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Original article

Genetic variation of maize silage ingestibility in dairy cattle

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Abstract — During a three-year experiment, twelve registered or experimental maize hybrids were investigated for their ingestibility in dairy cows. Their digestibility values in sheep were also available from simultaneous experiments. Significant intake differences were observed between maize hybrids, ranging from 14.4 to 17.9 kg·cow^{-1}·day^{-1}. The highest intake was observed for the bm3 hybrid. Among normal hybrids, DK265 had a higher ingestibility than other hybrids. However, two recently registered hybrids and an experimental hybrid had only little lower values of intake than DK265. In vivo NDF digestibility explained about 50% of the intake variation (bm3 hybrid excluded), but in vitro cell wall digestibility (DINAGZ) explained only 25% of the intake in similar conditions. Ingestibility variation were probably related to both rate of cell wall degradation and friability traits, that are not relevantly measured through usual digestibility or lignin content estimates.

ingestibility / maize / genetic variation / cell wall digestibility / lignin / breeding

Résumé — Variabilité génétique de l'ingestibilité du maïs ensilage mesurée sur des vaches laitières. L'ingestibilité de douze hybrides de maïs, inscrits ou expérimentaux, a été étudiée sur vaches laitières au cours d'une expérimentation répartie sur trois années consécutives. Leurs valeurs de digestibilité sur moutons étaient également disponibles à partir d'expérimentations simultanées aux mesures sur vaches laitières. Des différences significatives d'ingestibilité ont été observées entre hybrides, comprises entre 14.4 et 17.9 kg·vache^{-1}·jour^{-1}, l'hybride bm3 ayant la valeur la plus élevée. Au sein des hybrides normaux, DK265 avait une ingestibilité supérieure aux autres hybrides, mais un hybride récemment inscrit et un hybride expérimental avaient des valeurs d'ingestibilité proches. La digestibilité in vivo du NDF expliquait environ 50 % de la variabilité observée pour l'ingestibilité (hybride bm3 exclu), mais la digestibilité in vitro des parois estimée par le critère DINAGZ n'en expliquait dans les mêmes conditions que 25 %. La variabilité de l'ingestibilité est très probablement à relier autant à des caractéristiques de vitesse de dégradation et de friabilité des parois, non évaluées à travers les critères classiques, qu'à la digestibilité des parois proprement dite.

ingestibilité / maïs / variabilité génétique / digestibilité des parois / lignine / amélioration génétique

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1. INTRODUCTION

In European conditions of dairy cattle rearing, whole-plant maize silage often comprises more than three quarters of the animal diet. Genetic variation for maize silage digestibility and energy value was proved in numerous works from in vivo measurements, either between normal hybrids or in comparisons with bm3 hybrids (review in [9]). Recent unpublished data of Inra Lusignan showed that organic matter digestibility measured on wethers in digestibility crates ranged from 65.3 to 74.4% in a set of 232 registered early maize hybrids (mean value was 69.9%), and reached 76.8% in bm3 hybrids. Genetic variation in maize silage efficiency for milk or meat yield and quality was also proved in comparison (i) between normal hybrids [1, 7, 20], (ii) between normal and bm3 hybrids [4, 5, 17, 26] and (iii) between normal and leafy hybrids [10, 22, 25] despite the fact that in these last experiments normal and leafy hybrids were not isogenic, and therefore the higher milk yield could not definitely be related to the leafy trait. Efficient methods are available for breeding maize of higher whole plant and cell wall digestibility. These methods are based on NIRS measurement of enzymatic solubilities, and computed cell wall digestibilities [3, 8, 11].

Voluntary intake is also a primary nutritional factor controlling animal production. Ruminants consuming diets high in cell wall content are often unable to eat sufficient quantities of forage to meet their energy demands, especially for perennial grasses and alfalfa, but also for forage with a high energy content such as whole-plant maize. Different equations of intake prediction have been established by ruminant nutritionists, allowing the formulation of relevant and economical diets by farmers (reviews in [12, 15]). However, due mostly to the great impossibility for plant breeders to work with cattle, there was "a failure of most scientists to recognize the importance of voluntary intake, that has led to an unnecessary and undesirable gulf between the science and the practice" [24]. Very few works were then devoted to studies of genetic variation of ingestibility related to plant genotypes in fixed environmental conditions. From feeding experiments previously quoted [1, 7], it appeared that the intake of maize hybrids of significantly lower whole plant or cell wall digestibility was lower than the intake of hybrids of rather good cell wall digestibility. But the results when comparing hybrids of higher digestibility were not so clear. Although it has been reported only in very few experiments, some hybrids have seemingly a higher intake in dairy cows. A better ingestibility was shown by Ciba-Semences (personal communication) in kindred hybrids Briard and Bahia. The intake was increased by 0.5 and 1.0 kg respectively, compared to a "commonly used hybrid". The voluntary intake of hybrid DK265, which is of high cell wall digestibility, was also found greater than that of other hybrids, including hybrids of similar digestibility [7]. When maize silage was given as about 80% of the diet, dairy cows fed a DK265 silage had an average intake reaching 1.3 $kg \cdot day^{-1}$ more than that of a hybrid with the same dry matter and grain contents, and the same cell wall digestibility.

Today, no in vitro or in vivo routine traits are seemingly available to breed maize hybrids of higher ingestibility. Large genetic variation in in situ degradation kinetic parameters was found by Verbic et al. [30], and Tovar-Gomez et al. [27], and has been considered as related to ingestibility. But further works proved that (i) it was not possible to use this method on a great number of hybrids and samples, and to establish relevant NIRS calibration, and that (ii) the in situ kinetics parameters were not sufficiently related to ingestibility [1, and INRA Lusignan unpublished data], especially because samples had to be ground, leading thus to the loss of mechanical characteristics of plant tissues.

This work was devoted to a study of the genetic variation in ingestibility by dairy cattle of a set of hybrids. These hybrids represented a large variation range of organic matter digestibility (OMD) and NDF digestibility (NDFD) in sheep. The objectives of the work was (i) to investigate the potential variation in ingestibility between maize hybrids on a much larger genetic basis, and to compare it to the ingestibility of DK265 and (ii) to give plant breeders information on the feasibility of breeding maize for specific traits related to ingestibility.

2. MATERIALS AND METHODS

2.1. Dairy cattle experiments

Twelve hybrids were used in this 3 year experiment (1999, 2000, 2001), according to the distribution given in Table I, including (i) hybrid DK265, which is of high cell wall digestibility, and which appeared more ingested than control hybrids in previous experiments [7], (ii) 8 hybrids registered in France between 1996 and 2001 (namely Rh hybrids), (iii) a leafy hybrid (Rh390) available on the Northern American market, (iv) a bm3 hybrid and its isogenic counterpart (F7026bm3 is a bm3 isogenic of F7025), and (v) an experimental hybrid, resulting of a cross of a bm3 line (F7026bm3) with the Inra line F4, which is the normal flint line with the highest known cell wall digestibility (higher than that of F2bm3). One hybrid (Rh357) was discarded from the first year experiment, because of erratic results. Two hectares of 6 maize hybrids were grown each year at INRA Lusignan (Vienne, France) in fields with homogeneous agronomic conditions. Row spacing was 0.75 m and density was 95 000 plants per hectare. Irrigation was given three times at 30 mm, to prevent summer water stress. In mid-September, the maize hybrids were harvested at the (hard)-dough stage to yield a silage with a DM content close to 30%, with the same machine without a grain cracker (John Deere 5730), and then ensiled in bunker silos according to standard farming practices.

Six sets of 4 Prim'Holstein cows {1 (or 2) primiparous and 3 (or 2) multiparous} yielding about 8000 kg of milk per year were used in these experiments. Cows were paired and

Table I. Hybrids used in the experiments (Hi number referred to the design given in Tab. II, ^{O} = hybrid discarded of the experiment).

Hybrid	Year of registration	Hybrids experimented in		
		1999	2000	2001
Dk265	1987	H6	H5	H1
Rh317	1998	H5	H6	
Rh318	1997	H1		
Rh325	1997	H2		
Rh357	1996	H4^{O}		
Rh383	2001		H1	
Rh384	1999		H4	
Rh390 leafy hybrid	1995 (about)	H3	H2	
Rh412	1999			H3
Rh441	1997			H6
F7025 × F2bm3	–			H5
F7026bm3 × F4	–			H4
F7026bm3 × F2bm3	–		H3	H2

Table II. Experimental design used each year of experiment (6 hybrids H1 to H6 according to Tab. I, 6 sets of cows, and 4 successive periods of experiments).

	Cows					
	Set 1	Set 2	Set 3	Set 4	Set 5	Set 6
Period 1	H5	H6	H3	H4	H1	H2
Period 2	H1	H2	H5	H6	H3	H4
Period 3	H4	H5	H2	H3	H6	H1
Period 4	H2	H3	H6	H1	H4	H5

assigned experimental diets according to their parity, body weight (average value was 600.5 kg), date of calving (average value at the beginning of experiment was 61 days after calving), and milk yield during a pre-experimental period (2 weeks, average value was 30.5 $kg{\cdot}cow^{-1}{\cdot}day^{-1}$). The feeding experiments were performed each year according to an incomplete balanced design (Tab. II) from mid-November to February. Each set of cows was fed successively only 4 hybrids out of the 6 tested hybrids, during 4 periods. For each hybrid and each set of cows, measurements were performed for 10 days over 2 weeks, after 2 weeks of pre-experimental feeding with the involved hybrid. Cows were individually fed ad libitum the experimental maize diets daily in the morning, using Calan type feeding doors, for approximately 10% refusals.

Chemical composition of hybrids was estimated from daily sampling of silage during feeding experiments, but samples were weekly grouped together before analysis (Tab. III, values were not corrected from volatile component contents). Average starch contents of hybrids were only estimated from samples taken at harvest time, because the Ewers method (AFNOR, 1981, EEC ISO 10520.2) cannot be used on silage samples. The diet of cows was balanced with a nitrogen rich concentrate (2.2 kg), urea (50 g), and an energy rich concentrate (3–5 kg, according to the milk yield), (Tab. IV). Because of the balanced assignation of cows within and between each of the sets, quantities of concentrates were similar between sets during each of the experimental period, and for a same year the percentage of concentrate was thus similar for each hybrid. Some wheat straw from the litter was also eaten in very low amounts by the cows. A premix of minerals and vitamins (250 g) was given in accordance with the usual requirements. The average maize silage/concentrates ratio was 75/25, and the concentrate ratio ranged from 23 to 27%. In Table IV, the protein truly digestible in the small intestine (PDI), giving the nitrogen value of the silage for dairy cattle, was given according to Jarrige [19] as (i) PDIN, when energy is not limiting for microbial synthesis, and (ii) PDIE, when degraded nitrogen is not limiting for microbial synthesis. The net energy value for milk production in dairy cattle was also given according to the French standards [19], and expressed as UFL (UFL = Unité Fourragère Lait, with 1 UFL = 7.1 $MJ{\cdot}kg^{-1}$ DM).

Basic data for analysis were elementary observations for each diet, period, cow and day of experiment. Mean estimates and variance analysis were then computed according to the following statistical model, with

$$Y_{ijlk} = \mu + Y_l + P_j \times Y_l + S_j \times Y_l + H_i + H_i \times Y_l + H_i \times S_j \times Y_l + \varepsilon_{ijlk}$$

where Y_{ijlk} = observed response; μ = overall mean; Y_l = year effect; $P_j \times Y_l$ = period of experiment nested in year effect; $S_j \times Y_l$ = set of cow nested in year effect; H_i = hybrid

Table III. Average chemical composition of maize silages used in the experiments (organic matter, crude protein and NDF as percent of DM, ADL/NDF as percentage).

Hybrid	Organic matter	Crude protein	NDF	ADL/ NDF
Year 1999				
Dk265	95.8	8.2	35.7	5.8
Rh317	96.1	7.1	40.0	6.4
Rh318	96.4	7.1	40.1	7.0
Rh325	95.7	6.8	39.3	6.3
Rh390 leafy hybrid	96.0	7.0	46.1	7.3
Year 2000				
Dk265	95.1	7.2	41.2	5.5
Rh317	96.2	6.3	44.6	6.1
Rh383	95.5	7.2	43.4	6.4
Rh384	94.2	7.5	37.7	5.7
Rh390 leafy hybrid	94.3	7.7	41.3	7.3
F7026bm3 × F2bm3	95.2	7.5	43.2	4.2
Year 2001				
Dk265	94.9	8.5	36.7	5.0
Rh412	95.6	8.1	42.1	5.4
Rh441	95.5	7.9	42.1	5.5
F7025 × F2bm3	95.1	7.9	45.1	5.5
F7026bm3 × F4	95.5	8.1	34.2	4.8
F7026bm3 × F2bm3	95.3	8.9	36.2	3.6

effect; $H_i \times Y_l$ = hybrid × year interaction effect; $H_i \times S_j \times Y_l$ = hybrid × set of cows nested in year interaction effect; and ε_{ijlk} = residual error.

Significance of hybrid effect was estimated as the F ratio between hybrid mean-square (MS) and hybrid set of cows nested in year interaction MS, because of the repeated measurement statistical design, and according to Little and Hills [23]. The effect of variation of DM content on intake was also tested by added the DM content as covariate in the variance analysis of the intake trait, which also led to the estimate of corrected means for each genotype. Milk yield data were not reported, because they were measured on too short periods, and considered then to be insufficiently reliable.

2.2. Sheep experiments

The feeding value measurements in sheep were included in a long term experiment managed at Inra Lusignan, with repeated control hybrids allowing multi-year mean estimates for each genotype (experiment previously described in [6]). Two plots (each of them measuring 150 m^2) of each hybrid studied in cows were simultaneously cropped for sheep experiments, with an extra year of cropping for hybrids Rh318, Rh325, Rh384, Rh412, and for the bm3 hybrid which was cropped every year. Maize cropping conditions were similar to those used for dairy cattle experiments, and hybrids for cow and sheep experiments were cropped in two close fields. Plants were harvested according to hybrid earliness (maturity) at the (hard-)dough stage,

Table IV. Ingredients, chemical composition and feeding values of concentrates fed to dairy cows (PDIN is protein value when energy is not limiting for microbial synthesis, and PDIE is protein value when degraded nitrogen is not limiting for microbial synthesis).

	Nitrogen rich concentrate "Protival©"	Energy rich concentrate "Diapason©"
Ingredients		
Soybean cake (%)	65	10
Rapeseed cake (%)	20	12
Sunflower cake (%)	15	7
Wheat, barley, maize grains (%)	-	41
Wheat issues (%)	-	21
Soluble proteins (%)	-	3
Sugar beet molasses (%)	-	3
Mineral premix ($g \cdot kg^{-1}$)	-	5
$CaCO_3$ ($g \cdot kg^{-1}$)	-	20
NaCl ($g \cdot kg^{-1}$)	-	5
Chemical composition (DM)		
Organic matter (%)	92.7	93.2
Crude protein (%)	46.0	21.0
Starch (%)	2.5	32.0
Crude fiber (%)	12.9	9.2
Fat (%)	3.4	3.8
Feeding value (DM)		
Net energy for lactation ($UFL \cdot kg^{-1}$)	1.09	1.05
PDIN ($g \cdot kg^{-1}$)	333	144
PDIE ($g \cdot kg^{-1}$)	228	126

and yielded silage DM contents of 30–35%. Each maize plot was ensiled in one cylindrical mini-silo (1.30 height, 1.45 diameter) according to standard farming practices [28]. Each silage was then fed twice a day to six Texel wethers, housed individually in digestibility crates. Only nitrogen (1.5% urea), minerals and vitamins were added to balance the maize diet [6]. Feeding was adjusted to the maintenance requirement of each animal according to its metabolic weight (40 $g \cdot kg^{-0.75}$). For each of the mini-silos, measurements were done during one week, after a week of pre-experiment. Data were collected for five days, after a seven day pre-experimental period. NDF (neutral detergent fiber) and ADL (acid detergent lignin) were estimated according to Goering and van Soest [16]. In vivo digestibilities of organic matter (OMD) and NDF (NDFD) were determined from contents in offered forage and in feces, according to Jarrige [19]. The net energy value for lactation (NEL) in dairy cattle was computed according to the French standards [19], and expressed as UFL. In vitro cell wall digestibility was estimated through the DINAGZ criterion {in vitro digestibility of the "non starch (ST), non soluble carbohydrates (SC) and non crude protein (CP) part"} [3, 8], based on the Aufrère and Michalet-Doreau [2] enzymatic solubility

(IVDMD) as DINAGZ = 100 × (IVDMD – ST – SC – CP) / (100 – ST – SC – CP).

Basic data for analysis were average observations for each mini-silo. Genotype mean estimates were then computed after variance analysis according to the usual statistical model, with a year effect, a genotype effect, and a hybrid × year interaction effect.

This methodology, developed for the long time experiment of maize digestibility assessment in sheep, did not allow to compare directly the same silage in sheep and cows. But, conversely, it allowed to obtain higher accurate maize values in sheep, due to a higher number of replicates. It was then possible to study the relationships between values observed in cows and these value in sheep considered as average acute values, all the more because genotype × year interactions were proven low for cell wall digestibility traits [3, 6, 9]. Moreover, this methodology allowed to obtain robust in vivo feeding values for a large collection of maize hybrids, and then to study, from a breeding point of view, the genetic variation for feeding value in maize [6, 9].

3. RESULTS AND DISCUSSION

3.1. Feeding value in sheep

A great variation was observed between hybrids for their energy values and cell wall digestibility, as expected (Tab. V). NEL ranged from 0.82 to 0.98 UFL (5.8 to 6.9 MJ·kg^{-1}), and NDFD ranged from 45.3 to 62.1%. However, according to previous experiments of hybrids involving maize lines genetically related to F7025, values observed in hybrid F7025 × F2bm3 were probably under-estimated, possibly as it was measured in 2 mini-silos only, and because of an abnormally low starch content. The DINAGZ value of this hybrid indeed corroborated this assumption. OMD of the highest normal hybrids were only 2 or 3 points lower than that of the bm3 hybrid, but their NDFD were 9 or 11 points lower. These results illustrated once more the efficiency of the bm3 gene for the improvement of wall digestibility, mainly because of a decrease in lignin content higher than 30%. Because the bm3 trait is recessive, only hybrids having this trait in both parental lines produce the

Table V. In vivo feeding value of hybrids measured in sheep (OMD and NDFD are in vivo digestibility of OM and NDF, respectively, and NEL is computed from in vivo data according to the French standard [19]). In vitro traits related to digestibility of hybrids (DINAGZ is an in vitro cell wall digestibility trait, and lignin in the cell wall is given as ADL/NDF).

	Silo number	OMD (%)	NEL (UFL·kg^{-1})	NDFD (%)	DINAGZ (%)	ADL/NDF (%)
F7026bm3 × F2bm3	6	75.2	0.98	62.1	57.9	4.4
Dk265	6	73.4	0.95	52.8	50.5	6.1
F7026bm3 × F4	2	75.0	0.98	50.8	52.1	5.5
Rh325	4	72.2	0.92	51.0	51.0	6.0
Rh317	4	71.8	0.92	51.4	50.2	6.2
Rh383	2	73.2	0.94	52.1	49.6	6.4
Rh318	4	68.4	0.87	45.1	44.9	7.2
Rh441	2	67.8	0.85	48.5	46.6	6.9
Rh390leafy	4	68.6	0.86	48.8	47.5	6.6
Rh384	4	72.9	0.94	47.5	48.7	6.2
F7025 × F2bm3	2	66.0	0.82	45.3	49.6	6.8
Rh412	4	70.6	0.91	48.0	47.7	6.8
Residual error	-	2.4	0.001	13.2	3.7	0.1

brown-midrib phenotype. The F7026bm3 × F4 hybrid lignin content was intermediate between that of normal and bm3 hybrids, whereas F7025 × F2bm3 had a normal lignin content. Line F4, which is of low lignin content and high digestibility, could be a normal genetic resource allowing significant progress in normal maize feeding value improvement (but the agronomic value of this line is very poor).

3.2. Dairy cattle experiments

Silage preserving was suitable according to the usual parameters (pH, ammonia, acetic, propionic, and butyric acids, data not shown). Variation for NDF content was observed between hybrids, with a slight tendency for a lower content in DK265 (Tab. III). DK265 had also a slightly lower ADL/NDF content than other normal hybrids, whereas the bm3 hybrid had the lowest one. As it was observed from experiments with sheep, the experimental hybrid F7026bm3 × F4 had a lower ADL/NDF content than all normal hybrids. Contrarily, the leafy hybrid had the highest lignin content. The average starch content of hybrids at harvest was 33.7%, and ranged across years and hybrids between 30.6 and 36.9%, except a low value in F7025 × F2bm3 close to 27%.

The hybrid effect was highly significant for intake ($P < 0.01$, Tab. VI), and this effect remained significant even though the bm3 hybrid was removed from the analysis. Dry matter contents equal to 30 ± 2% were obtained for most of the hybrids, except for a higher content in 3 hybrids and a lower content in 2 hybrids (Tab. VII). When DM content was added as a covariate, the hybrid effect was only slightly increased, highlighting the importance of the genotypic effect over DM content in intake variations. When computed over mean values, the correlation between intake and DM content was only equal to 0.35. The regression between DM content and intake gave a higher intake of 0.11 kg per percent point increase in DM.

The bm3 hybrid had the highest value for intake, 0.6 $\text{kg·cow}^{-1}\text{·day}^{-1}$ higher than that of DK265 on raw data, and 1.1 kg more on data corrected of DM content. DK265 had also a significantly higher intake than all other hybrids, except F7026bm3 × F4. The bm3 hybrid and DK265 had an intake higher by 2.2 and 1.5 $\text{kg·cow}^{-1}\text{·day}^{-1}$, respectively, than the average value of all other investigated hybrids (15.5 $\text{kg·cow}^{-1}\text{·day}^{-1}$) on raw data (2.4 and 1.3 $\text{kg·cow}^{-1}\text{·day}^{-1}$ on data corrected of dry matter content, respectively). Whereas the intake variation range in DM corrected data was 3.5 $\text{kg·cow}^{-1}\text{·day}^{-1}$ among

Table VI. Variance analysis for maize intake.

	Without covariate			With DM content as covariate		
	Degree of freedom	Mean square	F	Degree of freedom	Mean square	F
Year	2	486.1	55.1	2	486.1	55.1
Period × Year	9	100.9	11.4	9	100.9	11.4
Set of cows × Year	15	231.3	26.2	15	231.3	26.2
DM content	-	-	-	1	2426.9	311.9
Hybrid	11	177.9	7.5	11	197.2	9.0
Hybrid × Year	3	51.4	5.8	3	32.9	4.2
Hybrid × Set × Year	27	23.6	2.7	27	21.8	2.8
Residual error	2420	8.8	-	2419	7.8	-

Table VII. Intake and dry-matter mean values of hybrids.

	Dry matter (%)	Dry-matter confidence limit	Intake (kg·cow^{-1}·day^{-1})	DM corrected intake	Intake confidence limit
F7026bm3 × F2bm3	28.4	0.3	17.6	17.9	0.4
Dk265	32.5	0.3	17.0	16.8	0.3
F7026bm3 × F4	35.0	0.5	16.4	15.9	0.6
Rh325	35.2	0.5	16.1	15.6	0.6
Rh317	30.7	0.3	15.9	15.9	0.4
Rh383	28.4	0.5	15.9	16.1	0.6
Rh318	35.0	0.5	15.7	15.2	0.6
Rh441	29.6	0.5	15.4	15.5	0.6
Rh390leafy	30.0	0.3	15.3	15.4	0.4
Rh384	28.1	0.5	15.2	15.5	0.6
F7025 × F2bm3	27.2	0.5	15.0	15.4	0.6
Rh412	27.9	0.5	14.1	14.4	0.6

the 12 investigated hybrids, 6 hybrids were in a 0.4 kg·cow^{-1}·day^{-1} range (from 15.2 to 15.6 kg·cow^{-1}·day^{-1}). Only one hybrid had a much lower intake (14.4 kg·cow^{-1}·day^{-1}). According to confidence limit values, 3 hybrids were close to the highly ingestible DK265, with an intake ranging from 15.9 and 16.1 kg·cow^{-1}·day^{-1}. Even if the comparison was not performed between isogenic hybrids, the leafy traits did not appear of interest in dairy cattle feeding.

3.3. Relationships between intake in cows and digestibility traits

Correlations between intake (in cows) and digestibility values (in sheep or in vitro), computed over mean values, are given in Table VIII. High correlation values were found between NDFD and intake when the bm3 hybrid was taken into account, but without this bm3 hybrid, the NDFD explained only 50% of the variation observed in intake (estimated by the r^2 value). However, cell wall digestibility appeared more related to intake than whole plant digestibility or energy value. Without the bm3 hybrid, the DINAGZ cell wall digestibility explained only a quarter of the total phenotypic variation in intake, slightly more than in vivo OMD. When using multiple regression, the second regressor after NDFD, or DINAGZ respectively, was not significant. Up to now, for breeding maize hybrids with a higher ingestibility, DINAGZ, or preferably a NIRS calibrated NDFD, are

Table VIII. Correlations between intake and digestibility traits (definition of traits is given in Tab. V).

	OMD	UFL	NDFD	DINAGZ
Raw values				
Intake (all hybrids)	0.65	0.61	0.80	0.73
Intake (without bm3)	0.55	0.52	0.66	0.52
DM corrected values				
Intake (all hybrids)	0.61	0.56	0.89	0.82
Intake (without bm3)	0.50	0.46	0.71	0.56

the best available traits. As a tentative conclusion, it appeared that the cell wall digestibility explained 50% (75% with bm3 hybrids) of the genetic variation in ingestibility. Maize breeding for a higher cell wall digestibility should have favorable effect on ingestibility. However, a significant part of the genetic variation for this trait remains unexplained, even if this unexplained part could be partly overestimated because sheep and cows were not fed silages exactly from the same silos.

3.4. Consequences in further breeding for a higher ingestibility of maize silage

The regulation of the appetite of animals fed maize silage is considered above all as resulting from a physical regulation, even if chemical and palatability traits cannot be excluded. It is also usually considered that the ingestibility of a forage is controlled by the time this forage is retained in the rumen [reviews in 13, 21, 24]. Particles have to be broken down to a size close to 2–4 mm before they can go out of the bovine rumen through the digestive tract [1]. Chewing during eating and ruminating is responsible for most of this particle breakdown in chopped forage [24]. Fernandez and Michalet-Doreau [14], quoting Ulyatt [29] and Inoué et al. [18], also mentioned that food is chewed during eating to a common end point, so that the bolus may be easily swallowed. As a consequence, from a plant breeder standpoint, the ingestibility and the filling capacity of maize forage probably depends on genetic traits of the maize related to its cell wall digestibility value, its cell wall digestibility rate, and its resistance to friability. Most of modern forage maize hybrids are based on a germplasm previously bred and/or also used in grain maize hybrid. It is then very likely that alleles allowing a good digestibility and a good friability of plants were eliminated during breeding for stalk standability and breakage resistance. The search of highly ingestible maize will require a new investigation of old genetic resources that are not currently used, or that were never used in maize breeding. However, some recently registered hybrids have appeared of higher ingestibility than other ones of similar registration time, but probably lower than DK265. Significant progress in understanding traits related to ingestibility will be based first on new results obtained by animal nutritionists that will give new data on the mechanical and chemical regulation of animal appetite. Progress will also arise from new results in molecular determinants of traits involved in cell wall biogenesis, that could lead to targeted genetic modifications of the cell wall structure in hybrids. The consequences on intake of these cell wall modifications could then be tested on animals, evidencing the more efficient plant traits related to a higher intake of maize silage by cattle.

4. CONCLUSIONS

The highest intake was observed in this experiment with the bm3 hybrid, confirming that the high nutritional value of such genotypes comes from both their high ingestibility and digestibility. However, these favorable feeding traits are probably highly related to the significantly lower lignin content of these plants, with the unfavorable related consequences on water and nutriment transport, due to the possible collapsing of vessels not lignified enough. Among normal hybrids, DK265 had the highest ingestibility. One experimental hybrid (F7026bm3 × F4) and one normal hybrid (Rh383), which are close to DK265, could however be considered as interesting model for plant breeders. Rh383 could be particularly of interest as it had a “normal” ADL/NDF content. Rh317 and, to a lesser extent Rh325, could also be considered as interesting model for breeders, because these two hybrids had both high NDFD and normal ADL/NDF content.

From a plant breeder standpoint, the improvement of the ingestibility of maize forage probably depends on genetic traits related to both plant cell wall digestibility and plant tissue friability. Up to now, during forage maize breeding, the best trait allowing the discarding of hybrids with poor ingestibility is probably a cell wall digestibility trait, either investigated in vivo or in vitro. However, breeding maize for a significantly higher silage ingestibility (and also for a higher cell wall digestibility) will demand new investigation of genetic resources that are not currently used in maize breeding. Moreover, only targeted introgression of new favorable alleles, using marker assisted selection, will allow the improvement of forage maize feeding value without decrease in agronomic value. Another relevant way in breeding forage maize for higher digestibility and ingestibility would be to devise specific genetic resources through genetic engineering in the cell wall biogenesis pathways. But this way will be conceivable only if this technology is definitively proven to be safe for environment and health, and with a public acceptance of genetically modified crops.

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REFERENCES

[1] Andrieu J., Baumont R., Digestibilité et ingestibilité du maïs fourrage, facteurs de variation et prévision, Fourrages 163 (2000) 239–252.

[2] Aufrère J., Michalet-Doreau B., In vivo digestibility and prediction of digestibility of some by-products, EEC seminar, Mlle Gontrode, Belgium, 26-29 September, 1983.

[3] Argillier O., Barrière Y., Hébert Y., Genetic variation and selection criteria for digestibility traits of forage maize, Euphytica 82 (1995) 175–184.

[4] Bal M.A., Shaver R.D., Al-Jobeile H., Coors J.G., Lauer J.G., Corn silage hybrid effects on intake, digestion, and milk production by dairy cows, J. Dairy Sci. 83 (2000) 2849–2858.

[5] Ballard C.S., Thomas E.D, Tsang D.S., Mandevu P., Sniffen C.J., Endres M.I., Carter M.P., Effect of corn silage hybrid on dry matter yield, nutrient composition, in vitro digestion, intake by dairy heifers, and milk production by dairy cows, J. Dairy Sci. 84 (2001) 442–452.

[6] Barrière Y., Traineau R., Emile J.C., Hébert Y., Variation and covariation of silage maize digestibility estimated from digestion trials with sheep, Euphytica 59 (1992) 61–72.

[7] Barrière Y., Emile J.C., Traineau R., Hébert Y., Genetic variation in the feeding efficiency of maize genotypes evaluated from experiments with dairy cows, Plant Breed. 114 (1995) 144–148.

[8] Barrière Y., Emile J.C., Le maïs fourrage. III – Évaluation et perspectives de progrès génétique sur les caractères de valeur alimentaire, Fourrages 163 (2000) 221–238.

[9] Barrière Y., Guillet C., Goffner D., Pichon M., Genetic variation and breeding strategies for improved cell wall digestibility in annual forage crops. A review, Anim. Res. 52 (2003) 193–228.

[10] Clark P.W., Kelm S., Endres M.I., Effect of feeding a corn hybrid selected for leafiness as silage or grain to lactating dairy cattle, J. Dairy Sci. 85 (2002) 607–612.

[11] Dolstra O., Medema J.H., An effective screening method for genetic improvement of cell-wall digestibility in forage maize, in: Proceedings of the 15th congress maize and sorghum section of Eucarpia, Baden, Austria, June 4-8 (1990), pp. 258–270.

[12] Faverdin P., Alimentation des vaches laitières. Comparaison des différentes méthodes de prédiction des quantités ingérées, INRA Prod. Anim. 5 (1992) 271–282.

[13] Fernandez I., Influence de la finesse de hachage des ensilages de maïs sur leur digestion (amidon et parois) et leur ingestibilité par les vaches laitières, Thèse Université Blaise Pascal, Clermont-Ferrand, 2003, 168 p.

[14] Fernandez I., Michalet-Doreau B., Effect of chop length of silage and corn hybrid on short-term feed intake control, J. Dairy Sci. (2003) in press.

[15] Fuentes-Pila J., Ibanez M., De Miguel J.M., Beede D.K., Predicting average feed intake of lactating Holstein cows fed totally mixed rations, J. Dairy Sci. 86 (2003) 309–323.

[16] Goering H.K., van Soest P.J., Forage fiber analysis (apparatus, reagents, procedures and some applications), Agric Handb 379, US Gov Print Office, Washington DC (1971).

[17] Hoden A., Barrière Y., Gallais A., Huguet L., Journet M., Mourguet M., Le maïs brown-midrib plante entière. III. Utilisation sous forme

d'ensilage par des vaches laitières, Bull. Tech. CRZV Theix INRA 60 (1985) 43–58.

[18] Inoué T., Brookes I.M., John A., Kolver E.S., Barry T.N., Effects of leaf shear breaking load on the feeding value of perennial raygrass (Lolium perenne) for sheep. II. Effect on feed intake, particle breakdown, rumen digesta and animal performance, J. Agric. Sci. (Camb.) (1994) 137–147.

[19] Jarrige R., Ruminant nutrition. Recommended allowances and feed tables, INRA, John Libbey Eurotext Editions, Monrouge, France, 1989, 389 p.

[20] Johnson L.M., Harrison J.H., Davidson D., Swift M., Mahanna W.C., Shinners K., Corn Silage management. II. Effect of hybrid, maturity, and mechanical processing on digestion and energy content, J. Dairy Sci. 85 (2002) 2913–2927.

[21] Jung H.G., Allen M.S., Characteristics of plant cell wall affecting intake and digestibility of forages by ruminants, J. Anim. Sci. 73 (1995) 2774–2790.

[22] Kuehn C.S., Linn J.G., Johnson D.G., Jung H.J.G., Endre M.I., Effect of silages from corn hybrids selected for leafiness or grain to lactating dairy cattle, J. Dairy Sci. 82 (1999) 2746–2755.

[23] Little T.M., Hills F.J., Subplot as repeated observations, In Agricultural Experimentation, Design and Analysis, John Wiley and Sons, New-York, 1978, pp. 125–137.

[24] Minson D.J., Wilson J.R., Prediction of intake as an element of forage quality, in: Fahey G.C. (Ed.), Forage quality, evaluation and utilisation, American Society of Agronomy, Inc, Crop Science Society of America, Inc, Soil Science Society of America, Inc, Madison, Wisconsin, 1994, pp. 533–563.

[25] Thomas E.D., Mandebvu P., Ballard C.S., Sniffen C.J., Carter M.P., Beck J., Comparison of corn silage hybrids for yield, nutrient composition, in vitro digestibility, and milk yield by dairy cows, J. Dairy Sci. 84 (2000) 2217–2226.

[26] Tine M.A., McLeod K.R., Erdman R.A., Baldwin R.L., Effects of brown midrib corn silage on the energy balance of dairy cattle, J. Dairy Sci. 84 (2000) 885–895.

[27] Tovar-Gomez M.R., Emile J.C., Michalet-Doreau B., Barrière Y., In situ degradation kinetics of maize hybrid stalks, J. Sci. Food Agric. 68 (1997) 77–88.

[28] Traineau R., Mise au point d'un matériel de récolte et de confection de silo adapté à des parcelles expérimentales, Fourrages 128 (1991) 465–470.

[29] Ulyat M.J., Plant fibre and regulation of digestion in the ruminant, fibre in human and animal nutrition, G. Wallace & L. Bell (Ed.), Massey University New Zealand, 1983, p. 103.

[30] 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 in breeding, Anim. Feed Sci. Technol. 54 (1995) 133–148.

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