

ANIMAL RESEARCH PAPER

In situ ruminal degradation of phenolic acid, cellulose and hemicellulose in crop brans and husks differing in ferulic and *p*-coumaric acid patterns

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SUMMARY

Lignification-associated phenolic acids are widely distributed in graminaceous plant cell walls. Nylon bags containing maize bran, wheat bran, millet husk and rice husk were incubated in the rumens of five Charolais (♂) × Nanyang (♀) crossbred steers for 6, 12, 24, 36, 48 and 72 h. The *in situ* ruminal disappearance of ester-linked phenolic acids linearly increased in the brans with increasing incubation time, and the disappearance was greater for ester-linked ferulic acid (FAest) than for ester-linked *p*-coumaric acid (PCAest). The disappearances of FAest and PCAest were positively correlated with disappearances of neutral detergent fibre (NDF), cellulose and hemicellulose. The effective degradabilities of NDF, cellulose and hemicellulose in the brans were markedly greater than the effective degradabilities of these components in the husks, and were negatively correlated with the contents of Lignin (sa), ether-linked ferulic acid, PCAest and ether-linked *p*-coumaric acid in both the cereal brans and husks. These findings suggested that breeding forage crops with modified phenolic acid contents could represent an alternative strategy to promote further increases in fibre digestibility of cereal residue feeds for ruminant animals.

INTRODUCTION

The plant cell wall, mainly consisting of cellulose, hemicellulose and lignin, is the most important fraction of fibrous feeds. It can be degraded by rumen microorganisms to provide energy and maintain rumen health. Increasing plant cell-wall digestibility is therefore a key strategy for maximizing ruminant performance. However, lignin in the plant cell wall is the primary factor limiting cellulose and hemicellulose degradation (Casler & Jung 1999; Casler 2001; Jung & Lamb 2003); also lignified tissues are difficult for microorganisms to digest compared with non-lignified tissues (Engels & Jung 2005). Jung (2012) reported that lignin accounted for 40–60% of the variation in cell-wall digestion observed in ruminants.

Phenolic acids, such as ferulic acid (FA) and *p*-coumaric acid (PCA), occur mainly in grasses and are important components of the cell wall. Ferulic acids form ether and ester bonds with lignin and/or other cell-wall polymers, while PCAs are mainly ester-linked to lignin (Fig. 1). The binding of phenolic acids to the cell wall through these covalent bonds can impose additional restriction on cell-wall digestion (Cremin *et al.* 1994).

Previous studies noted that the presence of ester-linked ferulic acid (FAest) was positively correlated with cell-wall degradation (Jung & Casler 1990; Casler & Jung 2006), whereas ether-linked ferulic acid (FAeth), an indicator of cross-linking between lignin and arabinoxylans, was negatively correlated with cell-wall digestibility (Rodrigues *et al.* 2007; Jung *et al.* 2011). Ester-linked *p*-coumaric acid (PCAest), also an indicator of cell-wall lignification

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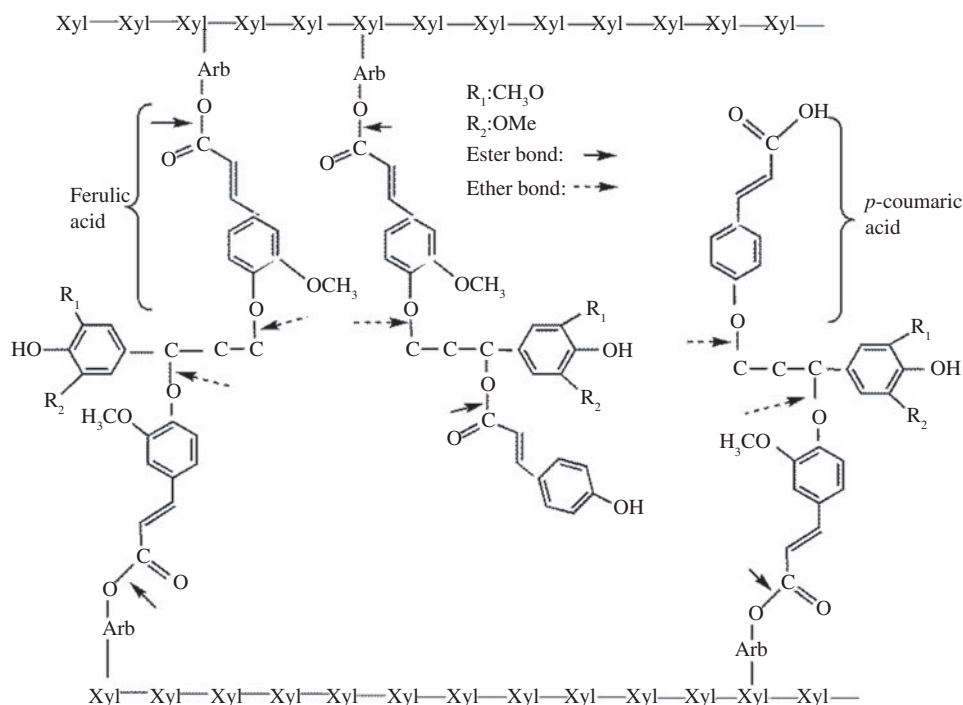


Fig. 1. Ferulic and *p*-coumaric acids linkages in the plant cell wall through ester and ether bonds. Ferulic acids are mainly ester-linked with arabinosyl and ether-linked with lignin, while *p*-coumaric acids are ester- and ether-linked with lignin (Grabber *et al.* 1996).

(Jung & Bernardo 2012), was also found to be negatively correlated with cell-wall degradation (Argillier *et al.* 1996), whereas no consistent correlations with cell-wall degradation were reported for ether-linked *p*-coumaric acid (PCAeth) (Casler & Jung 2006; Rodrigues *et al.* 2007). Previous studies have focused mainly on the effects of phenolic acids on ruminal digestibility of cell-wall material in crop straw (Grabber *et al.* 1998), meadow hay (Rodrigues *et al.* 2007) and grasses (Casler & Jung 2006).

Cereal brans are the outer layer fractions of grains, while cereal husks are the hard protective seed coverings. Both are by-products of milling processes and are therefore a potential source of readily available animal feed. Cereal brans are rich in FA and PCA, with the actual contents depending on the grain species (Saulnier & Thibault 1999; Kim *et al.* 2006; Wang *et al.* 2008). No similar information is available for phenolic acid contents in cereal husks.

Cereal brans (e.g. maize, wheat and rice) are extensively formulated into animal rations due to the presence of highly digestible fibre (Karppinen *et al.* 2000; Ryan 2011). In contrast, millet and rice husks are comparatively inferior fibrous feeds due to the low degradability of their fibre (Beg *et al.* 1986; Vadiveloo *et al.* 2009). The objectives in the present

study were to compare the *in situ* ruminal degradability of ester-linked phenolic acids, cellulose and hemicellulose in the cereal brans and/or husks, and to explore their associations with original Lignin (sa) and phenolic acid contents in the plant cell wall.

MATERIALS AND METHODS

Collection of cereal brans and husks

Representative samples of maize bran, wheat bran and millet husk were gathered from different local milling plants (37°11'N, 112°10'E, 1200 m a.s.l.) in PingYao city, ShanXi province in China. Rice husk samples were collected from different local milling plants (28°50'N, 112°22'E, 33 m a.s.l.) in Yuanjiang city (HuNan, China). Samples were collected in October of 2010 and pooled together in equal proportions according to the grain variety and numbered, resulting in five test samples (1.0 kg) for each cereal bran and/or husk. All samples were dried at 65 °C for 48 h, ground to pass through a 1 mm screen and stored at room temperature for later chemical analysis and *in situ* rumen incubation.

Animals and feeding

Five healthy Charolais (♂) × Nanyang (♀) yellow cattle crossbred steers, fistulated with ruminal cannulas,

weighing $c. 650 \pm 50$ kg (mean \pm SD) and aged 1.5 years old, served as experimental animals for *in situ* rumen incubation. The steers were housed in tie stall barns with free access to water, and they were fed a total mixed ration containing 3.5 kg Chinese wild ryegrass, 2.5 kg alfalfa hay and 8.7 kg commercial concentrate. The concentrate (per kilogram of dry matter (DM)) consisted of 565.5 g maize, 138 g wheat bran, 239.7 g soybean meal, 35.2 g cotton seed meal, 8.1 g salt, 5.4 g calcium carbonate and 8.1 g premix. The ration was offered in two equal portions and fed to the steers at 06:00 and 18:00 h. The study was carried out under the Guidelines of the Beijing Municipal Council on Animal Care.

In situ rumen incubation

Nylon bags (120 \times 80 mm, pore size 50 μ m) containing 3.0 g tested brans or husks were incubated in the rumens of the steers for 6, 12, 24, 36, 48 and 72 h. The bags were withdrawn at the appropriate time and washed with running cold water to remove any feed particles adhering to the bags until the water ran clear. The washed bags were dried at 65 °C for 48 h to a constant weight. The bags containing samples at 0 h were rinsed separately with the same washing procedure. The residues left in the bags were collected and stored for later chemical analyses of neutral detergent fibre (NDF), acid detergent fibre (ADF), Lignin (sa), FAest and PCAest contents.

Chemical analysis

The methods of the Association of Official Analytical Chemists (AOAC 1999) were used to determine DM (ID 930.5), crude protein (CP; ID 984.13), ether extract (EE; ID 920.30) and ash (ID 942.05) contents in the feed samples. Both NDF and ADF were determined following the detergent procedures of Van Soest *et al.* (1991) and corrected for residual ash content. Lignin (sa) content was determined by the solubilization of cellulose with 72% sulphuric acid (Robertson & Van Soest 1981).

Feed samples (100 mg) in 5.0 ml 2.0 M sodium hydroxide solution were incubated at 39 °C in the dark for 24 h to extract FAest and PCAest (Jung & Shalita-Jones 1990). Total FA and PCA were released by incubating 100 mg feed samples with 5.0 ml 4.0 M sodium hydroxide solution at 170 °C for 2 h (Iiyama *et al.* 1990). After the incubation, the solutions were acidified to a pH below 2.0 with concentrated phosphoric acid, extracted with ethyl ether which was then

evaporated under a nitrogen stream, and resolved with 1.0 ml methanol (Jung & Shalita-Jones 1990).

The FA and PCA standards were purchased from Sigma-Aldrich Co. (St. Louis, USA). The contents of FA and PCA released by the alkaline extractions were quantified by high-performance liquid chromatography with a Wufeng analytical instrument (Wufeng Co., Ltd, Shanghai, China) consisting of LC-P100PLUS pump, LC-UV100PULS UV detector and LC-CO100PLUS column heater. The analytical column was a symmetry reversed-phase C18 column (250 \times 4.6 mm², 5 μ m, pH 2–8, Waters, Milford, MA, USA). The method of Wang *et al.* (2013) was used and set as follows: acetonitrile proportion was increased from 20 to 35% within the first 16 min, kept at 35% for 1 min and then decreased from 35 to 20% for the remaining 0.5 min. The column was operated at 15 °C and the flow rate was 1.0 ml/min. Ferulic acid and PCA were detected at 320 nm. Samples (10 μ l) dissolved in methanol were injected into the sampling loop.

Calculations

Cellulose content was calculated as the difference between ADF and Lignin (sa), and hemicellulose content was the difference between NDF and ADF, while FAeth and PCAeth were calculated as the differences between total phenolic acids and ester-linked phenolic acids (Iiyama *et al.* 1990).

Ruminal degradation of FAest, PCAest, NDF, cellulose and hemicellulose in the cereal brans and/or husks at different incubation times was calculated as: $D_t = (w_0 - w_1)/w_0$, where D_t is the disappearance at incubation time t , w_0 is initial analyte (g) and w_1 is the residual analyte (g) at the incubation time t .

To estimate the degradation extent and rate of NDF, cellulose and hemicellulose, *in situ* degradation kinetics were described by the exponential equation of Ørskov & McDonald (1979): $D_t = a + b \times (1 - e^{-ct})$, where D_t is the disappearance at incubation time t , a is a rapidly soluble fraction, b is an insoluble but potentially degradable fraction and c is the degradation rate of b fraction. Effective degradability (ED) was calculated as: $ED = a + [bc/(c + k)]$ (Sniffen *et al.* 1992), where k is the ruminal outflow rate and was set arbitrarily at 0.06.

Statistical analysis

Data were subjected to analysis of variance with the General Linear Model procedure of SAS (1999). The model was applied as: $Y_{ijk} = \mu + F_i + T_j + A_k + e_{ijk}$, where Y_{ijk} is the dependent variable, μ is the overall

Table 1. Chemical composition of cereal bran/husk feeds on a DM basis

Items	Maize bran	Wheat bran	Millet husk	Rice husk
<i>Nutrient composition (g/kg)*</i>				
CP	139 ± 5.1	198 ± 4.3	57 ± 2.0	34 ± 2.2
EE	37 ± 1.9	30 ± 1.6	20 ± 1.2	3 ± 0.2
NDF	740 ± 9.7	526 ± 10.0	708 ± 8.5	858 ± 8.7
ADF	161 ± 4.9	106 ± 4.3	540 ± 8.7	631 ± 10.1
Cellulose	149 ± 5.7	79 ± 2.9	389 ± 8.9	457 ± 11.3
Hemicellulose	575 ± 15.1	420 ± 12.9	168 ± 8.9	226 ± 7.6
Lignin (sa)	12 ± 0.8	26 ± 2.3	151 ± 7.9	174 ± 6.8
<i>Phenolic acid content (mg/kg)†</i>				
FAest	13.10 ± 1.2	2.3 ± 0.22	1.25 ± 0.093	1.5 ± 0.12
FAeth	0.01 ± 0.009	0.04 ± 0.009	1.31 ± 0.024	1.3 ± 0.21
PCAest	1.3 ± 0.21	0.08 ± 0.023	9.1 ± 0.45	8.2 ± 0.23
PCAeth	1.0 ± 0.12	0.10 ± 0.024	2.8 ± 0.23	2.8 ± 0.32

* NDF and ADF represent neutral detergent fibre and acid detergent fibre, respectively, corrected for residual ash content.

† FAest and FAeth represent ester- and ether-linked ferulic acids; PCAest and PCAeth represent ester- and ether-linked *p*-coumaric acids.

Values are means ± s.e.

mean, F_i is fixed effect of the feed ($i = 4$), T_j is effect of the incubation time ($j = 6$), A_k is random effect of the animal ($k = 5$) and e_{ijk} is the error term. Least-square means were separated using a multiple comparison test (Tukey). The relationships between ester-linked phenolic acids, cellulose and hemicellulose digestion with original Lignin (sa) and phenolic acid contents in the tested cereal brans and/or husks were analysed with the correlation (CORR) procedure of SAS (1999). Significance was declared at $P < 0.05$.

RESULTS

Chemical composition

Crude protein, EE and hemicellulose contents were greater in the brans than in the husks (Table 1), but cellulose and Lignin (sa) contents were substantially greater in the husks than in the brans. The total FA content was greater in the brans than in the husks, while total PCA content was markedly greater in the husks than in the brans. The levels of both FAeth and PCAeth were clearly lower than the corresponding ester-linked contents, and the husks had higher levels of FAeth and PCAeth compared with the brans.

In situ rumen disappearance of ester-linked phenolic acids

As shown in Table 2, the time-dependent ruminal disappearance of ester-linked phenolic acids occurred in the brans ($P < 0.001$). No similar effects were observed

for the husks. Consequently, FAest disappearance was at least two times greater in the brans than in the husks as the incubation time was extended up to 72 h ($P < 0.001$). The disappearance of PCAest was at least five times greater in the brans than in the husks ($P < 0.001$), although no differences were observed between the brans or between the husks.

As shown in Table 3, the ruminal disappearances of ester-linked phenolic acids were negatively correlated with the original contents of Lignin (sa) and ether-linked phenolic acids, and these negative correlations became more pronounced with increasing incubation time.

Degradation kinetics of neutral detergent fibre, cellulose and hemicellulose

Table 4 shows that the *in situ* ruminal disappearances of NDF, cellulose and hemicellulose were positively correlated with *in situ* ruminal disappearances of FAest ($r = 0.87$, $P < 0.001$) and PCAest ($r = 0.82$, $P < 0.001$). The degradation kinetics shown in Table 5 indicate that the levels of rapidly soluble fractions (a) of NDF, cellulose and hemicellulose varied among the cereal brans and/or husks ($P < 0.001$), while the levels of the insoluble but potentially degradable fraction (b) with different degradation rates were consistently greater in the brans than in the husks ($P \leq 0.012$). Consequently, ED values of NDF, cellulose and hemicellulose were markedly greater in the brans than in the husks ($P < 0.001$).

Table 2. *In situ* ruminal disappearances of ester-linked phenolic acids in cereal brans and/or husks at different incubation times

Items	Incubation time (h)						<i>P</i> value*	
	6	12	24	36	48	72	L	Q
<i>Ester-linked ferulic acid disappearance (%)</i>								
Maize bran	31	37	65	84	88	89	<0.001	0.004
Wheat bran	36	42	72	82	87	90	<0.001	0.312
Millet husk	35	35	36	36	37	38	0.435	0.843
Rice husk	26	27	27	27	27	28	0.094	0.481
S.E.M†	10.2	17.4	19.0	9.7	5.2	11.3		
<i>P</i> value	0.494	0.004	<0.001	<0.001	<0.001	<0.001		
<i>Ester-linked p-coumaric acid disappearance (%)</i>								
Maize bran	13	32	50	74	79	85	<0.001	0.192
Wheat bran	53	60	72	77	84	86	<0.001	0.189
Millet husk	14	14	14	13	13	15	0.088	0.912
Rice husk	14	13	14	14	15	14	0.981	0.323
S.E.M	12.1	15.4	14.2	11.7	17.2	8.6		
<i>P</i> value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001		

* L and Q represent linear and quadratic effects of incubation time.

† S.E.M., standard error of means.

Table 3. Pearson correlation coefficients (*r*) between *in situ* ruminal ester-linked phenolic acid disappearance at different incubation times and original Lignin (sa), ether-linked phenolic acid contents in maize bran, wheat bran, millet husk and rice husk

Items	Lignin (sa)	FAeth	PCAeth
<i>FAest disappearance</i>			
6 h	-0.17 (0.40)	-0.15 (0.46)	-0.16 (0.45)
12 h	-0.49 (<0.01)	-0.48 (<0.01)	-0.52 (<0.01)
24 h	-0.73 (<0.01)	-0.72 (<0.01)	-0.70 (<0.01)
36 h	-0.75 (<0.01)	-0.74 (<0.01)	-0.70 (<0.01)
48 h	-0.68 (<0.01)	-0.69 (<0.01)	-0.63 (<0.01)
72 h	-0.76 (<0.01)	-0.77 (<0.01)	-0.67 (<0.01)
<i>PCAest disappearance</i>			
6 h	-0.40 (0.04)	-0.45 (0.02)	-0.54 (<0.01)
12 h	-0.57 (<0.01)	-0.60 (<0.01)	-0.62 (<0.01)
24 h	-0.66 (<0.01)	-0.68 (<0.01)	-0.74 (<0.01)
36 h	-0.72 (<0.01)	-0.74 (<0.01)	-0.76 (<0.01)
48 h	-0.70 (<0.01)	-0.71 (<0.01)	-0.74 (<0.01)
72 h	-0.75 (<0.01)	-0.74 (<0.01)	-0.70 (<0.01)

FAest, FAeth represent ester- and ether-linked ferulic acids; PCAest, PCAeth represent ester- and ether-linked *p*-coumaric acids.

Values in parentheses are noted for *P* value.

Table 6 shows that the ED values of NDF, cellulose and hemicellulose were negatively correlated with the contents of Lignin (sa) ($r = -0.96$, $P < 0.05$), FAeth ($r = -0.98$, $P < 0.05$) and PCAest ($r = -0.94$, $P < 0.05$) in the cereal brans and/or husks.

DISCUSSION

Phenolic acids profile in cereal brans and/or husks

As the major phenolic acids, FA and PCA are present at 2–20 g/kg in the cell wall of forages (Fahey & Jung 1989).

Table 4. Pearson correlation coefficients of *in situ* rumen disappearances between fibre and ester-linked phenolic acids in maize bran, wheat bran, millet husk and rice husk at different incubation times

Items	FAest	PCAest
NDF	0.96 (<0.001)	0.93 (<0.001)
Cellulose	0.87 (<0.001)	0.82 (<0.001)
Hemicellulose	0.90 (<0.001)	0.85 (<0.001)

NDF, neutral detergent fibre corrected for residual ash; FAest, ester-linked ferulic acid; PCAest, ester-linked p-coumaric acid. Values in parentheses are noted for *P* value.

Table 5. Rumen degradation kinetics of neutral detergent fibre, cellulose and hemicellulose in cereal brans and/or husks

Items*	a (%)	b (%)	c (%/h)	ED (%)
<i>Neutral detergent fibre</i>				
Maize bran	0	100	3.4	36
Wheat bran	9	79	3.1	34
Millet husk	0	32	2.3	4
Rice husk	2	10	2.9	7
S.E.M.†	1.4	6.0	0.56	1.1
<i>P</i> value	<0.001	<0.001	<0.001	<0.001
<i>Cellulose</i>				
Maize bran	0	100	3	35
Wheat bran	1	77	4	29
Millet husk	7	42	5	11
Rice husk	5	61	2	8
S.E.M.	1.1	9.5	1.1	1.2
<i>P</i> value	<0.001	0.012	0.366	<0.001
<i>Hemicellulose</i>				
Maize bran	1	99	3.6	38
Wheat bran	20	74	3.0	44
Millet husk	0	29	4.0	4
Rice husk	1	13	6.3	7
S.E.M.	2.2	6.5	0.82	1.5
<i>P</i> value	<0.001	<0.001	0.042	<0.001

* a, Immediately soluble fraction; b, insoluble but potentially degradable fraction; c, rate constant for the degradation of fraction b; ED, effective degradability.

† S.E.M., standard error of means.

Assuming that NDF represents the cell-wall fraction, total FA in the NDF fraction in the present study accounted for 1.8, 4.5, 3.6 and 3.2 g/kg in maize bran, wheat bran, millet husk and rice husk, respectively. These values were in accordance with those reported previously (Fahey & Jung 1989). Compared with ester-linked phenolic acid content in the present study, higher FAest (4.2–6.5 mg/kg DM) and lower PCAest (0.12–0.22 mg/kg DM) contents were reported in de-starched wheat bran (Beaugrand *et al.* 2004). The FAest content in maize bran in the present study was higher than that reported (0.33 mg/kg DM) in de-

starched maize bran by Lapierre *et al.* (2001). The content of ether-linked phenolic acids has not been reported previously in cereal brans and/or husks. In the present study, a lower ratio of PCA to FA content was found in the cereal brans than in the husks, in agreement with a previous report (Wang *et al.* 2013).

Microbial phenolic acid degradation in the rumen

Previous studies examining *in vitro* digestion of parenchyma and sclerenchyma cell walls isolated from cocksfoot (Grabber & Jung 1991) and *in situ* ruminal

Table 6. Pearson correlation coefficients of rumen effective degradability with original contents of Lignin (sa) and phenolic acids in maize bran, wheat bran, millet husk and rice husk

Items	Effective degradability		
	NDF	Cellulose	Hemicellulose
Lignin (sa)	-0.98 (0.016)	-0.99 (0.005)	-0.96 (0.031)
FAest	0.66 (0.340)	0.75 (0.247)	0.54 (0.457)
FAeth	-0.99 (0.001)	-0.98(0.015)	-0.98 (0.011)
PCAest	-0.98 (0.010)	-0.94 (0.050)	-0.99 (<0.001)
PCAeth	-0.94 (0.052)	-0.87 (0.124)	-0.98 (0.018)

FAest, FAeth represent ester- and ether-linked ferulic acids; PCAest and PCAeth represent ester- and ether-linked *p*-coumaric acids; NDF, neutral detergent fibre corrected for residual ash.

Values in parentheses are noted for *P* value.

degradation of barley (Du & Yu 2011) demonstrated that FA was more digestible than PCA. The higher FAest disappearance and lower PCAest disappearance were mainly observed in the cereal husks in the present study. This could be due to differences in specific enzyme activity of FA esterase and PCA esterase in the rumen. O'Neill *et al.* (1996) reported that the enzyme activity of fungal FA esterase was greater than PCA esterase, although the microorganisms in their study were not isolated from the rumen. Another explanation could possibly be that FAest mainly existed in the primary cell walls of cereal brans and were readily accessible by microbial FA esterase in the rumen, whereas PCAest localized mainly in the secondary cell walls of cereal husks was less accessible to enzymes. Phenolic acids are primarily linked to lignin or arabinoxylan through ester bonds that can be disrupted by microbial esterases, but the ether-linked phenolic acids do not appear to be digested (Rodrigues *et al.* 2007). This could explain why the *in situ* ruminal disappearances of ester-linked phenolic acids were negatively correlated with Lignin (sa) and also with FAeth and PCAeth contents.

Ruminal fibre degradation and its association with original phenolic acid content

Previous studies have reported that the digestible nutrients in rice husks were present at <100 g/kg DM (Juliano 1985), and the *in vitro* DM digestibility was only 0.16 (Vadiveloo *et al.* 2009). In contrast, the *in situ* ruminal DM digestibility of maize bran has been shown to be as high as 0.80 (Tedeschi *et al.* 2009). Ether-linked ferulic acid content was used as a

measurement of cross-linking between lignin and arabinoxylans. This cross-linking creates a barrier that protects cell-wall carbohydrates from enzymatic hydrolysis and microbial attack (Casler & Jung 2006), which could explain the much lower effective degradabilities of NDF, cellulose and hemicellulose in the cereal husks than in the brans, and the negative correlation between these degradabilities and the contents of Lignin (sa) and FAeth observed in the present study.

The formation of FAest in the primary cell wall is accompanied by the synthesis of other cell-wall components (Rodrigues *et al.* 2007). Previous studies have indicated that plants with higher FAest contents had higher cell-wall digestibility (Jung & Allen 1995; Mandevvu *et al.* 1999), reflecting the deposition of FAest accompanies the appearance of other cell-wall components (Rodrigues *et al.* 2007). Rodrigues *et al.* (2007) speculated that a negative correlation would exist between PCAeth content and cell-wall digestibility, and that the ether bond cannot be broken down under anaerobic conditions by microorganisms. Both PCAest and PCAeth contents, like Lignin (sa) in the present study, were negatively correlated with insoluble but degradable *b* fractions of NDF, cellulose and hemicellulose, and this resulted in lower ED of the cereal husks compared with the brans. One explanation, based on the previous findings, may be that PCA limited the plant cell-wall degradation in the rumen by indirectly influencing the extent of lignification of the plant cell wall (Argillier *et al.* 1996; Zhang *et al.* 2011).

In summary, cereal brans and/or husks exhibited different phenolic acid patterns. Besides Lignin (sa) content, phenolic acids in the ether-linked form, rather than the ester-linked form, were confirmed as

major factors that restricted microbial degradation of ester-linked phenolic acids, cellulose and hemicellulose in the rumen. Breeding forage crops with modified phenolic acid profiles could be an alternative strategy for further increasing the fibre digestibility of cereal residues for ruminant animals.

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