Original article

Ruminal degradability of corn forages depending on the processing method employed

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Abstract – The in sacco degradabilities of starch and fibre in corn were compared between kernel grains and the whole corn plant before and after ensiling using the nylon bag technique. The same plants were used, in order to exclude the effects of genotype or maturity at harvest. The incubation time course was carried out over 48 h on four cannulated dairy cows. The effective degradability of starch was lower in kernel grains (70.2%) than in the whole plant before (83.9%) and after (92.3%) ensiling. Starch degradation in whole plants was accelerated compared to kernel grains by a shift from the slowly degradable (from 61.3% to 31.9%) to the rapidly degradable fraction (from 35.9% to 65.6%) without significantly affecting the degradation constant rate (7.7 and 8.0% per h respectively for kernel grains and whole corn plants). The ensiling process improved starch degradation even further compared to whole fresh plants by significantly increasing the rapidly degradable fraction (80.7% versus 65.6%) and by a higher degradation constant rate (12.4% per h versus 8.0% per h). The fibre degradation was similar between grains and whole corn plants despite differences in their content and composition of NDF. However, ensiling significantly increased the rapidly degradable NDF fraction (15.2 versus 9.9%) and doubled its degradation constant rate (from 1.6% per h to 3.2% per h). This effect was probably due to improved hemicellulose degradation, because cellulose and lignin were not degraded differently between corn plants before and after ensiling. Mechanical cracking such as chopping at harvest improves ruminal starch degradation without altering fibre degradation but the ensiling process simultaneously increases the degradability of starch and fibres.

ruminal degradation / corn processing / corn starch / corn fibres

Résumé – Dégradation ruminale du maïs fourrage en fonction de sa forme de présentation. Les dégradations in sacco de l'amidon et des fibres ont été comparées entre le maïs grain et la plante entière avant et après fermentation en utilisant la technique des sachets nylon. L'utilisation des mêmes plantes a permis de contrôler les effets du génotype ou du stade de maturité à la récolte. L'étude a porté sur 48 h d'incubation avec 4 vaches fistulées. La dégradabilité théorique de l'amidon du maïs grain (70,2 %) est plus faible que celle de l'amidon de la plante entière avant (83,9 %) et après (92,3 %) fermentation. La dégradation d'amidon de la plante entière a été accélérée par rapport à celle du maïs grain par un déplacement d'une partie de la fraction lentement dégradable (de 61,3 à

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31,9 %) vers la fraction rapidement dégradable (de 35,9 à 65,6 %) sans effet significatif sur le taux horaire de dégradation (7,7 et 8,0 % par h respectivement pour le grain et la plante entière). La fermentation de la plante entière améliore la dégradation de l'amidon par une augmentation significative de la fraction rapidement dégradable (de 65,6 à 80,7 %) et du taux horaire (8,0 contre 12,4 % par h). Les dégradations des fibres ont été similaires entre grains et plante entière malgré des différences de la teneur en NDF et de sa composition. Par contre, la fermentation de la plante augmente significativement la fraction rapidement dégradable des NDF (15,2 contre 9,9 %) et double son taux horaire (de 1,6 à 3,2 % par h). Cet effet semble dû à une augmentation de la dégradation de l'hémicellulose puisque aucune différence de dégradation avant ou après fermentation pour la lignine et la cellulose n'est observée. Le broyage mécanique, comme le hachage à la récolte, améliore la dégradation de l'amidon de maïs dans le rumen sans modifier la dégradation des fibres. Par contre, la fermentation de la plante entière en ensilage augmente simultanément la dégradabilité de l'amidon et des fibres.

dégradation ruminale / traitement du maïs / amidon de maïs / fibres de maïs

1. INTRODUCTION

Corn silage is currently used as forage in the diet of high yielding dairy cows to assure an elevated energy supply, mainly because of its high starch content. The starch of corn grains harvested at maturity has been reported as being slowly degraded by micro-organisms in the rumen [28]. In contrast, the starch in ensiled corn is rapidly degraded in the rumen [21, 23, 25] and an increased amount of starch degraded in the rumen has been shown to depress fibre digestion [2]. Thus the risk of acidosis, at least in a subclinical state, is present. Different hypotheses can be put forward to explain the acceleration of starch degradation in ensiled corn when compared to starch from corn grains harvested at maturity.

A first possible explanation for modified ruminal degradation of corn is the genetic variability between cultivars. This has been shown not only for cell wall degradation in the rumen [7, 11, 35] but also for starch between grains of dent and flint genotypes [24, 35]. Other authors [25] have noted increased ruminal starch degradability after ensiling, independently of corn genotypes. Secondly, the literature [3, 8, 14, 24] has reported a decreased starch degradability of corn silage in the rumen when the maturity of harvested plants increases. Because silage cultivars are harvested at a less mature stage than crop cultivars, the starch fraction in

corn silage can be degraded more rapidly in the rumen than that found in crop cultivars. Thus the effect of the genotype, i.e. cultivar, and the vegetation stage at harvest on starch degradation in the rumen has always been demonstrated. Another explanation for a higher starch degradation after ensiling may be plant processing. The mechanical cracking that takes place prior to ensiling reduces particle size and there is an increased ruminal degradability of ensiled corn starch compared to the starch of identically prepared corn plants even before ensiling [25]. Moreover the solubilisation of endosperm proteins during corn fermentation has been observed [16], and this may improve enzyme access to starch, alongside mechanical cracking. Starch granules (especially in corn) are embedded in a protein matrix [9] that grows with the maturation of the kernel [14] and thus protects starch grains from hydrolysis by amylolytic enzymes [12]. Mainly made up of zeins, the core of these protein bodies is negatively correlated to starch degradation [27].

The first aim of this study was therefore to determine whether the more rapid degradation in the rumen of starch in ensiled corn is due to processing, i.e. not dependent upon differences in genotype or maturity. Finally, the supplementation of readily fermentable carbohydrates is known to reduce fibre digestion in vivo [2, 30], at least when using rapidly degradable grains such as barley or

wheat. The second aim of this study was to determine whether corn processing, especially fermentation, would affect the degradation of corn fibres and hence the nutritive value of corn forages.

2. MATERIALS AND METHODS

2.1. Experimental design and plant growing conditions

The characteristics of ruminal degradation of corn kernel grains, fresh whole corn plants (FWCP) and ensiled whole corn plants (EWCP) were compared using the same raw material throughout the trial.

Corn was grown on a calcic vertic combisol (FAO classification). During the spring, it was necessary to seed two cultivars (2265® hybrid, Force Limagrain, Saint-Quentin-Fallavier, 38, France and Etendard® hybrid, Sémences de France, La Chapelle d'Armentières, 59, France) because of the different moisture conditions which prevailed in the same field. Grains were sown in equivalent proportions with a corn population density of 113,000 plants per ha on May 5th and harvested 152 days later, on October 4th, 2000. The entire field was fertilised with 252 units of N per ha and the rainfall during the growing period was 402 mm. Growth and harvest characteristics are shown in Table I. Corn plants at silage maturity (dent stage) were chopped with a forage harvester to a particle size of 1 cm.

Fifteen kernels from each cultivar were randomly sampled from the field one day before harvest. The grains were manually separated and weighed. Because both cultivars were mixed in the same flat silo (width 13 m, depth 18 m, height 4 m) at similar proportions (as in the field), we also mixed the two cultivars together before incubating the grains (50:50 wt/wt). A representative sample of the whole fresh corn plant (FWCP) before fermentation was collected just after filling the silo, and another sample was taken from the same place in the

Table I. Growth and harvesting characteristics of the two corn cultivars.

	2265®	Etendard®
Grain texture	dent-flint	dent / dent-flint
Precocity (FAO index)	255	270
Vegetation period (days)	152	152
Fertilisation (units N per ha)	252	252
1000-grain weight (g)	271	233
Whole plant yield (T DM per ha)	12.9	12.4

silo after fermentation for 2 weeks (EWCP) in order to determine the chemical composition.

2.2. Incubation

In sacco measurements were carried out using four ruminally cannulated lactating multiparous Holstein cows housed in a free stall barn. The animals were fed ad libitum with a total mixed ration composed of corn silage (55.3% of DM), wheat straw (2.8%), cracked wheat (29.9%), soybean meal (10.4%) and minerals (1.6%). Cows had an average intake of 19.2 (± 2.6) kg DM per d and a daily yield of 31.4 (± 5.1) kg milk. The corn silage fed to them was the same as that used for incubation samples. The animals were adapted to the experimental diet for 2 weeks before measurements were performed.

All feed samples were oven dried (48 h at 65 °C) and ground (centrifugal force mill SK100, Retsch GmbH & Co KG, Haan, Germany, sieve 1.5 mm). The nylon bag technique [17] was then carried out and approximately 4 g of each tested feedstuff were placed separately into bags (internal dimension 9 × 14 cm, Blutex 120, Saati France Co., Sailly Saillisel, France) with a pore size of 50 μm.

The incubated bags were soaked and then inserted into the rumen just before giving access to the morning meal. The bags

were removed after 1, 3, 6, 12, 24, and 48 h of incubation, rinsed in cold water and washed in a washing machine (2 cycles of 5 min). Tests with different incubation times were performed on different days to avoid disturbing ruminal conditions by too many manipulations on the same day. However all bags for a given incubation time were introduced into the rumen at the same day. Three replicates were carried out for each feedstuff, each cow and each incubation time. Experimentally measured solubility (a_0) corresponds to non-degraded dry matter loss and the soluble fraction, measured by the difference between non-incubated feedstuff and samples (n = 4) in nylon bags spun in cold water in a washing machine (2 cycles of 5 min).

After incubation, all the bags were freeze-dried and weighed. The bags of the same feedstuff and the same incubation time in all cows were pooled prior to chemical analysis.

2.3. Chemical analyses

The samples of each tested feedstuff before incubation and their pooled residues after incubation were analysed for their starch content (enzymatic method, AFNOR NF V 18–121, 1997). The fibre fraction of all samples was described by analysing NDF, ADF [33] and ADL [32], in order to calculate cellulose and hemicellulose levels according to the method described by Staples [29]. In addition, ash (6 h at 550 °C) and crude protein (Kjeldahl method) were analysed in feedstuffs before incubation. The chemical composition of all feedstuff samples prior to incubation is shown in Table II.

2.4. Data analyses

The DM before and after incubation was averaged for each cow, a given feedstuff and a given incubation time. These DM amounts were then multiplied by the contents in starch or fibre of the pooled sample in order to calculate the disappearance rates of DM, starch, NDF, cellulose and hemicel-

Table II. Chemical characteristics of feedstuffs before incubation.

	2265[1]	Etendard[1]	FWCP[2]	EWCP[3]
Dry matter (%)	49.7	56.4	33.6	37.6
Chemical Composition (% of DM)				
starch	78.0	76.9	37.2	37.0
NDF	9.8	9.4	46.3	40.1
ADF	3.0	3.7	24.7	21.2
ADL	1.1	0.8	4.3	3.2
cellulose[4]	6.8	5.7	21.6	18.9
hemicellulose[5]	1.9	2.9	20.4	18.0
crude protein	7.7	7.9	6.7	6.4
ash	1.3	1.4	4.8	3.0

[1] cultivars of used kernel grains;
[2] FWCP fresh whole corn plant;
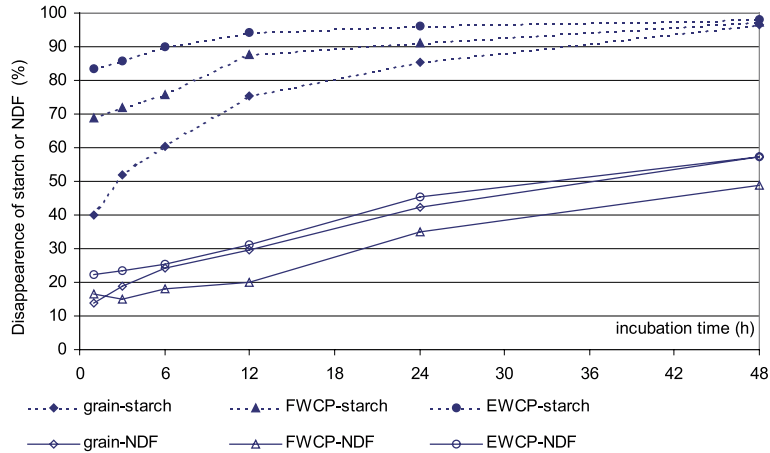[3] EWCP ensiled whole corn plant;
[4] cellulose = NDF – ADF according to Staples et al. [29];
[5] hemicellulose = ADF – ADL according to Staples et al. [29].

lulose individually for each cow, each feedstuff and at each incubation time.

The values for experimentally measured solubility (a_0) were statistically compared using the Student t test.

The disappearance kinetics obtained for each feed were then fitted to an exponential model according to the method described by Ørskov & McDonald [22]. Parameters (a_m: rapidly degradable fraction, b_m: slowly degradable fraction, c_m: degradation constant rate exponentially reduced over time) were estimated by an iterative procedure of STAT-ITCF (version 5.0, 1991, Institut Technique des Céréales et des Fourrages – renamed ARVALIS Institut du Végétal, Paris) in order to determine the smallest sum of squares after convergence. A statistical difference between feedstuffs for a given parameter was concluded if the values were outside the calculated confidence interval of $\pm 2\delta$ (i.e. $P < 0.05$). The fibre disappearance curves (i.e. NDF), differed from those of starch: a latency period of 3 h was observed (Fig. 1). Thus, the exponential

Figure 1. Mean disappearances of starch (dotted line) and NDF (solid line) in grains ($\Diamond$), fresh (FWCP: $\triangle$) or ensiled whole corn plants (EWCP: O) in the rumen during the incubation time course.

model has to be adjusted to the values only after this lag time, especially for cellulose and hemicellusose fractions.

The effective degradability (eD) of DM and all fractions were calculated using average parameters calculated by the exponential model for a given feedstuff at a ruminal outflow rate of 0.06 per h, as is classically applied [13].

This approach privileged the use of observed variability to statistically compare the model parameters (i.e. a_m, b_m, c_m). Their resulting effective degradability is indicated without statistical comparison.

3. RESULTS

Before incubation, the dry matter content of kernel grains ranged from 49.7 to 56.4% depending on the cultivar, which confirms that the plants were harvested at silage maturity. The dry matter of the whole corn plants before incubation increased from 33.6% before to 37.6% after ensiling (Tab. II). The kernel grains of both cultivars were similarly composed, mainly of starch (respectively 78 and 76.9% of the DM). Moreover,

the kernel grains of both cultivars contained nearly 10% total fibres (i.e. NDF), 7.8% crude protein and 1.3% ash (Tab. II). The starch content of the plants before and after ensiling was very similar (respectively 37.2 and 37.0% of the DM, Tab. II). But plants after ensiling had lower contents of total fibres, i.e. NDF (40.1 vs. 46.3%), crude protein (6.4 vs. 6.7%) and ash (3.0 vs. 4.8%). Proportions of cellulose and hemicellulose within the fibre fractions were similar for both forage forms (Tab. II).

The incubation kinetics show that experimentally measured DM solubility of kernels (37.3%) was similar to that of the whole fresh corn plant (38.4%) but significantly lower than the DM solubility of ensiled corn (57.4%, $P < 0.05$; Tab. III). These experimentally measured values (a_0) were confirmed by the values for the rapidly degraded fraction (a_m) calculated using the model. Thus, the rapidly degradable DM of grains or whole fresh plants was significantly lower than this fraction in ensiled corn (36.0% and 39.0% vs. 55.7% respectively, $P < 0.05$). The slowly degraded fraction (b_m) was significantly ($P < 0.05$) higher in grains (57.6%), followed by FWCP (41.6%)

Table III. Effect of corn presentation forms on the ruminal degradation characteristics of DM and its main fractions.

Variable of the kinetic model		grains	FWCP	EWCP
Dry matter degradation				
a_0		37.3[b]	38.4[b]	57.4[a]
a_m		36.0[b]	39.0 [b]	55.7[a]
b_m		57.6[a]	41.6 [b]	27.1[c]
c_m		0.073[a]	0.028[b]	0.042[b]
	r	0.99	0.99	0.99
	SE	5.5	2.3	2.1
Starch degradation				
a_0		34.7[c]	63.0[b]	81.2[a]
a_m		35.9[c]	65.6[b]	80.7[a]
b_m		61.3[a]	31.9[b]	17.2[c]
c_m		0.077[b]	0.080[b]	0.124[a]
	r	0.99	0.99	0.99
	SE	5.2	1.7	0.7
NDF degradation				
a_0		14.2[b]	15.8[b]	22.9[a]
a_m		11.3	9.9	15.2
b_m		70.7[a]	74.6[a]	53.6[b]
c_m		0.022	0.016	0.032
	r	0.78	0.98	0.99
	SE	18.8	4.9	3.3

Degradation parameter values in the same column within the same fraction and without a common superscript differ significantly at $P < 0.05$;
FWCP: fresh whole corn plant;
EWCP: ensiled whole corn plant;
a_0: experimentally measured solubility (%);
a_m: rapidly degradable fraction (%) calculated by the model [22];
b_m: slowly degradable fraction (%) calculated by the model [22];
c_m: rate of degradation (per h) calculated by the model [22].

and then EWCP (27.1%). The degradation rate (c_m) of grain DM was significantly higher (7.3% per h, $P < 0.05$) than that in whole corn plants, ensiled or not (4.2 or 2.8% per h respectively).

The experimentally measured solubility of starch was the highest in ensiled corn (81.2%) followed by the whole fresh plant (63.0%) and was the lowest for starch in grains (34.7%). This significant hierarchy of starch solubility between tested feedstuffs was also observed for their rapidly degradable starch fraction (a_m) calculated by the model (Tab. III). The slowly degradable fraction (b_m) varied significantly in the opposite order: the highest value was

seen for starch in grains (61.3%) followed by the whole fresh plant (31.9%) and finally starch in ensiled corn (17.2%). The degradation rates (c_m) of grain starch and starch from the whole fresh plant were very similar (respectively 7.7% and 8.0%) and significantly ($P < 0.05$) lower than those seen for starch in ensiled corn (12.4%). Nevertheless, the degradation constant rate (c_m) for starch of the three feedstuffs was diametrically opposite that of the slowly degradable fraction: the smaller the slowly degraded fraction, the steeper the slope of the degradation curve (Tab. III), and the starch in all forms was almost completely degraded in sacco after 48 h of incubation (Fig. 1).

Table IV. Effect of corn presentation form on the ruminal degradation characteristics of fibre fractions.

Parameter of the kinetic model		cellulose		hemicellulose	
		FWCP	EWCP	FWCP	EWCP
a_0		22.9	17.7	10.8	11.3
a_m		18.8	5.5	– 4.2	– 0.6
b_m		52.9	60.4	80.2	77.7
c_m		0.023	0.037	0.019	0.036
	r	0.99	0.99	0.96	0.98
	SE	4.6	4.1	5.3	4.5

FWCP: fresh whole corn plant;
EWCP: ensiled whole corn plant;
a_0: experimentally measured solubility (%);
a_m: rapidly degradable fraction (%) calculated by the model [22];
b_m: slowly degradable fraction (%) calculated by the model [22];
c_m: rate of degradation (per h) calculated by the model [22].

Since the values of fibre disappearance kinetics were adjusted to the exponential model after a lag time of 3 h (see Sect. 2.4), the alignment between experimentally measured solubility (a_0) and rapidly degraded fractions (a_m) was less evident for all fibre fractions (Tab. III and IV). The large confidence interval of the model parameters and the very high standard error, mainly for NDF in grains (SE = 18.8%, Tab. III), limited the statistical signification of observed differences. However, several trends for the kinetics of fibre degradation could be reported. The rapidly degraded NDF fractions of grains (11.3%) and whole fresh plants (9.9%) seemed to be lower than this NDF-fraction in ensiled corn plants (15.2%). This tendency was confirmed by significantly ($P < 0.05$) lower NDF-solubility in grains and fresh plants when compared to NDF in ensiled plants. In contrast, the slowly degradable fraction was significantly ($P < 0.05$) lower in ensiled plants (53.6%) than in grains (70.7%) or the whole fresh plant (74.6%). As seen previously for starch, the degradation constant rate (c_m) of NDF in grains and in whole fresh plants was quite similar (respectively 2.2 and 1.6% per h),

and the slope seemed to be lower than for NDF in ensiled corn (3.2%).

The fact that grains exhibited a low fibre content (before incubation: <4% ADF and approximately 1% ADL in the DM, Tab. II) limited the interest of monitoring the degradation kinetics of the different fibre fractions in grains. Therefore, these degradation kinetics were only determined in forages. In both forage forms, no increase in ADL disappearance rates (data not shown) was seen, since lignin (i.e. ADL), is generally not degraded in the rumen [34]. They remained close to the initial values (i.e. experimentally measured solubility) throughout the time course, but differed between fresh ($31.2\% \pm 7.6$) and ensiled whole corn plants ($51.8\% \pm 4.9$). The degradation models were calculated for cellulose and hemicellulose using the same lag time as that described above for NDF.

The rapidly degradable fraction of cellulose appeared to be higher in fresh corn plants than in ensiled plants ($a_0 + 5.2\%$, $a_m + 13.3\%$; Tab. IV) but the threshold of significance was not reached. The slowly degradable cellulose fractions of both forages were close (52.9 and 60.4% respectively for FWCP and EWCP). Finally, the degradation constant rate of cellulose in ensiled corn tended to be slightly higher than that seen in whole fresh corn plants (+ 1.4% per h). Thus, the calculated degradation curves of cellulose in both corn forms were very similar (Fig. 2) and differences between model parameters remained within their confidence intervals. Indeed, the exponential models for the degradation of cellulose and particularly for hemicellulose did not reach their asymptotes during the time course (Fig. 2). Indeed, the classically applied exponential model [22] described these degradation curves less precisely than a linear model would do. So, the exponential model for hemicellulose degradation in corn plants showed only tendencies and no difference reached the signification threshold. The experimentally measured solubility (a_0) and slowly degradable fraction (b_m)
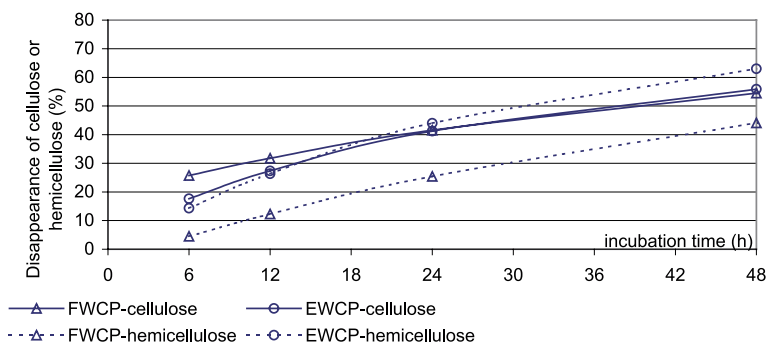
Figure 2. Degradation of cellulose (solid line) or hemicellulose (dotted line) in the rumen for fresh (FWCP: △) or ensiled whole corn plants (EWCP: O) fitted to the exponential model after a lag time of 3 h.

of hemicellulose were similar in both forages. The lag time used for the exponential model enhanced an artefact of negative values for the rapidly degradable fraction (a_m) of hemicellulose in both forms (Tab. IV). Indeed, these values tended to reflect a very low baseline point for the fitted model curve rather than true degradation features. The degradation constant rate of hemicellulose in ensiled corn was apparently higher than that seen in fresh corn plants (3.6 vs. 1.9% per h respectively), which was well illustrated by the steeper incline of the degradation curve for EWCP when compared to FWCP (Fig. 2).

The effective degradability of DM was similar in grains and ensiled corn (67.6 and 66.8% respectively, Tab. V) but was higher than in whole fresh plants (52.1%). The lower solubility of DM in grains compared to ensiled corn was counterbalanced with a smaller slowly degradable fraction and an increased degradation constant rate. The effective degradability of starch was the highest for ensiled corn (92.3%) followed by whole fresh plants (83.9%). Kernel starch reached only 70.2% of effective degradability (Tab. V). The effective degradability of NDF ranged from 25.2% (whole fresh plants) to 34.0% (ensiled plants), with an intermediate value of 30.5% for grains (Tab. V). Figure 1 illustrates this tendency of lower effective NDF degradation in FWCP compared to kernels or ensiled plants. Thus the effective degradability of cellulose using the parameters calculated within a broad confidence interval was slightly higher in fresh than in ensiled corn plants (+4.9%). The higher degradation constant rate of hemicellulose in ensiled corn enhanced an effective degradability, which was almost double that seen in fresh corn plants (Tab. V).

Table V. Effect of corn presentation forms on their effective degradability[1].

Item	grains	FWCP	EWCP
Dry matter	67.6	52.1	66.8
Starch	70.2	83.9	92.3
NDF	30.5	25.2	34.0
cellulose		33.6	28.7
hemicellulose		15.2	28.3

[1]: effective degradability (%) calculated using the equation $a + bc/(c + k)$, where k = outflow rate assumed to be 0.06 per h [13];
FWCP: fresh whole corn plant;
EWCP: ensiled whole corn plant.

4. DISCUSSION

4.1. Starch degradation

Corn starch disappeared completely after 48 h of incubation in the rumen whichever processing method was employed. However, the parameters of the degradation model differed considerably between corn forms.

In the literature, a broad range of values of starch degradation parameters are reported in corn grains depending on genotype [7, 24, 25], maturity at harvest [7, 14, 24, 26] and sample preparation [18, 24, 25]. We observed a high rapidly degradable fraction but a relatively small slowly degradable fraction of starch compared to others [24] working at similar maturity (37% of DM at harvest). A high grinding fineness of samples has been shown [5, 20, 24, 36] to increase starch lost through the bag pores and the grinding of our samples over a 1.5 mm sieve may, because of the small particle size, have favoured these particulate losses. This methodological weakness affected all tested corn forms similarly in our trial, and possibly led to an overestimation of ruminal starch degradability under our experimental conditions. We therefore preferred to focus the discussion of our results on differences in degradation between corn forms, rather than their absolute values.

Nevertheless, corn starch in the whole plant was more rapidly degraded than in kernel grains. Since the same plants and vegetation stage at harvest were used, an explanation due to differences in genotype or maturity can be excluded. The low starch content in plant residue (2% of DM, [8]) let us conclude that starch in the whole corn plant is nearly identical with starch in the grains. The more rapid degradation in the FWCP could be due to the chopping of the plant at harvest as suggested in the literature [36]. The double mechanical treatment during harvest and grinding prior to ruminal incubation could have weakened the protective layers of starch granules and

the fine grinding in our trial could amplify this effect by increased particulate losses. Another hypothesis to explain for the more rapid degradation of starch in both forage forms was the higher moisture level of the whole plant when compared to dry kernel grains. The starch structure would be softened by moisture and therefore favour enzymatic hydrolysis, even if the forages were dried during sample preparation prior to incubation. Indeed, the literature reports an increase in the soluble fraction and the fractional rate of degradation in the rumen for high moisture corn versus dry cracked [1] or dry rolled [6] corn, even though the effects of the maturity stage may distort these comparisons.

Thus, double cracking and/or a softened starch structure lead to a higher rapidly degradable starch fraction in the whole fresh plant when compared to the starch in grains. In our trial, the higher starch degradability observed for the fresh plant was mainly due to a shift from slowly degradable starch to the rapidly degradable fraction which let us privilege the mechanical hypothesis.

In agreement with other studies [21, 23, 25], starch in ensiled corn was degraded very rapidly. Ensiling increases ruminal digestion of cornstarch more than mechanical treatments such as grinding, rolling or cracking [23]. Indeed, ensiling enhanced a second shift of slowly degradable starch to the rapidly degradable fraction (Tab. III), and increases the effective degradability of cornstarch [25]. In our trial we also observed an increase of 4.4% per h in the degradation constant rate of starch in ensiled corn when compared with the whole fresh plant. These observations should be linked to the fermentation process, because both forages underwent identical chopping during harvest and sample preparation. Moreover, their moisture contents were also similar (Tab. II). Baron [4] reported a partial solubilisation of endosperm proteins in corn grains after ensiling which involved a reduction in the protective aptitude of the protein matrix. It would be interesting to test whether
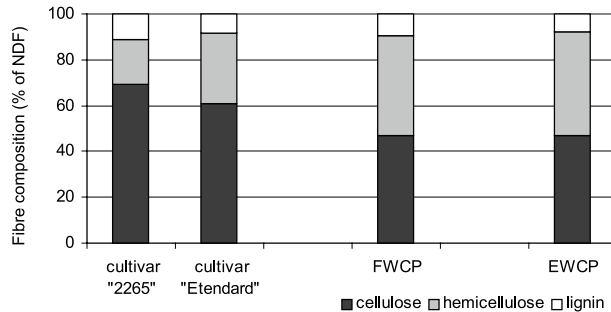
Figure 3. Fibre (i.e. NDF) composition before incubation in grains of both used cultivars, fresh (FWCP) or ensiled whole corn plants (EWCP).

zeins, the main factor causing reduced starch access [27], are sensitive to variations in pH and if starch degradation can so be improved. This hypothesis is strengthened by the fact that enzymes used in analytical procedures that hydrolyse starch usually require an acid pH to ensure their optimum activity.

4.2. Fibre degradation

The velocity of starch degradation in the rumen determines the in vivo postprandial pH drop [19] and a moderate drop in pH would favour the cellulolytic activity of micro-organisms [8]. But this widely reported negative relationship between starch and fibre degradation [2, 10, 30], especially in corn silage [31], cannot be studied in sacco. Nevertheless, determining the effects of plant processing on corn fibre degradation in a given ruminal environment would clarify their nutritive value.

Unlike the starch fraction, fibres (i.e. NDF) in grains and in the whole corn plant differ in terms of both their quantity (NDF content) and their quality (fibre composition). In our study, fibres in kernel grains represented less than 10% of the dry matter in this organ, versus approximately 4-fold more in whole corn plant forms (Tab. II). The indigestible lignin (i.e. ADL) represented nearly 10% of the fibre fraction (i.e. NDF) regardless of the considered corn

form (Fig. 3). But kernel fibres of both cultivars were mainly composed of cellulose and in the whole plant cellulose and hemicellulose were present at similar proportions in the fibre fraction (Fig. 3).

The experimentally measured solubility data (a_0) for all fibre fractions were higher than their corresponding rapidly degradable fraction as determined by the model (a_m; Tab. III, Tab. IV). This difference may have been due firstly, to an overestimation of a_0 because of particulate losses (see above), and secondly, to the lag time applied in the model, which lowered the calculated value of the rapidly degradable fraction (a_m).

The degradable fractions of NDF in grains were similar to those found in the whole fresh plant, despite the different composition of NDF in both feedstuffs. Chopping at harvest did not seem to affect fibre degradation. It can be concluded that mechanical effects such as chopping will similarly affect cellulose and hemicellulose degradation in the rumen. An evoked effect of the higher moisture content in the whole plant compared to grains on fibre degradation is unknown. The tendency of a slightly lower effective degradability in the plant before ensiling (–5.3%) should be considered with caution because of the lack of significance. Thus, no difference of fibre degradation between kernels and the whole fresh plant

has been observed in sacco despite initial variations in its composition.

It was surprising that before incubation all the characteristics of the fibre fraction in EWCP exhibited lower initial values than in FWCP (Tab. II). The fibre levels in EWCP were low but within the usual range observed for this site (38 to 48% NDF in DM) and in line with the high starch contents seen in corn silage harvested at later maturity [3], such as at the dent stage. No data were found in the literature to explain for any disappearance of fibre during ensiling. FWCP values therefore seemed to be quite high [13]. In spite of the numerous precautions taken during sampling, we advance the hypothesis that some sampling errors, linked to the heterogeneity of feed stock, were the most likely explanation for the higher fibre contents found in FWCP when compared with the levels seen after ensiling.

Fibre degradation (i.e. NDF) in ensiled plants was higher than in whole fresh plants: there was a significantly increased solubility (a_0), confirmed by a similar trend with respect to rapidly degradable NDF (a_m). The lower slowly degradable fraction (b_m) in ensiled plants reflected the initially more rapid disappearance of NDF at the beginning of the time course for ensiled plants. This difference between fresh and ensiled plants was maintained throughout the time course (Fig. 1). The doubled degradation constant rate slightly increased the fibre degradability in favour of ensiling, when compared to fresh plants. The literature [29] has generally associated a more acid environment in the rumen with a reduced fibre degradation *via* a shift in the microbial population balance [15] and a more rapid passage rate by the small size of concentrate particles [8]. On the contrary, we observed an increased fibre degradation in the acidified (i.e. ensiled) compared to fresh plants. Passage rate and particulate size were standardised in sacco. These factors can therefore not explain in sacco differences in ruminal fibre degradation between plants

before and after ensiling, in agreement with others [8]. Nevertheless, it is possible that the acidity provoked by microbial fermentation of fresh plants in the rumen would affect fibre structures differently than the acidity created by fermentation in a silo. Perhaps fibre structures would be weakened in the silo prior to degradation in the rumen. Indeed, acid chemicals such as ADF [33] enable the solubilisation of some fibre particules.

Within the fibre fraction, the disappearance of lignin was too small to conclude as to true degradation. Cellulose degradation varied little and in a non-significant manner between the two forage forms. The calculated effective degradation of cellulose in our corn silage of 28.7% was close to the 24% reported by Jochmann [14] in similar conditions (36% DM at harvest, $k_p = 6\%$ per h) but for a more fibrous silage (49% NDF, 25% ADF). The main difference in fibre degradation in our study was due to the hemicellulose fraction that tended to be degraded at an increased degradation constant rate in ensiled rather than fresh plants, leading to a higher effective degradability. Indeed, degradation of the very regular cellulose structure (glucose monomers with β-glucosidic links only) did not vary notably between fresh and ensiled plants, but the very heterogeneous structure of hemicellulose (varying monomer composition and numerous lateral chains) seemed to be more sensitive to weakening by the fermentation in the silo.

Thus the ensiling process increased the total fibre degradation in the rumen. This difference in favour of ensiling seemed to be due to a higher degradation of hemicellulose since cellulose and lignin degradation did not differ between fresh and ensiled plants. Complementary studies in vivo should be focused on the question if an apparently improving effect of ensiling on starch and fibre degradation of corn plants in the rumen would be lowered by changes in microbial populations and modified passage rate.

5. IMPLICATIONS

Cornstarch in the plant before and especially after ensiling was more rapidly degraded than that found in kernel grains. The higher degradability of starch in the whole corn plant compared to kernel grains was mainly due to the increased rapidly degradable fraction. More work is necessary to elucidate whether the mechanical cracking of grains during harvest or a softened starch structure by higher moisture level in the whole fresh plant were responsible for improved starch degradability. The fermentation of cornstarch during ensiling increased its degradation. Acidification probably solubilises the protective protein layer surrounding the starch granules. The sensitivity of endosperm proteins to pH variations should be tested to see whether acidification could improve starch access, even in dry corn grains.

Fibre degradation did not vary between kernels and whole plants despite the different composition of NDF. Thus chopping at harvest does not seem to modify in sacco degradation. These results should be confirmed using more roughly ground samples so as to reduce particulate losses and less variable parameters of the degradation model. Nevertheless, ensiling increased in sacco NDF degradation in the rumen and mainly the degradation of the hemicellulose fraction was higher in plants after than before ensiling. The responsible mechanisms should be determined in studies focusing on the resistance of hemicellulose in fresh plants to pH variations or on the effect of microorganisms specific of the ensiling process.

Mechanical cracking such as chopping at harvest improves ruminal starch degradation without altering fibre degradation. Even though these results need confirmation in vivo, higher starch availability by cracking and similar fibre degradation can be a way to improve the energy furniture to the animals while limiting the risk of acidosis. The ensiling process increases the degradability of starch and fibres. In spite of the better nutritive value of ensiled corn plants, this process would also enhance a higher risk of acidosis. Therefore, the fibre supply of corn silage to the diet should not be overestimated.

REFERENCES

[1]   Alvarez H.J., Santini F.J., Rearte D.H., Elizalde J.C., Milk production and ruminal digestion in lactating dairy cows grazing temperate pastures and supplemented with dry cracked corn or high moisture corn, Anim. Feed Sci. Tech. 91 (2001) 183–195.

[2]   Archimède H., Sauvant D., Schmidely P., Quantitative review of ruminal and total tract digestion of mixed diet organic matter and carbohydrates, Reprod. Nutr. Dev. 37 (1997) 173–190.

[3]   Bal M.A., Coors J.G., Shaver R.D., Impact of the maturity of corn for use as silage in the diets of dairy cows on intake, digestion, and milk production, J. Dairy Sci. 80 (1997) 2497–2503.

[4]   Baron V.S., Stevenson K.R., Buchanan-Smith J.G., Proteolysis and fermentation of corn-grain ensiled at several moisture levels and under several stimulated storage methods, Can. J. Anim. Sci. 66 (1986) 451–461.

[5]   Cerneau P., Michalet-Doreau B., In situ starch degradation of different feeds in the rumen, Reprod. Nutr. Dev. 31 (1991) 65–72.

[6]   Cooper R.J., Milton C.T., Klopfenstein T.J., Scott T.L., Wilson C.B., Mass R.A., Effect of corn processing on starch digestion and bacterial crude protein flow in finishing cattle, J. Anim. Sci. 80 (2002) 797–804.

[7]   Flachowsky G., Peyker W., Schneider A., Henkel K., Fibre analyses and in sacco degradability of plant fractions of two corn varieties harvested at various times, Anim. Feed Sci. Tech. 43 (1993) 41–50.

[8]   Flachowsky G., Einsatz von maisstärkehaltigen Futtermitteln, Kraftfutter 6 (1994) 224–232.

[9]   Gallais A., La physiologie du maïs, INRA (Ed.), Versailles, France, 1983, 574 p.

[10] Grant R.J., Mertens D.R., Influence of buffer pH and raw corn starch addition on in vitro fiber digestion kinetics, J. Dairy Sci. 75 (1992) 2762–2768.

[11] Hunt C.W., Kezar W., Vinande R., Yield, chemical composition, and ruminal fermentability of corn whole plant, ear, and stover as affected by hybrids, J. Prod. Agric. 75 (1992) 852–867.

[12] Huntington G.B., Starch utilization by ruminants: from basics to the bunk, J. Anim. Sci. 75 (1997) 852–867.

[13] Jarrige R., Alimentation des bovins, ovins et caprins, INRA (Ed.), Versailles, France, 1988, 471 p.

[14] Jochmann K., Lebzien P., Daenicke R., Flachowsky G., Zum Einfluss des Reidestadiums von Maispflanzen und des Einsatzes von Milchsäurebakterien bei ihrer Einsilierung auf die Nährstoffumsetzungen im Verdauungstrakt von Milchkühen, J. Anim. Physiol. An. N. 82 (1999) 178–192.

[15] Martin C.B., Michalet-Doreau B., Variations in mass and enzyme activity of rumen microorganisms: Effect of barley and buffer supplements, J. Sci. Food Agr. 67 (1995) 223–228.

[16] McAllister T.A., Phillippe R.C., Rode L.M., Cheng K.J., Effect of the protein matrix on the digestion of cereal grains by ruminal microorgansims, J. Anim. Sci. 71 (1993) 205–212.

[17] Michalet-Doreau B., Vérité R., Chapoutot P., Méthodologie de mesure de la dégradabilité in sacco de l'azote des aliments dans le rumen, Bull. Tech. CRZV INRA Theix 69 (1987) 5–7.

[18] Michalet-Doreau B., Philippeau C., Doreau M., In situ and in vitro ruminal starch degradation of untreated and formaldehyde-treated wheat and maize, Reprod. Nutr. Dev. 37 (1997) 305–312.

[19] Monteils V., Jurjanz S., Colin-Schoellen O., Blanchart G., Laurent F., Kinetics of ruminal degradation of wheat and potato starches in total mixed rations, J. Anim. Sci. 80 (2002) 235–241.

[20] Nozière P., Flors S., Rémond D., Philippeau C., Michalet-Doreau B., Prise en compte de la taille des particules dans la détermination de la dégradation in sacco de l'amidon, 9e Renc. Rech. Ruminants, 2002, p. 335.

[21] Offner A., Bach A., Sauvant D., Quantitative review of in situ starch degradation in the rumen, Anim. Feed Sci. Tech. 106 (2003) 81–93.

[22] Ørskov E.R., McDonald J., The estimation of protein degradability in the rumen from incubation measurement weighted according to rate of passage, J. Agr. Sci. 92 (1979) 499–503.

[23] Owens F.N., Zinn R.A., Kim Y.K., Limits to starch digestion in the ruminant small intestine, J. Anim. Sci. 63 (1986) 1634–1648.

[24] Philippeau C., Michalet-Doreau B., Influence of genotype and stage of maturity of maize on rate of ruminal starch degradation, Anim. Feed Sci. Tech. 68 (1997) 25–35.

[25] Philippeau C., Michalet-Doreau B., Influence of genotype and ensiling of corn grain on in situ degradation of starch in the rumen, J. Dairy Sci. 81 (1998) 2178–2184.

[26] Philippeau C., Le Deschault de Mondredon F., Michalet-Doreau B., Relationship between ruminal starch degradation and the physical characteristics of corn grain, J. Anim. Sci. 77 (1999) 238–243.

[27] Philippeau C., Landry J., Michalet-Doreau B., Influence of the protein distribution of maize endosperm on ruminal starch degradability, J. Sci. Food Agr. 80 (2000) 404–408.

[28] Sauvant D., Chapoutot P., Archimède H., La digestion des amidons par les ruminants et ses conséquences, INRA Prod. Anim. 7 (1994) 115–124.

[29] Staples C.R., Fernando R.L., Fahey G.C., Berger L.L., Jaster E.H., Effects of intake of a mixed diet by dairy steers on digestion events, J. Dairy Sci. 67 (1984) 995–1006.

[30] Tamminga S., Van Vuuren A.M., Van Der Keulen C.J., Ketelaar R.S., Van Der Togt P.L., Ruminal behaviour of structural carbohydrates, non-structural carbohydrates and crude protein from concentrate ingredients in dairy cows, Neth. J. Agr. Sci. 38 (1990) 513–526.

[31] Valentin S.F., Williams P.E.V., Forbes J.M., Sauvant D., Comparison of the in vitro gas production technique and the nylon bag degradability technique to measure short- and long-term processes of degradation of maize silage in dairy cows, Anim. Feed Sci. Tech. 78 (1999) 81–99.

[32] Van Soest P.J., Use of detergents in analysis of fibrous feeds. 2. A rapid method for the determination of fiber and lignin, J. Assoc. Off. Agr. Chem. 46 (1963) 829–835.

[33] Van Soest P.J., Wine R.H., Use of detergents in analysis of fibrous feeds. Determination of plant cell-wall constituents, J. Assoc. Off. Agr. Chem. 50 (1967) 50–55.

[34] Van Soest P.J., Nutrional Ecology of the Ruminant, Durham and Downey Inc. (Eds.), Portland OR, USA, 1982, 374 p.

[35] Verbic J., Stekar J.M.A., Resnik-Cepon M., Rumen degradation characteristics and fibre composition of various morphological parts of different maize hybrids and possible consequences for breeding, Anim. Feed Sci. Tech. 54 (1995) 133–148.

[36] Wadhwa M., Dharam P., Kataria P., Bakshi M.P.S., Effect of particle size of corn grains on the release of nutriments and in sacco degradability, Anim. Feed Sci. Tech. 72 (1998) 11–17.