). By affecting digesta properties, certain fibers may alter the intestinal mucus barrier and increase endogenous secretions, also contributing to reduced apparent nutrient digestibility (Grala et al., 1998). Nevertheless, fibers are an essential fuel for the microbiota present in the digestive tract. They can influence the microbiome, which in turns may affect the intestinal health of the host (Bach Knudsen et al., 2012; Bouhnik et al., 2004; Ravn et al., 2017; Williams et al., 2001).

The lack of specific data on fibers present in RSM and SFM, and the limited understanding of their fate in the animal, currently hampers accurate predictions of their nutritional value in feed formulations. It also prevents the development of technologies to further improve degradation of the recalcitrant fiber fractions and enhance the utilization of those meals. To pinpoint the major barriers for degradation and define the scope for improvement for each of these oilseed meals, this review aims to (1) summarize information on the composition of RSM, SFM, and SBM fibers, (2) compare the degradation of RSM, SFM, and SBM fibers in the gastrointestinal tract of pigs and chickens, and, (3) identify possibilities to enhance degradation of RSM, SFM, and SBM fibers, in order to further exploit the potential of these feed ingredients in monogastric diets.

2. Methodology

To quantify RSM, SFM, and SBM fiber composition and degradation in pigs and chickens, peer reviewed scientific articles were selected, where fiber composition was analyzed by rational methods, as a sum of NSP (enzymatic-chemical methods) and lignin, or total dietary fiber according to AOAC 2009.01 (reviewed by Van der Poel et al., 2018). Commonly used gravimetrical methods to analyze fiber fractions, such as CF, NDF, acid detergent fiber (ADF), acid detergent lignin (ADL), or Klason lignin, are unspecific and represent a variable part of the NSP- and lignin fractions, depending on the feed material and the physical characteristics of the sample, which complicates prediction of the nutritive value of fiber fractions from ingredients in monogastric diets (Choct, 2015; de Vries, 2015; de Vries et al., 2012; Van der Poel et al., 2018; Van Erven et al., 2017). Hence, studies reporting only crude fiber (CF) or neutral detergent fiber (NDF) contents were excluded. In the case of lignin, results from ADL and Klason lignin were still included, due to the absence of data from more specific analysis. Coefficients of apparent ileal (CAID) and total tract fiber degradation (CATTD) reported -either at the end of the ileum or total tract - correspond to the disappearance of (poly)saccharides from the gastrointestinal tract by hydrolysis into smaller molecules (e.g. sugar- and uronic monomers deriving from NSP), assuming they are absorbed as such or metabolized by microorganisms, and therefore not recovered as NSP in ileal digesta or fecal material.

3. Fiber composition of rapeseed, sunflower seed, and soybean meals

RSM, SFM, and SBM are obtained after the oil extraction of the parent seeds. This process concentrates proteins and fibers in the meal. In these meals, the fiber fraction mainly consists of NSP and lignin. Within NSP from RSM, SFM and SBM, cellulose, pectic polysaccharides, and hemicelluloses are present, and are mostly insoluble (Table 1). Some oligosaccharides are also found, and mainly consist of galacto-oligosaccharides (GOS) in RSM, SFM, and SBM (Table 1). These GOS consist of 1, 2, or 3 α-(1→6)-linked units of galactosyl residues, linked through an α-(1→3)-bond to a terminal fructosyl-glucosyl dimer (sucrose) (Mul and Perry, 1994). All three meals do not contain starch (all below 30 g/kg DM; Bach Knudsen, 1997). The processing method used to obtain RSM, SFM, and SBM directly influences the fiber content of these meals. To enhance the oil extraction of the seed dehulling is often applied to soy beans and

sunflower seeds (Heuzé et al., 2020a; Kartika, 2005), but it is not so frequent for rape seeds (Heuzé et al., 2020b). Following oil extraction, all or part of the hulls can be added back to the meal. The amount of hulls added back influences greatly the final fiber content of the meal, because rapeseed-, sunflower seed-, and soybean hulls are rich in fibers relative to the cotyledon (Table 1). Fiber contents also depend on the amount of residual oil present in the meal. Oil is usually extracted using a solvent (e.g. hexane), which results in low residual oil (<30 g/kg DM), and concentrated fibers and proteins in the so-called meal. Oil can also be mechanically extracted by a screw press. This results in a higher residual oil (>50 g/kg DM) and, therefore, lower fiber content in the so-called expeller or cake (Heuzé et al., 2020b, 2020a). Part of the variation reported for RSM, SFM, and SBM fiber contents also arises from the multiple methods used among publications, to analyze fiber fractions (Table 1). For instance, during NSP analysis, starch is first removed by specific enzymes, after which contingent soluble fibers should be precipitated in ethanol prior to discarding the soluble phase. However, the type of enzyme, buffer, temperature and ethanol concentration used, differ among methods. This can lead to variation in recovery of certain fiber fractions, such as small ethanol-soluble fibers, and contributes to discrepancies in the fiber content analyzed (Monro, 1993).

3.1. Rapeseed meal fibers

RSM can be obtained from multiple rapeseed species, e.g. *Brassica napus*, *B. campestris* or *B. rapa*. These species have a slightly different fiber composition (Mejicanos et al., 2016; Pustjens et al., 2013; Simbaya et al., 1995). The term canola meal (CM) is also used for rapeseed meal and refers to low erucic/low glucosinolate varieties of rapeseed developed in North America, but is also used for mustard seed meal (*B. juncea*) (Heuzé et al., 2020b). NSP, notably cellulose (46 and 60 g/kg DM), are the most abundant components of the fiber fraction in RSM. The pectic polysaccharides in RSM are mainly insoluble and include homogalacturonans (4–20 g/kg DM), highly branched arabinans (20 g/kg DM), (arabino-) galactans (20 g/kg DM), and rhamnogalacturonans. Insoluble homogalacturonans in *B. napus* have been described to consist of α-(1→4)-linked galacturonic acid residues (Hirst and Jones, 1946; Pustjens et al., 2013). The arabinans are composed of a backbone of α-(1→5)-linked arabinosyl residues, which can be substituted with additional arabinosyl residues (Levigne et al., 2004). The (arabino-) galactans consist of a β-(1→4)-linked galactosyl backbone, which can be substituted with arabinosyl and/or galactosyl residues (Ralet et al., 2009; Voragen et al., 2009; Wong, 2008). The rhamnogalacturonans are composed of a backbone of α-(1→4)-linked galacturonic acid residues alternating with α-(1→2)-linked rhamnosyl residues. Rhamnosyl residues can be further linked to arabinan or arabinogalactan side chains (Sengkhamparn et al., 2009). In RSM, these pectic polysaccharides can interact with cellulose, forming cellulose-arabinan and cellulose-rhamnogalacturonan complexes (Pustjens et al., 2013). In *B. campestris*, some arabinans and arabinogalactans are present in the soluble fraction (Siddiqui and Wood, 1972). RSM hemicelluloses are mostly insoluble, and include xyloglucans, xylans, and galactomannans. The xyloglucans consist of a β-(1→4)-linked glucosyl backbone substituted with xylosyl residues (Fry et al., 1993), which can be further decorated with galactosyl, arabinosyl and fucosyl residues in RSM (Pustjens et al., 2013). Xylans, which consist of a β-(1→4)-linked xylosyl backbone, are also present in RSM (40 g/kg DM) (Ebringerová et al., 2005; Pustjens et al., 2013). The glucuronoxylans consist of xylans substituted with (4-*O*-methyl)-glucuronic acid (Kabel et al., 2003; Pustjens et al., 2013; Rogowski et al., 2015). The galactomannans are composed of a β-(1→4)-linked mannosyl backbone, which can be substituted with α-(1→4)-galactosyl residues (Buckeridge et al., 2000). Besides, lignin content fluctuates between 28 and 134 g/kg DM in RSM. Among the GOS present in RSM, stachyose is the most abundant (12 g/kg DM), followed by raffinose (4 g/kg DM), whereas verbascose is absent (Bach Knudsen, 1997).

3.2. Sunflower seed meal fibers

In SFM, the fiber fraction mostly consists of NSP (264–350 g/kg DM). Among these NSP, cellulose is the most abundant one (87–136 g/kg DM). When added back to the meal, the hulls provide a substantial share of this cellulose (Table 1). Pectic polysaccharides content is about 84 g/kg DM in SFM. In these pectic polysaccharides, homogalacturonans are found, of which some can be branched with arabinosyl and rhamnosyl residues, yielding rhamnogalacturonans (Düsterhöft et al., 1992). Other pectic polysaccharides include arabinogalactans and arabinans (Canibe et al., 1999). Some of these pectic polysaccharides, such as rhamnogalacturonans, can interact with lignin, which contributes to their insolubility (Düsterhöft et al., 1992). SFM contains 119 g/kg DM of hemicelluloses. Glucuronoxylans, with approximately 10% (4-*O*-methyl)-glucuronic acid substitution, are the most abundant ones (84 g/kg DM) (Düsterhöft et al., 1992). Part of these polysaccharides can interact with cellulose, thereby limiting their solubility. (Gluco-) mannans (18 g/kg DM), and xyloglucans (16 g/kg DM) constitute the residual hemicellulose fraction. The (gluco-) mannans are composed of a β-(1→4)-linked mannosyl backbone which can be interrupted by glucosyl residues (Buckeridge et al., 2000). Some of these xyloglucans and (gluco-) mannans can interact with cellulose (Düsterhöft et al., 1992). The lignin content of SFM is in the same range as in RSM (95–160 g/kg DM), and can fluctuate depending on the amount of lignin-rich hulls added back to the meal (Table 1). No data on low molecular weight sugars in SFM could be found in the literature. Using data from sunflower cake and partly dehulled sunflower cake (Bach Knudsen, 1997), and the concentrated carbohydrate content in the meal (Centraal Veevoederbureau, 2018), GOS content from SFM can be estimated, and is in the same range as GOS from RSM, with approximately 17–18 g/kg DM raffinose, 3–7 g/kg DM stachyose, and no verbascose.

3.3. Soybean meal fibers

Like RSM and SFM, the fiber fraction mainly consist of NSP (159–233 g/kg DM). Cellulose content ranges from 29 to 62 g/kg DM, while pectic polysaccharides are the major NSP in SBM (192 g/kg DM) (Table 1; Choct et al., 2010). Among them,

Table 2
Coefficients of apparent ileal (CAID) and total tract degradation (CATTD) of non-starch polysaccharides (NSP), arabinosyl, galactosyl, uronyl, mannosyl, xylosyl, and glucosyl residues from non-starch polysaccharides originating from soybean meal (SBM), rapeseed meal (RSM), and sunflower seed meal (SFM), or from diets containing SBM, RSM, and SFM in pigs.

Item	RSM		SFM		SBM	
	CAID	CATTD	CAID	CATTD	CAID	CATTD
NSP	0.09–0.77	0.68–0.74	-0.05	0.48	-0.01–0.24	0.68–0.80
Arabinosyl	-0.01–0.21	0.85–0.87	0.07	0.74	-0.21–0.07	0.72–0.89
Galactosyl	0.09	0.66	-0.43	0.64	0.13–0.39	0.92–0.95
Uronyl	-0.50–0.18	0.51–0.56	0.02	0.69	-0.15–0.03	0.84–0.91
Mannosyl	0.11	0.64	0.07	0.80	0.23–0.35	0.90–0.91
Xylosyl	-0.06–0.25	0.79–0.87	-0.08	0.25	-0.06–0.03	0.61–0.65
Cellulosic glucosyl	0.06	0.65	-0.08	0.38	-0.06	0.57
Non-cellulosic glucosyl	0.38	0.76	0.15	0.60	-0.03	0.63
Reference[a]	(de Vries et al., 2016; Navarro et al., 2019; Pustjens et al., 2014a; Zhang et al., 2004)		Zhang et al. (2004)		(Gdala et al., 1997; Navarro et al., 2019; Zhang et al., 2004)	

[a] Body weight of the pigs was 28 kg for de Vries et al. (2016), 9 kg for Gdala et al. (1997), 31 kg for Navarro et al. (2019), 22 kg for Pustjens et al. (2014a), and 45 kg for Zhang et al. (2004). The contribution of NSP from the test ingredient to the total dietary NSP content in % as fed was, 100% of RSM for de Vries et al. (2016) and Pustjens et al. (2014a), 48% of SBM for Gdala et al. (1997), 50% and 54% of SBM for the two SBM diets, 29% and 55% of RSM for the two RSM diet for Navarro et al. (2019), 72% of SBM for the SBM diet, 78% of RSM for the RSM diet and 77% of SFM for the SFM diet for Zhang et al. (2004). To calculate these contributions, data were converted using data from Centraal Veevoederbureau (2018) when dry matter contents of feed ingredients were not reported. When dry matter contents of diets were not reported, data were converted assuming an average dry matter content of diets of 900 g/kg.

Table 3
Coefficient of apparent total tract degradation (CATTD) of non-starch polysaccharides (NSP) from soybean meal (SBM) and rapeseed meal (RSM), or from diets containing SBM and RSM in chickens.

Ingredient	Category	NSP[a]	CATTD		Reference
			Ingredient	Diet	
RSM	Broilers	52	0.24	0.20	de Vries et al. (2014)
CM	Broilers	55		0.08	Meng and Slominski (2005)
CM[c]	Laying hens	100	0.03		Slominski and Campbell (1990)
CM[c]	Caecectomised laying hens	100	0.02		Slominski and Campbell (1990)
CM[c], brown-seeded	Laying hens	100	0.03		Slominski et al. (1994a)
CM[c], yellow-seeded	Laying hens	100	0.09		Slominski et al. (1994a)
CM[c]	Laying hens	100	0.05		Slominski et al. (1994b)
CM[c,4]	Laying hens	100	0.09		Slominski et al. (1994b)
CM[c,4] + raffinose	Laying hens	100	0.05		Slominski et al. (1994b)
SBM	Cockerels	100	0.13		Carré et al. (1990)
SBM	Cockerels	57[b]		0.03	Carré (1995)
SBM	Broilers	57[b]		-0.06	Carré (1995)
SBM	Broilers	46		0.09	Meng and Slominski (2005)

[a] Contribution of NSP from SBM and RSM to the total dietary NSP content in % as fed.
[b] Calculated using data from Bach Knudsen (1997) and Centraal Veevoederbureau (2018).
[c] CM, canola meal.

rhamnogalacturonans are the most abundant, and can be branched with arabinogalactan, arabinan and galactan (Choct, 1997; Huisman et al., 1999). Xylogalacturonans are also found, especially in the insoluble fraction (Huisman et al., 1999, 1998). They consist of a homogalacturonan backbone substituted with β -(1→3)-linked xylosyl residues (Beldman et al., 2003). Hemicellulose represent a minor fraction of NSP in SBM (Choct, 1997), including water-soluble galactomannans, water-insoluble xyloglucans, and mannans (Huisman et al., 2000). The mannans consist of an unsubstituted backbone of β-(1→4)-mannosyl residues (Karr-Lilienthal et al., 2005). Xylans and galactomannans are also found in soybean hulls (Aspinall et al., 1966). Compared with RSM and SFM, SBM lignin content is low (2–18 g/kg DM). Among RSM, SFM, and SBM, SBM has the greatest GOS content (53–73 g/kg DM). Stachyose is the most abundant GOS in SBM (41–57 g/kg DM) followed by raffinose (8–14 g/kg DM). Unlike RSM and SFM, SBM contains some verbascose (2–3 g/kg DM) (Bach Knudsen, 1997; Grieshop et al., 2003; Huisman et al., 1998; Jankowski et al., 2009).

4. Degradation of rapeseed, sunflower seed, and soybean meal fibers in pig and chickens

The degradation of RSM, SFM, and SBM fibers differs among species. While 0.48–0.80 of NSP from RSM, SFM, and SBM is degraded in pigs (Table 2), only 0–0.24 of NSP is degraded in chickens (Table 3). The long mean retention time of solid digesta in pigs, especially in the large intestine (36–44 h) where most of the insoluble fibers are fermented, offers substantial opportunity for degradation (Bedford and Schulze, 1998; Le Goff et al., 2002; Wilfart et al., 2007a). In chickens, the ceca is the major site of fiber fermentation,

where mean retention time ranges from 7 to 15 h (de Vries, 2018; Vergara et al., 1989). However, the access to the ceca is restricted to liquids and small particles (<0.2 mm) (de Vries et al., 2014; Ferrando et al., 1987; Van der Klis and Van Voorst, 1993; Vergara et al., 1989). This hampers the degradation of insoluble fibers, which are abundant in RSM, SFM, and SBM (Table 1). The extent of fiber degradation also differs among meals, related to the differences in degradation of the various polysaccharides present (Table 2). Furthermore, degradation of RSM, SFM, and SBM fibers is influenced by other factors, such as the age, the body weight of the animal, and the dietary composition, including the presence of other fibers sources (de Vries et al., 2016; Le Goff et al., 2002; Wilfart et al., 2007b, 2007a). RSM, SFM and SBM fibers can also influence digesta physicochemical and rheological properties, thereby affecting digesta transit and nutrient digestibility. When broilers and cockerels were fed a RSM-based diet, the total mean retention time of digesta was significantly shorter (310 min) than when fed a SBM-based diet (388 min) (Shires et al., 1987). Viscosity may limit enzyme accessibility to nutrients, reducing their digestibility (Hardacre et al., 2016; Schop et al., 2020). However, NSP from RSM, SFM, and SBM, are expected to contribute little to digesta viscosity in contrast to some cereal NSP (Navarro et al., 2018; Pustjens et al., 2012). In broiler chickens, increased inclusion of RSM and SFM did not increase jejunal digesta viscosity (Amerah et al., 2015). Yet, data on digesta retention time in monogastric animals fed RSM, SBM, and SFM is scarce, and effects of their fibers on digesta physicochemical properties have been poorly investigated.

4.1. Degradation of rapeseed, sunflower seed, and soybean meal fibers in pigs

Soluble fibers from RSM and SBM, which consist of GOS and soluble NSP, are almost completely and rapidly degraded before the end of the terminal ileum in growing pigs (Pustjens et al., 2014a; Smiricky-Tjardes et al., 2003; Zhang et al., 2004). Even in early weaned pigs, CATTD of soluble carbohydrates from a SBM diet reached > 0.92 (Turlington et al., 1989). There are no data on degradation of soluble NSP from SFM, but they may be extensively degraded, although representing only a small fraction of NSP from SFM (Table 1).

4.1.1. Degradation of rapeseed meal pectic polysaccharides and hemicelluloses in pigs

The degradation of RSM arabinosyl, uronyl, and galactosyl residues, which are abundant in RSM pectic polysaccharides, in pigs is variable (Long et al., 2020). The CATTD of arabinosyl residues is substantial (CATTD of 0.85–0.87), predominantly in the cecum (0.53 units). In the feces, no arabinogalactans were present, whereas some arabinans were still found. The relative reduction in degree of branching of arabinans found in feces versus ileal digesta indicates that microbial enzymes in the large intestine have debranching activities (Pustjens et al., 2014a). The CATTD of galactosyl residues is more limited (0.66), and corresponds to partial degradation of (arabino-) galactans (Zhang et al., 2004). The CATTD of uronyl residues is only 0.51–0.56, and mostly occurs in the cecum (0.24 units). Analysis of undegraded NSP from RSM in pig feces indicated that 45% of the unfermented NSP from RSM were composed of tightly bound pectic polysaccharides anchored in a cellulose lignin matrix. This likely hampered the degradation of pectic polysaccharides. Another 50% of unfermented NSP from RSM were characterized by a high proportion of small uronyl-rich carbohydrates. Theses uronyl-rich polysaccharides were released by alkaline extraction, suggesting that ester-linkages or hydrogen-bonds are involved in the recalcitrant part of this fraction (Pustjens et al., 2014a). In addition, replacement of SBM by increasing levels of rapeseed expeller, reduced CATTD of uronyl residues by 0.14 units in 23 kg pigs, confirming the greater recalcitrant nature of RSM uronyl residues compared with SBM (Pérez De Nanclares et al., 2019). The CATTD of RSM xylosyl and non-cellulosic glucosyl residues, which are abundant constituents of RSM hemicellulose, is substantial (0.76–0.87), and corresponds to the degradation of RSM xylans and xyloglucans. Degradation of these polysaccharides already starts in the proximal gastrointestinal tract, mainly for xyloglucans as indicated by the CAID of non-cellulosic glucosyl residues (0.38), subsequentially followed by degradation of xylosyl residues in the cecum (0.36 units). In the feces of growing pigs, some xylans and xyloglucans from RSM were still found. The incomplete degradation of xyloglucans is likely due to the presence of hydrogen bonds between xyloglucans and cellulose (Pauly et al., 1999; Pustjens et al., 2014a). The CATTD of mannosyl residues was only 0.64, and corresponds to the partial degradation of the mannosyl backbone of RSM galactomannans. However, mannosyl residues represent a minor fraction of NSP from RSM (Table 1).

4.1.2. Degradation of sunflower seed meal pectic polysaccharides and hemicelluloses in pigs

Similarly to arabinosyl residues from RSM, the CATTD of arabinosyl residues from SFM is substantial (0.74). The CATTD of galactosyl residues from SFM (0.64) is in the same range as galactosyl residues from RSM, but they represent a minor fraction of NSP from SFM. Uronyl residues from SFM are better degraded (CATTD of 0.69) than those of RSM. Because of their low solubility, uronyl-rich polysaccharides from SFM are barely degraded before the end of the ileum. In the large intestine, their degradation is substantial, but not complete (Table 2). The ability of SFM uronyl-rich polysaccharides to interact with lignin (e.g. rhamnogalacturonans) certainly contributes to their recalcitrant properties (Düsterhöft et al., 1992). The CATTD of xylosyl residues which are abundant in SFM, is by far the lowest (0.25), among all NSP present in SBM, RSM, and SFM. In SFM, most of the xylosyl-rich NSP originate from the hulls (Table 1), where they can interact with cellulose and lignin. These structures prevent accessibility for microbial enzymes, and hamper the degradation of glucuronoxylans and xylans. The CATTD of non-cellulosic glucosyl residues (0.60), originating from xyloglucans, is also incomplete in SFM. This may be partly caused by the interaction between xyloglucans and cellulose (Düsterhöft et al., 1992). On the contrary, the degradation of mannosyl residues is substantial (CATTD of 0.80).

4.1.3. Degradation of soybean meal pectic polysaccharides and hemicelluloses in pigs

Arabinosyl, uronyl, and galactosyl residues from SBM are degraded to a greater extent than those from RSM and SFM in growing pigs. The CATTD ranges from 0.72 to 0.89 for arabinosyl, from 0.84 to 0.91 for uronyl, and from 0.92 to 0.95 for galactosyl residues.

This indicates a substantial degradation of SBM arabinans, arabinogalactans and uronyl-rich pectic polysaccharides. Such degradation is limited up to terminal ileum, except for galactosyl residues (CAID of 0.14–0.39). In the large intestine, the cecum is the main site of degradation for these polysaccharides (0.40 units for arabinosyl, 0.52 units for uronyl, and 0.67 units for galactosyl residues). Extensive degradation of SBM arabinosyl, uronyl, and galactosyl residues was also reported in piglets and by in vitro fermentation using pig fecal inoculum (Gdala et al., 1997; Jonathan et al., 2012). The considerable degradation of these SBM polysaccharides is related to their solubility, and their limited interaction with recalcitrant structures (Bach Knudsen, 2014).

The CATTD of SBM xylosyl and glucosyl residues from non-cellulosic glucose ranges from 0.61 to 0.65 total tract, and may correspond to the (partial) degradation of SBM xylans, xyloglucans and, to a lower extent, xylogalacturonans. Due to their recalcitrant characteristics, SBM xylans and xyloglucans are degraded in more distal parts of the digestive tract, as illustrated by the substantial colonic degradation of xylosyl residues (0.38 units) (Gdala et al., 1997). Most of these xylosyl-rich NSP originate from the hulls (Table 1) where they can interact with the abundant cellulose (Table 1), limiting their solubility and degradation. Mannosyl residues, which represent a minor fraction of NSP from SBM (Table 1), are almost completely degraded (CATTD ~0.90). Already before the end of the ileum, a substantial part of these mannosyl residues are degraded (CAID of 0.23–0.35). In the large intestine, mannosyl residues are mainly degraded in the cecum (0.42 units).

Although the diet composition differs among studies, greater CATTD of NSP from (mainly) SBM, such as uronyl-rich polysaccharides (0.07-units), were observed in growing pigs (Zhang et al., 2004) compared with piglets (Gdala et al., 1997). This suggests that SBM fiber degradation may increase with the age or body weight, as can be expected from the greater fermentation capacity in growing pigs compared with piglets. This age/body weight-related improvement, may, however, vary among feed ingredients. For instance, degradation of maize bran fibers was improved in sows compared with growing pigs, coinciding with a longer retention time and a lower feeding level, which provided more opportunity for degradation. Although wheat bran fibers are expected to be less recalcitrant than maize bran fibers (Wang et al., 2004), no improvement in fiber degradation was shown in sows compared with growing pigs. This may be due to the stimulating effect of wheat bran on colonic peristaltic motility, resulting in a reduced retention time in the large intestine, or to physical inaccessibility of wheat bran fibers to microbial enzymes (Le Goff et al., 2002).

4.1.4. Degradation of rapeseed, sunflower seed, and soybean meal cellulose in pigs

The degradation of cellulosic glucosyl residues, which represents most of the glucose of NSP from RSM, SFM, and SBM, is restricted to the large intestine and is equal or below 0.65 total tract (Table 2). For SFM, cellulose degradation is even more limited due to the high lignification of the hulls, where most of the cellulose originates from (Canibe et al., 1999; Table 1).

4.1.5. Interactions between degradation of meal fibers and other fibers

The degradation of RSM, SFM, and SBM fibers can be affected by the presence of other fibers in the diet. In growing pigs, the addition of resistant starch to a RSM-based diet reduced the CATTD of arabinosyl, uronyl, and xylosyl residues from RSM (de Vries et al., 2016). In the large intestine, resistant starch appeared to be preferentially degraded by the microbiota over pectic polysaccharides from RSM, reducing degradation of the latter compared with the control diet based on native maize starch (de Vries et al., 2016; Jonathan et al., 2012). The addition of β-glucans increased CATTD of non-glucosyl polysaccharides (NGP) by 6% units, mainly explained by increased degradation of xylosyl residues. Although, the mode of action remains unclear, the authors speculated that the addition of β-glucans might have increased retention time in the large intestine, therefore offering more time for recalcitrant xyloglucan degradation, or promoted microbiota that specifically degrade RSM xyloglucans (de Vries et al., 2016). More generally, physicochemical properties of the digesta such as bulking or viscosity, as affected by fibers, may influence all sort of digestive processes, e.g. mean retention time, nutrient accessibility and solute diffusion; which will interfere with fiber degradation as well (Le Goff et al., 2002; Lentle and Janssen, 2008, 2010; Smits and Annison, 1996; Wenk, 2001; Wilfart et al., 2007a,b).

4.2. Degradation of rapeseed, sunflower seed, and soybean meal fibers in chickens

The capacity of chickens to degrade RSM and SBM fibers is low, with CATTD of NSP ranging from 0 to 0.24 (Table 3). To our knowledge, degradation of NSP from SFM by chickens has never been reported. Because SFM fibers are even less soluble than RSM and SBM fibers, their degradation is expected to be low.

4.2.1. Degradation of rapeseed and soybean meals soluble fibers in chickens

Degradation of the soluble fiber fraction from RSM and SBM in chickens, is substantial, but not necessarily complete. CATTD of oligosaccharides from RSM was 0.69 in laying hens (Slominski et al., 1994b). In broilers fed RSM diets, characterization of carbohydrates remaining in the excreta revealed the presence of 1,6-linked galactose, likely originating from raffinose and stachyose. This confirms that the degradation of GOS from RSM is incomplete in chickens (Pustjens et al., 2014b). In cockerels (from broiler and layer strains) and in broilers, CATTD of GOS from SBM ranged from 0.82 to 0.99 (Carré, 1995; Carré et al., 1990). In adult roosters fed a SBM based diet, CATTD was 0.91 for raffinose and 0.83 for stachyose. When measured in the ileum, CAID of raffinose and stachyose were below 0.01, indicating that GOS degradation occurs in the distal digestive tract, most likely in the ceca (Coon et al., 1990). In broilers fed a maize-RSM diet, CATTD of NSP (0.08) corresponded to the amount of soluble NSP present in the diet, suggesting that the large majority of soluble NSP from RSM are degraded. Similar observations were made when broilers were fed a maize-SBM diet (CATTD of NSP of 0.09; Meng and Slominski, 2005). In 73-day-old cockerels (from a broiler strain), the CATTD of NSP from SBM was slightly larger than the amount of water-soluble NSP in the diet, supporting that most of the soluble NSP from SBM are degraded by chickens (Carré et al., 1990). However, in laying hens fed semi-purified RSM diets, CATTD of soluble NSP ranged from 0.42 to 0.51 (Slominski

Table 4
Total nitrogen (N), nitrogen present in the neutral detergent fiber fraction (N in NDF), nitrogen present in NDF as amino acid (AA) in g/kg as fed, and coefficient of standardized ileal digestibility of crude protein in pigs (CSID of CP) of rapeseed meal (RSM), sunflower seed meal -high protein (SFM HP) and -low protein (SFM LP), and soybean meal (SBM).

	RSM	SFM HP	SFM LP	SBM
N[a]	49	54	39	77
N in NDF[a]	13	3	4	6
of which present as AA[a,b]	9	2	2	4
CSID of CP[c]	0.74	0.81	0.83	0.87

[a] Data from: van Krimpen et al., unpublished and de Vries (2019)
[b] Excluding methionine, cysteine and tryptophan.
[c] National Research Council (2012).

Table 5
Effect of processing technologies and enzyme addition on change in coefficients of apparent ileal (CAID) and apparent total tract degradation (CATTD) of non-starch polysaccharides (NSP) from soybean meal (SBM) and rapeseed meal (RSM) or from diets containing SBM and RSM in broilers.

Ingredient	Processing	Enzyme	NSP[f]	Change in degradation			Reference
				CAID	CATTD		
				Diet	Ingredient	Diet	
RSM							
		Pectinases[a]	52		0.14	0.16	de Vries et al. (2014)
	Wet-milled	–	52		0.02	0.00	
	Wet-milled	Pectinases[a]	52		0.16	0.17	
	Extruded	–	52		0.02	0.03	
	Extruded	Pectinases[a]	52		0.08	0.08	
	Acid-extruded	–	52			0.04	Pustjens et al. (2014b)
	Acid-extruded	Pectinases[a]	52			0.06	
		Multi-carbohydrases[b]	55			0.09	Meng and Slominski (2005)
SBM							
		Extruded[c]	100	0.10–0.13			Marsman et al. (1997)
		Multi-carbohydrases[d,e]	100	0.12			
		Multi-carbohydrases[b]	46			0.12	Meng and Slominski (2005)

[a] Pectinex UltraSP (Novozymes, Bagsvaerd, Denmark) and Multifect Pectinase FE (Genecor, Rochester, USA); multi-carbohydrases with mainly pectolytic and hemicellulolytic activities, added at 8.75 mL per kilogram of dry feed for each enzyme mixture.
[b] 1000 U of xylanase, 400 U of glucanase, 1000 U of pectinase, 120 U of cellulase, 280 U of mannanase, 180 U of galactanase (Canadian Bio-Systems Inc., Calgary, Canada).
[c] Change in CAID of NSP was calculated as the difference between extruded SBM with a torpedo screw containing either zero, four or eight rows of flights on the screw and toasted SBM.
[d] Change in CAID of NSP was calculated as the difference between untoasted SBM supplemented with Energex (NOVO Enzyme Process Division, Novo-Nordisk a/s, Bagsvaerd, Denmark) and toasted SBM. [5]Multi-carbohydrases activities were not further specified.
[e] Contribution of NSP from SBM and RSM to the total dietary NSP content in % as fed.

et al., 1994b). Moreover, in broilers, characterization of excreta revealed the presence of branched arabinans, xyloglucans, linear xylans, galactomannans, and galactans in the water-soluble fraction, indicating that complete degradation of soluble NSP from RSM might be hampered by the lack of appropriate microbial enzymes (Pustjens et al., 2014b).

4.2.2. Degradation of rapeseed and soybean meals insoluble fibers in chickens

In laying hens fed RSM-based, semi-purified diets, CATTD of NSP from RSM was low (0.03). Furthermore, no difference between intact and caecectomised hens was observed (Slominski et al., 1990), certainly because most of the NSP from RSM are insoluble, which prevent their access to the ceca. In laying hens, CATTD of NSP of a yellow-seeded CM variety was greater than CATTD of NSP of brown-seeded CM (Table 4). This was in line with the lower cell lignification of the yellow-seeded CM (32 g/kg DM lignin and polyphenols) compared with the brown-seeded CM (80 g/kg DM lignin and polyphenols) (Slominski et al., 1994a). Poor degradation of insoluble fibers in chickens was also reported for other feed ingredients, indicating that the prediction of fiber degradation in chickens is strongly related to fiber solubility (de Vries, 2018).

5. Improving the use of rapeseed, sunflower seed, and soybean meal fibers in pig and chicken diets

With ~20–30% of fibers from RSM and SBM, and ~50% from SFM remaining undegraded in pigs, and ~75–100% from RSM and SBM in chickens, considerable improvements can be achieved if their recalcitrant fibers are successfully targeted. Identification of undegraded fibers in both species revealed that multiple structures are responsible for this recalcitrance, and are specific to each meal. Targeting such fractions is likely to enhance RSM, SFM, and SBM fiber degradation and the resulting energy derived from

Table 6
Change in solubilization (%, weight/weight) of constituent sugars from non-starch polysaccharides (NSP) from soybean meal (SBM) and rapeseed meal (RSM) after incubation with multi-carbohydrases[a] obtained from *Aspergillus aculeatus* as compared with incubation without multi-carbohydrases.

	RSM	SBM
Arabinosyl	20	36
Galactosyl	14	36
Uronyl	N.A.[b]	22
Mannosyl	7	14
Xylosyl	20	18
Glucosyl	7	39
Total NSP[c]	14	32
Reference	Pedersen et al. (2017)	Ravn et al. (2015)

[a] RONOZYME® VP; multi-carbohydrases containing hemicellulolytic and pectolytic activities (DSM Nutritional Products, Basel, Switzerland; Pedersen et al., 2017; Ravn et al., 2015)
[b] N.A.: not available
[c] Calculated as weighed average of analyzed constituent sugars. For RSM, uronyl residues are not included since they were not measured.

fermentation, improve digestion of other nutrients, modify digesta physicochemical and rheological properties as well as intestinal microbiome and the resulting fermentation metabolites (de Vries, 2019; Long et al., 2020).

Undegraded NSP represent a substantial part of the unused energy in RSM, SFM, and SBM in growing pigs. In addition, degradation of nutrients encapsulated in the cell-wall matrix, is hampered by physical inaccessibility. For instance, in RSM, it was reported that ~24% of the total nitrogen was found to be bound to the NDF-fraction, of which 74% was present as amino acids (Table 4). This contributes to its inferior crude protein (CP) digestibility compared with SBM and SFM (Table 4). To enhance fiber degradation by pigs and poultry, mechanical and thermal feed processing such as milling or extrusion, which lead to particle size reduction and can enhance NSP solubilization, have been investigated (de Vries et al., 2012; Table 5). However, these technologies mostly affect NSP that can be easily solubilized (de Vries et al., 2012). Extrusion and wet milling of RSM did not significantly improve NGP degradation in chickens, (Table 5). Interestingly, extensive particle-size reduction via wet milling increased solubilization of NGP from RSM and the flow of NGP entering the ceca by 40% compared with untreated RSM, but did not enhance NGP degradation (Pustjens et al., 2014b). This indicates that also the time available for fermentation or the lack of appropriate enzyme activities are possible limiting factors for degradation of NSP from RSM (de Vries et al., 2014). Unlike RSM, extrusion significantly increased degradation of NSP from SBM by enhancing NSP solubilization (Table 5).

The presence of recalcitrant fiber fractions in RSM, SFM, and SBM requires more severe or targeted treatments to degrade such fibers. Acid-extrusion of RSM did not improve degradation of NSP, neither in chickens nor in pigs (Pustjens et al., 2014a, 2014b). Alkali-extrusion of RSM did not improve in vitro degradation of RSM fibers using pig fecal inoculum (de Vries, 2014). However, alkali treatment of RSM did improve fiber degradation after *in sacco* fermentation in ileal cannulated growing pigs. Undegraded carbohydrate content was reduced by 10–21% units after alkali treatment compared with untreated RSM. Alkali treatment of RSM may have disrupted hydrogen bonds and ester linkages present in RSM fibers, which enhanced polysaccharide accessibility and microbial degradation (Long et al., 2020). Enzyme addition also improved RSM and SBM fiber degradation, both in vivo and in vitro. In broiler chickens, multi-carbohydrase addition significantly increased CATTD of NSP from a maize-RSM diet by 0.09 units and that of a maize-SBM diet by 0.12 units compared with non-supplemented diets (Meng and Slominski, 2005). The addition of pectolytic enzymes to RSM-based diets fed to broiler chickens increased NGP solubilization, but also modified the cell-wall structure, which increased polysaccharides accessibility to microbial enzymes (de Vries et al., 2014). This resulted in an increase in CATTD of NGP by 0.14 units, mainly explained by an improvement in CATTD of arabinosyl residues (0.19 units), indicating an enhanced degradation of RSM arabinans. This observation was confirmed by a decrease in the degree of branching of arabinans present in the soluble fraction of broiler excreta. CATTD of xylosyl residues was increased by 0.10 units after enzyme addition, indicating an improvement in RSM xyloglucans and xylans degradation. Despite the pectolytic activity of the enzyme mixture, only a trend for improved CATTD of uronyl residues was observed (0.12 units) (Pustjens et al., 2014b). This result highlights the specificity of RSM pectic polysaccharides, of which degradation is limited by the presence of hydrogen-bonds or ester linkages between pectic polysaccharides and the cellulose-lignin matrix (Pustjens et al., 2014a, 2014b). Addition of a commercially available multi-carbohydrase mixture from *Aspergillus aculeatus* increased in vitro solubilization of NSP from RSM and SBM (Table 6). This demonstrates the capacity of multi-carbohydrases to degrade NSP from RSM and SBM. In addition, exposure of isolated xyloglucans and glucomannans to multi-carbohydrases led to a significant reduction in substrate viscosity, indicating that multi-carbohydrases possess the capacity to degrade xyloglucan and galactomannans (Pedersen et al., 2017; Ravn et al., 2015). Multi-carbohydrases also increased the release of protein from RSM, supporting that enhanced fiber degradation, via multi-carbohydrases addition, could improve protein accessibility in RSM (Pedersen et al., 2017). Moreover, cellulase addition to RSM reduced carbohydrate content after *in sacco* fermentation in ileal cannulated growing pigs, by 10–12% units compared with untreated RSM (Long et al., 2020). The cellulase likely contributed to RSM cellulose degradation, but may have also improved microbial accessibility to other fibers such as arabinans, which can be associated with cellulose in RSM (Pustjens et al., 2013). Compared with untreated RSM, arabinosyl content in feces was reduced by 3–4% units after cellulase pre-treatment. However, pectinase pre-treatment did not improve RSM carbohydrate degradation, supporting the idea

Table 7
Total gas production, lag time till onset of gas production, maximum rate of gas production (Rmax) and time at which Rmax occurs (Tmax) during in vitro degradation of rapeseed meal- (RSM) and sunflower seed meal (SFM) fibers with or without addition of two commercially available multi-carbohydrases at different doses[1].

		24 h incubation					72 h incubation						
Substrate	Enzyme[3] x dose[4]	n[5]	Total gas production (mL/g DM)	SEM	Lag time (h)	SEM	n[5]	Total gas production (mL/g DM)	SEM	Rmax (mL/h)	SEM	Tmax (h)	SEM
RSM	Control	4	86.6^{a}	7.64	14.0^{d}	0.26	2	131.8^{a}	7.56	11.1^{a}	1.03	20.9^{e}	0.18
	VP Low	4	136.2^{b}	7.64	4.9^{a}	0.26	2	165.2^{ab}	7.56	10.0^{a}	1.03	10.2^{b}	0.18
	MG Low	4	152.1^{bc}	7.64	8.1^{c}	0.26	2	188.3^{bc}	7.56	11.5^{a}	1.03	15.8^{d}	0.18
	MG + VP Low	4	183.6 ^{cd}	7.64	4.7^{a}	0.26	2	222.1 ^{cd}	7.56	18.8^{b}	1.03	9.3^{b}	0.18
	VP High	4	202.2^{d}	7.64	4.3^{a}	0.26	2	237.1^{d}	7.56	21.1^{b}	1.03	7.6^{a}	0.18
	MG High	4	242.2^{e}	7.64	6.6^{b}	0.26	2	261.8^{de}	7.56	23.4^{b}	1.03	13.4^{c}	0.18
	MG + VP High	4	296.0 ^{f}	7.64	4.4^{a}	0.26	2	292.8^{e}	7.56	32.9^{c}	1.03	8.3^{a}	0.18
P-value[2]			< 0.001		< 0.001			< 0.001		< 0.001		< 0.001	
	Control	1	62.8	–	15.0	–	0	–	–	–	–	–	–
SFM	VP Low	1	93.1	–	4.8	–	1	98.5	–	6.3	–	9.4	–
	MG Low	4	107.4^{a}	7.25	6.8^{b}	0.31	2	125.4^{a}	13.25	6.6^{a}	1.24	11.8^{ab}	0.97
	MG + VP Low	4	130.0^{ab}	7.25	5.0^{a}	0.31	2	138.3^{a}	13.25	12.4^{a}	1.24	8.8^{ab}	0.97
	VP High	3	144.2^{b}	8.37	4.9^{a}	0.36	2	167.1^{ab}	13.25	12.6^{a}	1.24	7.3^{a}	0.97
	MG High	4	202.4^{c}	7.25	6.8^{b}	0.31	2	232.5^{bc}	13.25	21.0^{b}	1.24	13.2^{b}	0.97
	MG + VP High	4	258.3^{d}	7.25	4.8^{a}	0.31	2	258.8^{c}	13.25	30.0^{c}	1.24	8.5^{ab}	0.97
P-value[2]			< 0.001		< 0.001			0.003		< 0.001		0.032	

[a-f]Means within substrate and columns without common superscripts are significantly different ($P < 0.05$)
[1]Data are presented as least square means and standard error of the mean (SEM), except for SFM Control and SFM VP Low that are presented as raw values due to missing observations.
[2]Model established P-values from ANOVA comparing the fixed effect of treatments (enzyme and dose combination) within substrate, using Tukey adjustments for multiple comparisons (SAS, 2013). SFM Control and SFM VP Low were not included in this comparison due to missing observations.
[3]VP: RONOZYME® VP; multi-carbohydrases containing hemicellulolytic and pectolytic activities (DSM Nutritional Products, Basel, Switzerland; Pedersen et al., 2017; Ravn et al., 2015), MG: RONOZYME® Multigrain; multi-carbohydrases containing xylanolytic, cellulolytic and β–glucanolytic activities (DSM Nutritional Products, Basel, Switzerland; Rangel Pedersen et al., 2021).
[4]Low VP = 300 mg/kg substrate; low MG = 360 mg/kg substrate; high VP = 900 mg/kg substrate; high MG = 1080 mg/kg substrate.
[5]For each enzyme and dose combination, four replicate samples were incubated. Out of those four, two replicates were stopped at 24 h for further analysis, and the two others were incubated for 72 h. Missing observations were due to malfunctioning of the automated gas production system, therefore data from these replicates could not be analyzed.

that further degradation of RSM pectic polysaccharides is hampered by the presence of ester-linkages or hydrogen bonds (Pustjens et al., 2014a). Nevertheless, it is worth noting that care should be taken when interpreting effects of technologies on fiber degradation. In most analytical methods to analyze NSP, starch is first degraded by enzymes, after which soluble fiber should be precipitated in ethanol prior discarding the soluble phase (Bach Knudsen, 1997; Englyst and Cummings, 1984; Englyst et al., 1982; Prosky et al., 1985; Theander and Westerlund, 1986). This soluble fraction is normally not further analyzed. However, if processing and enzyme supplementation are used to enhance fiber degradation, some fiber polysaccharides could be partially hydrolyzed into small (oligo) saccharides. These small (oligo)saccharides may become soluble in ethanol and be discarded. This may lead to an underestimation of residual fibers depending on the material analyzed, and thereby, an overestimation of improvements in fiber degradation enabled by technologies.

Preliminary data from our research group indicate that multi-carbohydrase addition substantially increased in vitro degradation of deproteinized RSM and SFM by pig fecal microbiota (Table 7). Briefly, deproteinized RSM and SFM were obtained by depositing either SFM or RSM in a beaker placed in a water bath filled with water at 50 °C. Distilled water (14 g /g of substrate) was added in the beaker, and pH was set to 6.8. Then, 0.08 g of Alcalase per g of substrate was added. Incubation lasted 3 h during which pH was regularly checked and adjusted if needed to 6.8, by adding NaOH or HCl. After 3 h, the soluble fraction containing the hydrolyzed protein was removed by vacuuming the beaker content through a filter. The residue was incubated again with Alcalase following the same procedure to ensure that all the protein was removed. Final nitrogen content (NEN-ISO, 2008) was found to be lower than 0.05%. To inactivate the Alcalase, the substrate was heated at 100 °C for 30 min. Then, the substrate was oven dried at 70 °C for 48 h, and subsequently ground through a 1 mm sieve using a centrifugal mill at 12,000 rpm (ZM200; Retsch GmbH, Haan, Germany). Fermentation in the large intestine of pigs was simulated in duplicate using a batch culture method with continuous automated recording of gas production for 72 h (Cone et al., 1996). Fecal inoculum was prepared from pig feces, collected from 10 fattening pigs (~100 kg body weight) according to the method of Williams et al. (2005). Just prior to incubation, liquid multi-carbohydrases were added to the substrate/inoculum mixture using a pipette. Besides improving overall degradation, reflected by the total gas production, multi-carbohydrase addition accelerated substrate degradation. Indeed, multi-carbohydrase addition significantly increased

maximum rate of gas production (Rmax), reduced time at which Rmax occurred, and reduced the time till onset of gas production (Table 7). Effects were even more pronounced when enzymes were used in combination, at a high dose, indicating a synergistic action and a dose-dependent action. Although not statistically tested due to missing observations, improvements seem to be even greater for SFM, of which fibers are more recalcitrant than in RSM (Table 2).

Development of new feed technologies may help to further degrade RSM, SFM, and SBM fibers. As the presence of ester-linkages or hydrogen-bonds in RSM is involved in the recalcitrance of the fiber fraction (Pustjens et al., 2014a, 2014b), technologies targeting these linkages, like addition of esterase activities in the multi-carbohydrase cocktails, need to be considered in future research (de Vries, 2014; Van der Poel et al., 2018). In addition, fiber degradation might be improved by enhancing lignin degradation, which is abundant in RSM and SFM. Chemical and physicochemical pre-treatments of biomass to modify lignin already exist, like hydrothermal pre-treatment with alkali and acid catalysts. However, the drastic conditions they require prevent their implementation in the animal feed industry (Brodeur et al., 2011). The use of fungi with ligninolytic activities might offer more feasible opportunities to release additional NSP from RSM and SFM, as well as entrapped nutrients (Kuhad et al., 2013; Nayan et al., 2019). Finally, the differences in structure and degradation among fibers present in RSM, SFM, and SBM clearly indicate that quantitative information on only total NSP or dietary fiber contents is not sufficient to predict fiber degradation and their indirect effects on digestive processes, gastrointestinal health and -function, or (feeding) behavior and feed intake. To more accurately predict the nutritional value of fibers and develop technologies to successfully degrade fibers in RSM and SFM, the heterogeneity of the fiber fractions present among ingredients should be acknowledged. Detailed chemical characterization of fibers, their structural arrangement, their ability to interact with other fibers, and their resulting physicochemical and functional properties will help to better understand animal responses and design tailored technologies to improve utilization of RSM and SFM.

6. Conclusion

In pigs, the recalcitrant non-starch polysaccharide fraction represents ~65 g/kg dry matter for rapeseed meal and ~147 g/kg dry matter for sunflower seed meal, whereas it only represents ~39 g/kg dry matter for soybean meal. In chickens, the recalcitrant non-starch polysaccharides fraction is greater than in pigs due to the restricted access of liquids and small particles to the ceca, and represents ~165 g/kg dry matter for soybean meal, and ~197 g/kg dry matter for rapeseed meal. The recalcitrant nature of rapeseed and sunflower seed in pigs and chickens stresses the need to develop ingredient-specific strategies to improve fiber degradation. So far, mechanical, (hydro)thermal, or chemical treatments led to minor improvements in fiber degradation except alkali treatment, which substantially improved degradation of rapeseed meal fibers in pigs. Addition of multi-carbohydrases also improved degradation of rapeseed meal fibers in chickens and pigs, and showed potential to further degrade fibers from sunflower seed meal in pigs. To account for the diversity of recalcitrant structures present in rapeseed and sunflower meals, combinations of enzymes with synergistic activities seem promising. This is likely to open the cell-wall matrix of rapeseed and sunflower meals, increasing accessibility for microbial enzymes, improving fiber degradation and the energy supply to the animal. Successful fiber degradation may also improve utilization of nutrients entrapped in the cell-wall matrix, such as amino acids, particularly for rapeseed meal. This will contribute to further exploit their use in pig and chicken diets, and ultimately reduce the European Union dependency on soy imports.

Conflict of interest

Adam Smith and Anne-Lise Mary are employed by DSM Nutritional Products (Kaiseraugst, Switzerland), Eduardo Antonio Della Pia is employed by Novozymes A/S (Lyngby, Denmark).

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