Influence of the Biochemical and Physical Characteristics of the Maize Grain on Ruminal Starch Degradation

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This study was aimed at determining the influence of biochemical and physical features of the maize grain on ruminal starch degradation using genotypes differing in the texture of the endosperm (dent or flint) and in the starch composition (waxy [*wx*], normal [+], amylose extender [*ae*]). Ruminal starch degradation was (1) highest for dent types, (2) highest for (*ae*) strains irrespective the texture, and (3) dependent on the texture for (*wx*) strains. Ruminal starch degradation was independent of the amylose:amylopectin ratio in starch. The slowly degradable starch fraction which reflects the potentially degradable starch fraction that would be degraded by microorganisms given sufficient residence time in the rumen was negatively linked to the true glutelins including in the protein matrix. Ruminal starch degradability was also related to the proportion of coarse particles (1000 > d > 400 μm), which is an estimator of grain hardness.

Keywords: *Maize; genotype; ruminal digestion; starch; protein*

INTRODUCTION

In ruminants, starch of cereal grain is almost totally digested in the whole digestive tract, but the site of digestion, rumen vs intestine, varies widely (Waldo, 1973; Owens et al., 1986). Rates of ruminal starch digestion are variable and are influenced by several parameters such as the type and process of cereal grains, diet, and feeding level. In turn, the rate and extent of ruminal starch digestion may have an effect upon the composition of the microbial fermentation acid produced, the efficiency of starch utilization, and food conversion by the ruminant. Different approaches to control rate and extent of starch digestion were studied: management of feed consumption, grain process, and choice of cultivar (Poncet et al., 1995). Differences in site and extent of starch digestion, although not systematic for barley (Hatfield et al., 1993; Feng et al., 1995; Boss and Bowman, 1996) have been reported among varieties of sorghum (Streeter et al., 1990b,c) and barley (Khorasani, personal communication). For maize, in situ ruminal starch degradability has been shown to be strongly correlated with vitreousness, i.e., the ratio of vitreous endosperm to floury endosperm (Philippeau and Michalet-Doreau, 1997) which are two portions of the endosperm with specific physical and chemical features. Few studies have assessed, on the same maize samples, the influence of grain biochemical composition on ruminal starch digestion, and we do not know how structural and chemical factors of the protein endosperm affect starch availability for enzymatic hydrolysis. More information is needed to better assess these differences and to improve the potential to manipulate ruminal starch digestion rates and the efficiency of starch utilization by ruminant. The aim of this study was to determine how the biochemical composition and physical characteristics of maize grain influence ruminal starch degradation. Also of interest are the specific features of the grain such as texture, particle size distribution, content of cell wall, composition and content of starch, and proteins' effects on starch hydrolysis in the rumen.

Table 1. Description of the Growing Characteristics of the Six Maizes

texture	genotype	origin	year
flint	*wx*	France (south-west)	1993
flint	+	France (middle)	1989
flint	*ae*	France (south-west)	1993
dent	*wx*	France (south-west)	1993
dent	+	Chili	1993
dent	*ae*	France (south-west)	1993

MATERIALS AND METHODS

Plant Material. Two maize (*Zea mays* L.) cultivars differing in the texture of their endosperm, dent or flint, were used. Each type was made of waxy [*wx*], normal [+], and amylose extender [*ae*] starch, differing in the amylose content. The characteristics of the growing conditions are given in Table 1. Grains were harvested at 72% dry matter (DM) and then they were dried at a low temperature (<38 °C) to bring the DM content to 90%, on average. The morphological composition of the grain and the vitreousness were determined on 20 grains. Grains were hand dissected and separated into three fractions, envelopes (pericarp and pedicel), germ, and endosperm, by peeling off the pericarp and dissecting out the germ with a scalpel. The floury and vitreous portions of endosperm were then isolated. The vitreousness was exprimed as the weight proportion of vitreous endosperm in the degermed grain.

Physical Analyses. Each maize was ground through a 2 mm sieve in a hammer mill. The particle size distribution of maize was measured by wet sieving (Fritsch GMBH, Idar-Oberstein, Germany). Wet sieving was performed according to the method of Grenet (1984) with a system that provided water spray and vibration equipped with five sieves (1600,

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Table 2. Influence of Texture and Genotype of Maize on Morphological Composition of the Grain[a] and Particle Size Distribution

	flint			dent				statistical significance		
	wx	+	*ae*	*wx*	+	*ae*	SE	texture	genotype	interaction: texture × genotype
DM in grain, mg	304.8	269.6	217.8	288.9	254.5	259.9	6.2	0.1824	0.0001	0.0001
germ, %	9.6	13.6	14.5	9.8	12.5	13.9	0.6	0.1255	0.0001	0.1034
envelopes, %	7.4	6.1	12.6	8.4	8.8	10.0	0.8	0.3248	0.0001	0.0001
endosperm, %	83.0	80.3	72.9	81.8	78.7	76.1	1.5	0.9652	0.0001	0.1575
vitreousness[b]	75.3	81.9	50.4	72.7	55.6	42.2	2.6	0.0001	0.0001	0.0001
arithmetic mean, μm	99.1	110.4	104.5	94.3	97.8	97.0	2.5	0.0748	0.3189	0.6767
% particles										
$d > 1600\ \mu$m	0.5	0.4	2.7	0.3	1.2	0.4	0.4	0.3428	0.2900	0.1503
$1600 > d > 1000\ \mu$m	10.3	23.0	37.2	19.0	18.6	24.9	1.2	0.1689	0.0007	0.0066
$1000 > d > 400\ \mu$m	66.5	63.7	37.6	52.2	54.8	50.0	1.8	0.2066	0.0036	0.0113
$400 > d > 100\ \mu$m	20.1	12.1	21.8	24.7	21.5	22.4	2.6	0.2390	0.4407	0.6428
$100 > d > 50\ \mu$m	1.5	0.8	0.5	2.5	1.1	2.0	0.2	0.0240	0.0946	0.4138
$d < 50\ \mu$m	1.1	0	0.2	1.3	2.8	0.3	0.4	0.0912	0.2200	0.1393

[a] Weight percent of total grain for germ, envelopes, and endosperm. [b] Weight percent of degermed grain.

1000, 400, 100, and 50 μm). All samples underwent the complete procedure twice. The arithmetic mean particle size and the proportion of each class of particle size were reported.

Chemical Analyses. Dry matter was determined after oven drying at 80 °C for 48 h. Starch was assayed according to an enzymatic method (Faisant et al., 1995). Crude protein (CP) was determined by a Kjeldahl method (AOAC, 1990) and neutral detergent fiber (NDF) was measured according to Robertson and Van Soest (1977).

The amylose content was determined using an amylose/amylopectin assay kit (Megazyme International Ireland Limited, Bray Business Park, Bray Co., Wicklow, Ireland) by a modified method of Yun and Matheson (1990). A preliminary step consisted of removing lipids by precipitating the starch in ethyl alcohol. Amylopectin was specifically precipitated by the addition of the lectin, concanavalin-A, and amylose in the supernatant was enzymatically hydrolyzed in glucose and was measured colorimetrically by glucose oxidase/peroxidase. Two replicates were performed for each sample.

The distribution of the proteins in the endosperm was determined according to a modified method of Landry and Moureaux (1980). After separation of the grain, the endosperm was ground, defatted by stirring in hexane (1/10 v/v) for 20 min at room temperature. The solvent-imbibing meal was isolated by centrifugation and removed by evaporation at room temperature. The proteins from defatted endosperm were extracted successively by a series of solvents. Thus, 0.5 g of sample was kept in suspension with 5 mL of extract in 16 mL centrifuge tubes. The duration, the number ($n\times$) and the temperature of extraction with each solvent were as follows: (step 1) 0.5 M NaCl, 30 min (2×) at 4 °C; (step 2) 0.5 M NaCl with 0.6% 2-mercaptoethanol (2ME) (v/v), 30 min (2×) at 20 °C; (step 3) 0.1 M $C_2H_3NaO_2$; $3H_2O$ with 0.5 M NaCl and 0.6% 2ME buffered at pH 10 (0.0125 M $Na_2B_4O_7$; 12 H_2O and 0.02 M NaOH), 30 min (1×) at 20 °C; (step 4) 55% of isopropyl alcohol (w/w) with 0.6% 2ME, 30 min (3×) at 20 °C. The solid material was isolated from extractants by centrifugation at 30000*g* for 15 min. For each solvent, supernatants were combined to give the extract. By this way, salt-soluble proteins were isolated at step 1, γ-zeins (step 2), β-zeins (step 3), (α,β,δ)-zeins (step 4), and the residual proteins were made up of true glutelins. Each protein fraction was identified by amino acids analysis (data not shown). For each sample, the entire procedure was repeated twice. The protein distribution in the endosperm was expressed as a percentage of recovered endosperm proteins and as a percentage of starch contained in the grain to determine the limitation of the accessibility of starch granules to ruminal microorganisms by proteins.

Measurements of Ruminal Starch Degradation. Measurements of starch degradation were carried out in situ using three dry Jersey cows fitted with a ruminal cannula. They received a diet of 70% hay and 30% concentrate, composed of 43% barley, 40% beet pulp, 10% soybean, 5% beet molasses, and 2% mineral−vitamin premix. Daily ration was 6 kg of DM, given in two equal parts at 08:00 and 17:00. Cows were adapted to the diet for 4 weeks before measurements. Maize grains were ground through a 2 mm sieve in a hammer mill. Approximately 3 g of 2 mm ground grain were put into nylon bags (Ankom Co, Fairport, NY; pore size, 53 μm; internal dimensions, 5 × 10 cm) and introduced in the rumen at the same time just before the morning meal. They were removed after 3, 6, 9, 15, 24, 48, and 72 h of incubation. Six measurements (2 repetitions × 3 cows) were made for each incubation time. After removal, bags were washed in a washing machine with 3 successive 2 min washings, then dried at 80 °C for 48 h, and weighed. For each animal, the two bags of the same maize and the same incubation time were pooled to carry out starch content determination.

The degradation kinetic of starch obtained for each cow and for each maize was fitted with an exponential model: disappearance $(t) = a + b(1 - e^{-ct})$. This model assumes two degradable fractions: a rapidly degradable fraction in the rumen (a) and a slower degradable fraction (b) with speed reducing exponentially [e^{-ct}]. The three parameters a, b, and c were estimated by an iterative least-squares procedure of SAS (1988), and best fit values were chosen using the smallest sum of squares after convergence. Ruminal starch degradability was calculated according to the equation of Orskov and McDonald (1979) at a ruminal outflow rate of 0.06 per h (Poncet et al., 1995).

Statistical Analyses. Ruminal starch degradation parameters, and physical and chemical parameters, were analyzed in a split-plot model of SAS Institute (1990), with texture of the endosperm as whole plot treatment and genotype as subplot.

RESULTS AND DISCUSSION

Morphological Composition of the Grain. The data concerning the morphological composition of the six maizes were given in Table 2. The proportion of germ was independent ($p > 0.10$) of the texture but varied ($p < 0.0001$) with the genotype ranging from 9.6 (*wx*) to 14.5% (*ae*). Amylose extender (*ae)* maizes were the richest in envelopes and the difference with the other genotypes was more marked for flint than dent type. Therefore, the proportion of endosperm in the grain varied ($p < 0.0001$) with the genotype, amounting to 82.5, 79.5, 74.5% for the (*wx*), (+), and (*ae*) maizes, respectively. The differences in morphological composition, namely a higher content of pericarp and a lower content of endosperm recorded for (*ae)* maize, are in agreement with the observations of Zuber et al. (1960), Wolf et al. (1975), and Tsai et al. (1978). The higher

Table 3. Influence of Texture and Genotype of Maize on Biochemical Composition of the Grain

	flint			dent				statistical significance		
	wx	+	*ae*	*wx*	+	*ae*	SE	texture	genotype	interaction: texture × genotype
starch, % of DM	74.2	74.4	64.3	68.8	68.8	64.3	0.4	0.0006	0.0001	0.0087
amylose, % of starch	2.1	31.5	49.1	8.1	22.6	46.8	1.3	0.4018	0.0001	0.0434
CP, % of DM	11.8	13.7	11.5	13.0	14.6	13.4	0.1	0.0001	0.0001	0.0444
NDF, % of DM	9.1	8.1	17.5	12.8	15.1	18.9	0.3	0.0001	0.0001	0.0098

Table 4. Influence of Texture and Genotype of Maize on the Protein Distribution in the Endosperm[a]

	flint			dent				statistical significance		
	wx	+	*ae*	*wx*	+	*ae*	SE	texture	genotype	interaction
endosperm CP (%)	11.7	13.8	11.1	13.2	14.8	13.9	0.2	0.0002	0.0024	0.0246
salt-soluble proteins	6.7	3.4	11.1	8.0	10.2	13.0	0.2	0.0001	0.0001	0.0003
γ-zein	8.1	9.1	9.9	10.8	9.3	9.3	0.3	0.0748	0.6972	0.0209
(α,β,δ)-zeins	73.8	75.6	59.3	68.6	66.8	60.1	0.8	0.0095	0.0003	0.0402
true glutelins	11.4	11.9	19.7	12.6	13.7	17.6	0.5	0.6691	0.0003	0.0986

[a] Percentage of recovered endosperm proteins.

Table 5. Influence of Texture and Genotype of Maize on Ruminal Starch Degradation

	flint			dent				statistical significance		
	wx	+	ae	wx	+	ae	SE	texture	genotype	interaction: texture × genotype
rapidly degradable fraction, %	18.7	12.3	27.3	21.0	26.7	50.7	2.9	0.0064	0.0002	0.0221
slowly degradable fraction, %	81.3	87.7	72.7	66.3	73.3	49.3	2.4	0.0011	0.0001	0.1743
degradation constant rate, % h^{-1}	4.3	8.3	4.9	22.9	6.7	5.8	1.3	0.0314	0.0008	0.0001
effective degradability, %	52.5	51.9	69.5	73.5	62.7	76.7	0.9	0.0031	0.0001	0.0001

proportion of endosperm in *wx* maizes has not been reported previously. The vitreousness was higher for flint than dent grain, averaging 69.2 and 56.8%, respectively. The difference between the two textures were the most marked for (+) genotype whereas the difference was the lowest for (*wx*) genotype. Irrespective the texture, the (*ae*) grains were the lest vitreous.

Physical Characteristics. The dent and flint maizes differed in the proportion of fines particles ($100 > d > 50$ μm and < 50 μm), and these proportions remained low for all maize grains. The starch mutation altered the proportions of coarse particles. The arithmetic mean was lower ($p < 0.10$) for dent than flint maizes.

Biochemical Composition. Flint grains were seen ($p < 0.001$) to be the richest in starch (Table 3). Within a same texture of grain, (*ae*) grains had the lowest starch content in keeping with the lowest proportion of endosperm (Wolf et al., 1975). As might be expected, the amylose content of starch depended on the genotype, averaging 5.1, 27.0, and 48.0% for (*wx*), (+), and (*ae*) maizes, respectively. The CP content averaged 13.0% DM and was lower ($p < 0.0001$) for flint than dent type, i.e., 12.3 and 13.7%, respectively. Flint type was ($p < 0.0001$) the poorest in NDF content, i.e., 11.6% DM. For grain of the same texture, (*ae*) grain had ($p < 0.0001$) the highest NDF content, particularly in the flint type, in agreement with the highest proportion of envelopes.

The proportions of each protein fraction, expressed as a percentage of recovered total proteins, are given in Table 4. Protein recovery ranged from 95.0 to 103.0%. Salt-soluble proteins averaged 8.7%, amounting 7.1 and 10.4% for flint and dent maizes, respectively. The higher salt-soluble proteins content in dent than flint type confirms the data of Mestres et al. (1996). Zeins were the predominant fraction; (α,β,δ)-zeins averaged 67.4% and γ-zeins 9.4%. The lower proportion of salt-soluble proteins in the flint type resulted in a higher proportion of (α,β,δ)-zeins. These results conform with observations of Chandrashekar and Kirleis (1988), but the discrepancies recorded between flint and dent were lower in our study. This could be related to genetic and environmental factors altering the relative ratio of floury-to-vitreous ratio as suggested in the work of Hamilton et al. (1951). The proportion of true glutelins averaged 14.4% and did not differ ($p > 0.05$) for dent and flint types. Irrespective the texture, the distributions of endosperm proteins were almost similar for (*wx*) maize and the normal counterpart, whereas the endosperm proteins of (*ae*) maize differed greatly from those of the normal counterpart. The lower (α,β,δ)-zeins content in (*ae*) maize was in agreement with results of Wolf et al. (1975).

Ruminal Starch Degradation. Ruminal starch degradability was lower ($p < 0.01$) with flint than with dent maizes, averaging 58.0 and 71.0%, respectively (Table 5). This discrepancy was related to a lower proportion of rapidly degradable fraction (19.4 vs 32.8%) in detriment of the slowly degradable fraction (80.6 vs 63.0%) and to a depressed degradation constant rate (5.8 vs 11.8% h^{-1}). These observations were in agreement with those obtained in vitro by Kotarski et al. (1992) and Opatpatanakit et al. (1994) and in vivo by Ladely et al. (1995). Variation in starch composition was also an important factor of variation ($p < 0.001$), but its effects depended on the texture. Irrespective the texture, (*ae*) grains displayed a higher ruminal starch degradability than the normal counterpart, averaging 73.1 vs 57.3% and this superiority was due to a higher proportion of the rapidly degradable fraction. But, starch in (*wx*) grain compared to that of normal counterpart had the same ruminal starch degradability in the flint texture, whereas it was higher in the dent texture. The increase in the dent texture was mainly due to a higher degradation constant rate. In sorghum, starch in (*wx*) grain compared with that of normal grain was always more degradable in studies performed in

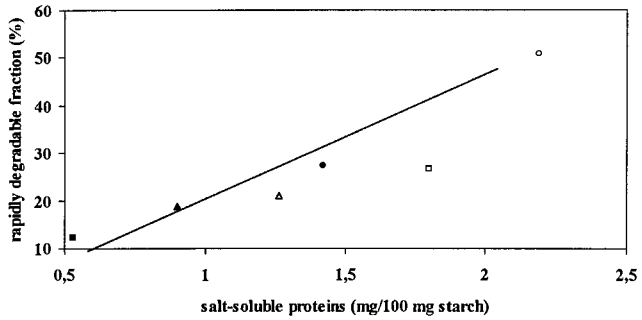

Figure 1. Relationship between the amount of salt-soluble proteins and the rapidly degradable starch fraction. % = 20.35 (SSP) − 1.21. r^2 = 0.84. Symbols: ▲, waxy (*wx*); ■, normal (+); ●, amylose extender (*ae*); ◇, dent; ◆, flint.

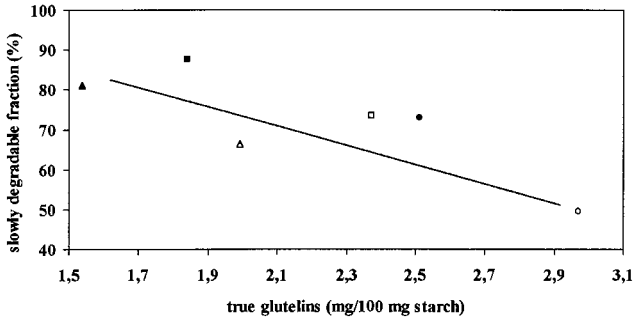

Figure 2. Relationship between the amount of true glutelins and the slowly degradable starch fraction. % = −20.8 (TG) + 117.79. r^2 = 0.65. Symbols: ▲, waxy (*wx*); ■, normal (+); ●, amylose extender (*ae*); ◇, dent; ◆, flint.

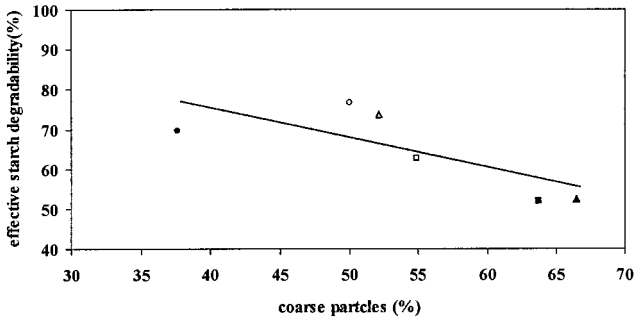

Figure 3. Relationship between the proportion of coarse particles and the effective starch degradability. *D* = −0.8% coarse particles + 106.7; r^2 = 0.59. Symbols: ▲, waxy (*wx*); ■, normal (+); ●, amylose extender (*ae*); ◇, dent; ◆, flint.

vitro (Streeter et al., 1986; Wester et al., 1992; Kotarski et al., 1992) and in vivo (Streeter et al., 1990a). But, the texture of the (*wx*) grain was not reported except for the study of Kotarski et al. (1992).

Influence of Biochemical and Physical Characteristics of Maize Grain on Ruminal Starch Degradation. Ruminal starch degradability was not related ($p > 0.05$) to the amylose content of starch. In the literature, starch in (*ae*) maize was less degradable by α-amylase than its normal counterpart (Davis and Harbers, 1974), whereas the amylose:amylopectin ratio did not affect digestion of isolated starch when incubated in ruminal fluid as shown in vitro Cone and Wolters (1990) in different cereals and Hibberd et al. (1982) in the same cereal. This last result confirms our finding. Ruminal starch degradability was positively related ($p < 0.05$) to the NDF content but this relation might be indirect. In this study, the (*ae*) maizes were the richest in parietal constituents and the lowest in vitreousness. This lowest vitreousness in (*ae*) maizes could explain their highest ruminal starch degradability, these two parameters are strongly correlated as it has been shown in a previous study (Philippeau et Michalet-Doreau, 1997). Regardless of the maize grain, starch degradability was dependent on endosperm texture ($p < 0.01$). This parameter could affect distribution of proteins in the endosperm and particle size distribution. To investigate the variation in ruminal starch degradation related to the features of protein distribution in the endosperm, we studied the relationship between the amount of each protein fraction (mg) expressed per 100 mg of starch contained in one grain and the starch degradation parameters. The rapidly degradable starch fraction was positively linked to the amount of salt-soluble proteins (Figure 1). The slowly degradable fraction was positively linked to the amount of true glutelins (Figure 2) but independent of the amount of (α,β,δ)-zeins. These different proteins do have not the same localization in the endosperm: true glutelins constitute the protein matrix (Christianson et al., 1969) and zeins make up the storage bodies (Duvick, 1961). Therefore, starch granules accessibility might be linked more to the protein matrix itself than to the storage bodies. But, regardless of the protein fraction, there was no relation between the amount of protein and ruminal starch degradability. Regardless of the maize genotype, the proportion of DM that passed through the 50 μm sieve was low (<2%). Consequently, variation in ruminal starch degradability could not be related to variation in particulate starch losses that passed through the pores of the bag without being degraded. Ruminal starch degradability was linked to the proportion of coarse particles (1000 > *d* > 400 μm) which averaged 54% of maize DM (Figure 3). The proportion of coarse particles was commonly used as a predictor of hardness and Shull et al. (1991) and Li et al. (1996) showed a strong relationship between these two parameters.

CONCLUSION

The accessibility of starch granules to ruminal microorganisms was related to the protein distribution in the endosperm and to the particles size distribution. This relationship was weak because maizes differed greatly in the endosperm texture and in starch composition.

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