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Composition and nutritive value of whole maize plants fed fresh to sheep. I. Factors of variation

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Summary — The composition and digestibility by sheep of 15 commercial maize varieties and 1 brown mid-rib experimental hybrid was measured over 2 yr in 7 locations, according to earliness as fresh-cut forage from the milky stage of the grain to the glazed stage. This study determined the effect of the main factors causing variations in plant composition and digestibility. Under satisfactory growing conditions, the digestibility of a given maize hybrid increases significantly with growth stage, whereas it changes very little under poor conditions (low temperatures, drought, etc). For a given dry matter content, genotype effects were significant in only 2 locations and were of similar importance to those of environment (location and year) on a given genotype. As for other forage crops, maize digestibility is closely linked ($R = 0.98$) to its undigestible cell wall content. In contrast, the digestibility of maize cell walls is not only independent of their content in the plant but also lower than that of other forage crops (–10 points for the same ADL/ADF ratio).

maize forage / fresh / composition / digestibility / sheep

Résumé — **Composition et valeur alimentaire de la plante entière verte de maïs pour les ovins. I. Facteurs de variation.** Dans le cadre d'une étude concertée (INRA, ITCF, AGPM, sélectionneurs de maïs), 15 hybrides commerciaux et un hybride expérimental Brown mid-rib (bm3) ont été répartis selon leur précocité (tableau I) dans 7 lieux (Clermont-Ferrand, Dijon, La Jaillière, Le Pin-au-Haras, Lusignan, Rennes et Toulouse) et, dans 5 de ces lieux, durant 2 années consécutives (tableau II). La composition (morphologique et chimique), la solubilité enzymatique (selon 3 méthodes) et enfin, la digestibilité in vivo (4 à 6 moutons alimentés en quantité limitée), ont été mesurées sur la plante verte durant 4 à 7 sem du stade laiteux au stade vitreux du grain, soit sur un total de 48 cultures de maïs. La valeur moyenne et le coefficient de variation de ces mesures figurent dans le tableau IV. Cette étude a permis de préciser l'influence du stade de récolte sur la composition de la plante de maïs et, plus particulièrement, sur celle de ses parois : leurs teneurs en hémicel-

luloses s'accroît au détriment de celles en cellulose et lignine (figs 4 et 5) quand la plante vieillit. À même stade de récolte, il existe des différences significatives de composition dues à l'hybride et aux conditions de milieu (lieu, année), mais il existe de nombreuses interactions entre facteurs (cf Annexes 2, 3 et 4). Les effets les plus constants d'un essai à l'autre sont ceux de l'année (MAT), du lieu (cendres) et de l'hybride (lignine). La digestibilité de la matière organique des hybrides du commerce a été en moyenne de 71,7% et a varié de 67 à 78%, ce qui est comparable aux résultats obtenus 15 ans auparavant dans notre laboratoire sur d'autres hybrides. Contrairement aux études antérieures, la digestibilité a augmenté significativement avec la teneur en matière sèche de la plante (jusqu'à une teneur de 35%) mais de manière variable selon les années. Cet aspect est discuté. À même teneur en matière sèche, les différences de digestibilité entre hybrides n'ont été significatives que dans 2 lieux (Clermont-Ferrand et Lusignan). Elles sont restées alors inférieures à 5 points et n'ont pas été toujours retrouvées d'un lieu à un autre. D'après des comparaisons plus partielles permises par le dispositif expérimental, l'influence du lieu et de l'année semble au moins équivalente à celle de l'hybride (Annexes 3 et 4). La digestibilité réelle des constituants cytoplasmiques étant voisine de 100%, la digestibilité de la plante entière est, comme celle des autres plantes fourragères, liée très étroitement à sa teneur en parois indigestibles ($R = 0,98$; fig 8). En revanche, les parois du maïs se différencient sensiblement de celles des autres plantes : leur digestibilité est liée de manière plus lâche à leur degré de lignification (rapport ADL/ADF) et, pour un même degré de lignification, est nettement plus faible (en moyenne de 10 points pour les hybrides du commerce, fig 11). Enfin, la digestibilité des parois du maïs est indépendante de leur teneur dans la plante. Ces éléments, qui sont discutés, sont invoqués pour expliquer la valeur prédictive relativement médiocre de la solubilité enzymatique, et surtout de la composition chimique, pour prévoir la digestibilité du maïs.

maïs fourrage frais / composition / digestibilité / ovin

INTRODUCTION

The last studies by INRA concerning the factors causing variation in the composition and food value of fresh or preserved (silage or dehydrated) maize were carried out > 15 yr ago (eg Demarquilly and Andrieu, 1974; Andrieu, 1975). These studies mainly concerned grain maize varieties. Since this date, commercial varieties with greater grain productivity or specially adapted to silage-making have been introduced. In addition, new methods (enzymatic, spectrometric) of predicting quality attributes have been developed and it appeared important to compare their accuracy with those of chemical methods of predicting *in vivo* digestibility of maize. For these reasons, a joint study by INRA, ITCF, AGPM and breeders ("Club Digestibilité") was undertaken on forage maize nutritive value. The main objectives were:

- to determine under French conditions, factors causing variation in composition and digestibility of fresh plants of 15 registered hybrids and 1 experimental hybrid (present article);
- to compare different methods for predicting *in vivo* digestibility (morphological and chemical composition, enzymatic digestibility, near infra-red spectrometry used in animal husbandry (Dardenne *et al*, 1992) or in plant breeding (Barrière *et al*, 1991);
- to constitute a bank of reference samples usable for testing methods of prediction.

MATERIALS AND METHODS

Although the main objective was to study the *in vivo* digestibility and energy value of maize silage, it was decided to use fresh maize for 2 reasons:

– firstly, digestibility of silage at > 25% dry matter (DM) is almost identical to that of the fresh plant (Andrieu and Demarquilly, 1974; Andrieu, 1985);

– secondly, trials with silage are more difficult to carry out satisfactorily (use of silos, necessity for correction of results according to losses of volatile substances during oven-drying of samples).

Over 2 yr, 15 commercial varieties which were as different as possible and 1 experimental hybrid, bm3, were selected (table I) by a working group and coded 1 to 17. The 16 hybrids were grown in 7 trial locations (Clermont-Ferrand, Dijon, La Jaillière, Le Pin-au-Haras, Lusignan, Rennes and Toulouse) where it was possible to measure *in vivo* digestibility on sheep (table II). As the variability due to environmental conditions (location, year) had been found (Andrieu, 1976) to be as or if not more important than that between genotypes, several hybrids (numbers 1, 2, 4, 5 and 10) were studied over 2 yr in several locations. Overall, 48 maize crops were studied.

The general conditions of the experimental design over the 2 yr are given in table III. It may be noted that sowing was deliberately late (June 5–6th) in Rennes in order to reproduce the case of maize crops sown in Brittany after Italian ryegrass silage crops.

Sowing conditions were good except at Le Pin-au-Haras, where, because of problems with a drill, plant populations were lower than elsewhere and also more irregular. Fertilization was according to soil agronomic characteristics and thus varied between locations (table III). It in-

Table I. Hybrids studied.

French catalogue	
Very early	Alsa
	Anjou 09
	Keo DK 182
Early	Artus
	Gracia
	Lixis LG 22.21
Half-early	Anjou 29
	Arcade
	Dea
	Mammoth
	Monarque 282
Half-late	Eva
Late	Ogalo
	Sabrina
European catalogue	
INRA Lusignan	Bastion
	HTV bm3

cluded some organic manure (liquid or solid manure) at Le Pin, Rennes, and la Jaillière. Growing conditions (temperature, rainfall) were generally good. 1987 was characterised by a rather cold spring and a particularly hot and dry September and October (table III). In 1988, temperatures were generally lower than in 1987 during the phase of grain maturation in September.

Table II. Hybrid trial locations (coded 1 to 17).

Locations	Hybrids *															
1 INRA Theix	1		3	4						11		13				
2 INRA Rennes		2							10						16	
3 INRA Lusignan	1			4	5	6										17
4 INRA Le Pin-au-Haras	1						7	8							15	
5 INRA-ENSAA Dijon	1	2										12				
6 ITCF La Jaillière	1	2			5				10			13				
7 ENSAT Toulouse						6								14		

* The hybrids codes in bold type indicate that they were studied in only 1 year.

Table III. Main characteristics of trials carried out in 1987 and 1988.

1987	(1) Clermont-Fd	(2) Rennes	(3) Lusignan	(4) Le Pin-au-Haras	(5) Dijon	(6) La Jallière
No of hybrids	5	3	5	4	3	4
Sowing date	4/24	6/5	4/22	4/24	5/7	4/24
Silking date						
Mean	7/21	8/23	7/29	8/3	7/28	7/24
Interval	7/17-7/23	8/21-8/26	7/20-8/12	7/30-8/3	7/25-8/1	7/20-7/29
Harvest dates						
Mean	9/5	10/6	9/15	10/3	9/12	9/12
Interval	8/18-9/22	9/22-10/20	8/25-10/6	9/22-10/13	9/1-9/22	9/1-9/22
DM content at harvest (%)						
R1	20.2	20.7	23.0	31.7	24.9	26.3
R2	22.6	22.4	25.1	32.0	28.2	32.3
R3	25.6	23.0	27.1	34.8	33.2	35.0
R4	27.7	22.5	31.9	36.3	36.4	42.4
R5	33.6	23.0	32.3			
R6	40.9		32.9			
R7			30.0			
Mean	28.4	22.3	28.9	33.7	30.7	34.0
Summed temperatures (base 6°C)						
From sowing to silking	871	877	880	742	735	837
From silking to mean	596	480	607	579	562	623
Harvest date						
Without						
With						
Irrigation	Without	Without	With	Without	With	Without
Fertilization						
Organic		40 m ³ /ha slurry		50 T/ha manure		45 T/ha manure
Mineral (NPK)		80-120-240		160-220-500		115-135-315
Plant population (plants/ha)	102 000	97 000	180-0-0	76 000	160-110-110	87 000
Yields (tonnes DM/ha)	18 to 24	9 to 14	87 000 12 to 21	14 to 17	99 000 15 to 24	

Table III. Continued

1988	(1) Clermont-Fd	(2) Rennes	(3) Lusignan	(4) Le Pin-au-Haras	(5) Dijon	(6) La Jallière
No of hybrids	5	3	5	4	5	2
Sowing date	4/21	6/6	5/10	4/27	5/14	5/31
Silking date						
Mean	7/15	8/20	8/7	7/31	8/6	8/13
Interval	7/12-7/18	8/17-8/24	8/1-8/14	7/28-8/4	8/3-8/10	8/12-8/14
Harvest dates						
Mean	8/30	10/21	7/19	10/1	9/25	9/27
Interval	8/16-9/13	10/10-10/31	8/24-10/11	9/14-10/18	9/7-10/12	9/7-10/18
DM content at harvest (%)						
R1	23.9	21.7	21.4	24.3	23.9	21.2
R2	26.1	23.4	23.9	36.5	28.0	23.3
R3	29.1	26.1	24.5	28.0	30.8	25.3
R4	31.6	28.7	27.3	29.2	33.7	27.8
R5	35.2		30.9	30.8	36.4	30.4
R6			32.5	33.3	33.8	33.1
R7			33.2			38.8
R8			33.2			
Mean	29.2	25.0	28.4	28.7	31.1	28.6
Summed temperatures (base 6°C)						
From sowing to silking	782	841	897	685	870	1044
From silking to mean	646	550	473	529	559	584
Harvest date						
Irrigation	With	Without	With	Without	Without	With
Fertilization						
Organic		30 m ³ /ha slurry		50 T/ha manure	45 T/ha manure	
Mineral (NPK)	195-160-160	145-150-300	180-0-0	150-210-410	95-135-315	170-110-200
Plant population (plants/ha)	97 000	107 000	92 000	80 000	102 000	86 000
Yields (tonnes DM/ha)	13.5 to 22.0	12 to 16	12 to 20	8.2 to 15.0	9.5 to 17.6	15.4 to 21.7

The main crop damage sustained was partial lodging of maize at Rennes in 1988 due to a storm just before the beginning of measurements and rapid drying of the 1987 La Jaillère crop as a result of a drought associated with a *Fusarium* attack.

Measurements on plants

For each hybrid, the date of silking (50% of plants with silks visible on the upper ear) was determined on 2 x 5-m rows. During each period of digestibility measurements (see below), the plants present in 1 or 2 5-m rows were counted, harvested and divided into 2 fractions (whole ear and stems + leaves), then weighed fresh. In order to determine the DM content and the respective proportions in DM of stems + leaves, ear and grain, a subsample of these constituents was oven-dried (48 to 72 h at 80°C). The mean yield/ha estimated from these samples was 15 tonnes DM, with a wide range of variation (7 to 25 tonnes; table III). This was due not only to the stage of grain maturation at sampling and to environmental conditions, but also to the precision of sampling methods and heterogeneity of plant populations (Le Pin-au-Haras). Similarly, the rate of increase in dry weight was very variable, and much lower at Rennes, le Pin-au-Haras and La Jaillère (in 1987) than in the other locations.

Measurements on sheep

The digestibilities of whole plants of each plot were measured on 6 castrated wethers in individual metabolic cages with feed in limited quantity (42 ± 3 g DM/kg $W^{0.75}$ in 2 meals per day) to avoid selection and limit digestive interactions. So that the protein and mineral contents were not limiting factors for maize digestion in the rumen (Andrieu and Demarquilly, 1974), the animals received at the trough a nitrogen (urea) and mineral (major and trace elements) supplement. This supplement was fed in order to provide 15 g urea/kg whole maize plant DM. After a 10-d period of adaptation, the main measurements were carried out continuously for each crop for 4 to 7 periods, from the milky stage to the glazed stage of grain: each period lasted for 6 d (5 d at Lusignan), separated from

the following period by 1 d (2 d at Lusignan). A representative sample of the forage provided (without the urea-mineral supplement) during each period was taken from the 12 sub-samples in order to determine the DM content of each of the 2 daily meals (dried at 80°C for 48 h). A representative sample of the faeces excreted by each sheep was taken from the daily collection of faeces. In spite of the limited diet, some animals refused feed at certain periods, and were eliminated from calculations when their DM digestibility differed by > 5 points from the mean value for the considered period. The number of sheep restrained per period ranged from 3 to 6. All the representative samples of maize fed to the animals and the corresponding faeces were ground in the same mill (Gondart, 1-mm mesh).

Under these experimental conditions, the precision of DM digestibility measurements (SD of error) was 2.34 and 1.89 points respectively before and after elimination of individual results differing by > 5 points from the mean value for each measurement period.

Analytical methods

For the 234 representative samples of maize and the corresponding faeces, the following characters were determined:

- usual chemical composition: ash, crude protein ($N \times 6.25$), Weende crude fibre;
- starch content by the Ewers (1910) method, water soluble carbohydrate (Somogyi, 1952), neutral detergent fibre (NDF), acid detergent fibre (ADF), acid detergent lignin (ADL) contents by method proposed by Van Soest (1967), and adapted by Giger *et al* (1979). The ADL was corrected by the ash content. The hemicellulose (NDF-ADF) and cellulose (ADF-ADL) contents were obtained by subtraction;
- enzymatic solubility by 3 methods (Aufrère and Michelet-Doreau, 1983; Lila *et al*, 1986; Limagrain, 1985). The methodologies are defined in Appendix 1.

In addition, on a more restricted number of samples (those from Clermont-Ferrand and Lusignan), the following additional measurements were made:

- plant starch content, determined by the enzymatic method of Thivend *et al* (1965), in order to make a comparison with the Ewers' method ($n = 53$);

– NDF, ADF and ADL contents of the faeces, in order to determine the digestibility of these constituents ($n = 99$);

– gross energy contents (adiabatic bomb calorimeter) of plants ($n = 59$) and of certain faeces ($n = 37$), in order to calculate relations allowing prediction of gross and digestible energy.

Statistical analysis

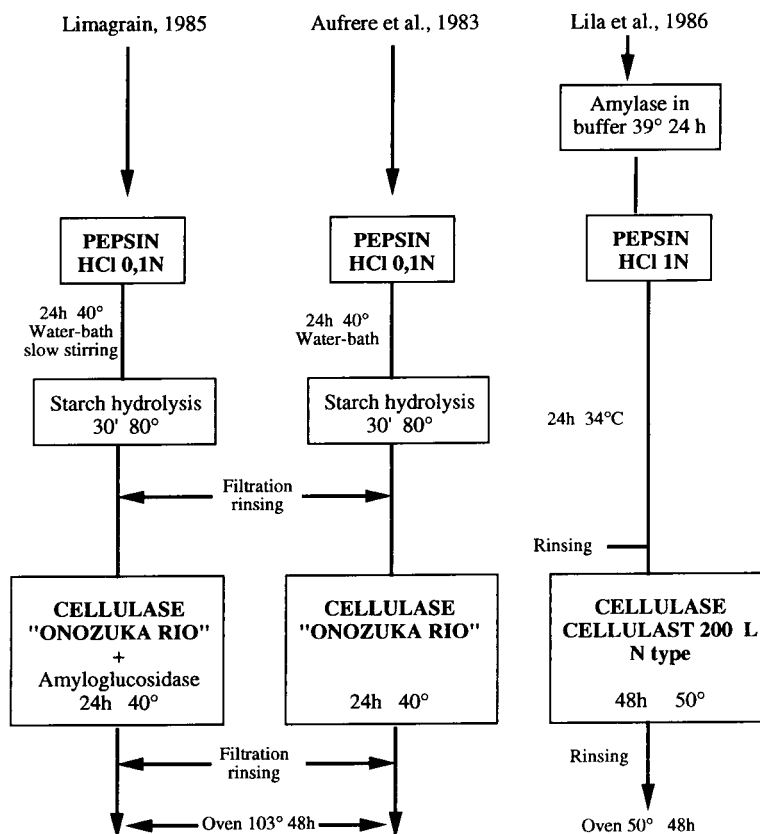
The analysis of variance and covariance (the covariate used was plant DM) were made using

the programme of Seebeck (1973) with calculation of factor x factor or factor x covariate (regression slope) interactions on the following equilibrated factorial plants:

Three-factor analysis

The following hybrids were studied in 2 consecutive yr (1987 and 1988): 1 and 4 at Clermont-Ferrand and Lusignan; 1 and 5 at Lusignan and La Jaillière; 2 and 10 at Rennes and La Jaillière.

Appendix 1. Methodologies for the 3 enzymatic methods used.



Two-factor analysis

The following hybrids were studied in 2 consecutive yr (1987 and 1988): 1, 3, 4, 11, 13 at Clermont-Ferrand; 2, 10, 16 at Rennes; 1, 4, 5, 6, 17 (bm3) at Lusignan; 1, 7, 8, 15 at Le Pin-au-Haras; 1, 2, 5, 10 at La Jaillière; 1 at Theix, Lusignan, Le Pin and La Jaillière.

Single-factor analysis

The following hybrids were studied in 2 consecutive years: 1, 2, 12 at Dijon in 1987; 6, 14 at Toulouse in 1988.

RESULTS

Gross energy contents and digestibility

The average gross energy content was 4660 ± 33 Kcal per kg organic matter (OM) for the 59 samples studied. For a given variety, the gross energy content dropped

slightly with age (expressed as d after silking); it is thus linked to some extent to chemical and morphological composition. The best prediction criteria appear to be DM, protein and lignin contents. Since DM content depends partly on climatic conditions, it is proposed to use, as for other forages (Demarquilly *et al*, 1978), the following relation between gross energy (GE in Kcal/kg OM) and crude protein content (CP in g/kg OM):

$$GE = 4487 + 2.019 CP \pm 25; R = 0.578; N = 59$$

However, this equation overestimates by ≈ 70 Kcal the hybrids carrying the gene bm3 with reduced lignin content. For these hybrids, it is preferable to use an equation also including the lignin content (ADL in g/kg OM):

$$GE = 4548 + 0.37 CP + 3.29 ADL \pm 26; R = 0.621; N = 53$$

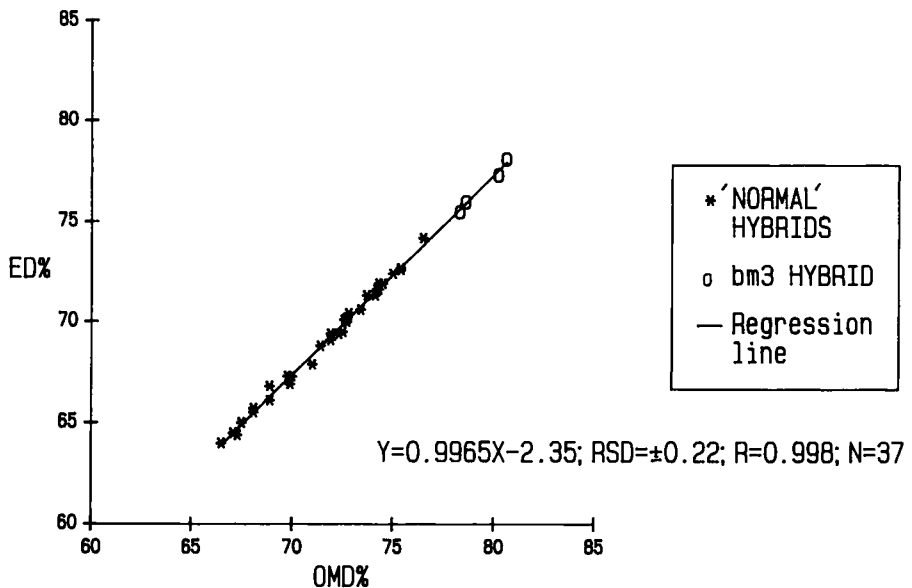


Fig 1. Relationship between energy digestibility (ED) and organic matter digestibility (OMD) of whole-plant maize fed fresh to sheep.

Energy digestibility (*ED* in %) with a mean of $69.9 \pm 3.6\%$ for the 37 measurements made is closely related to organic matter digestibility (*OMD* in %) (fig 1):

$$ED = 0.9965 OMD - 2.35 \pm 0.22;$$

$$R = 0.998; N = 37$$

These results were used to calculate the net energy values (following 1988 INRA standards) of the maize hybrids studied in part II (Dardenne *et al*, 1993).

Influence of growth stage

This study showed, sometimes with improved precision, the general rules concerning change in plant composition according to age. Age, expressed by d after silking, varied from 20 to 83 (with a mean of 49 d). For a given hybrid or for the series of hybrids, DM content increased with age (fig 2), mainly because of the relative increase in grain content ($R = 0.776$; fig 3). The development of grain results from the formation of starch (*STA* in g/kg DM ac-

cording to the Ewers method), from water-soluble carbohydrates (*WSC* in g/kg DM) synthesized after flowering or that were stored earlier (mainly in the stem) so that, as other authors have indicated (Demarquilly, 1969), a close inverse relation exists between these 2 constituents:

$$STA = 450 - 1.7986 WSC \pm 40;$$

$$R = 0.873; N = 234$$

During the same period, the contents of other constituents drop (fig 4) noticeably (crude fibre, *ADF*) or slightly (ash, crude protein, *NDF*, *ADL*). The composition of cell walls (as a percentage of *NDF*) varied little according to stage (fig 5): the hemicellulose content (mean $51.7 \pm 2.9\%$) increased at the expense of the cellulose content (mean $43.3 \pm 2.4\%$), whereas the lignin content (mean $5.1 \pm 0.8\%$) showed a tendency to decrease.

There exists quite close relations between certain morphological and chemical constituents. The following are the most significant (for abbreviations and units, see table IVa):

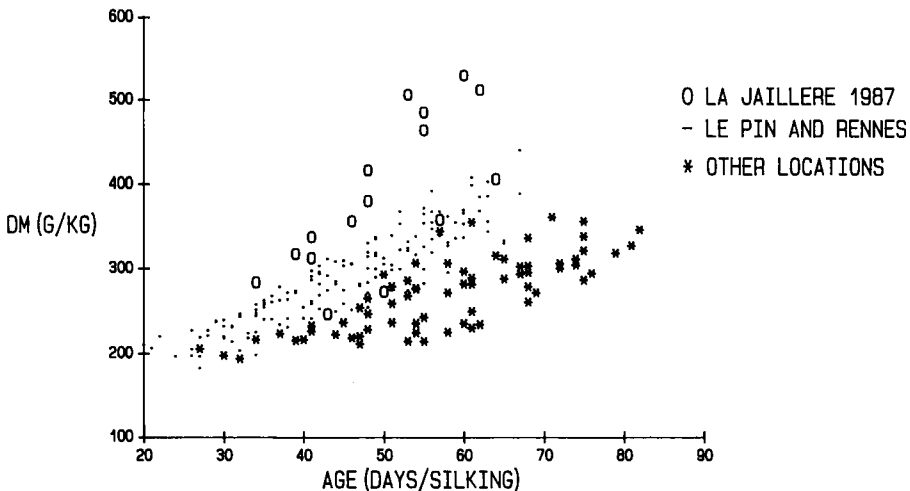


Fig 2. Relationship between DM content of maize plant and its age.

$$GRA = 754 - 0.008823 CF^2 \pm 73;$$

$$R = 0.761; N = 234 \text{ (fig 6)}$$

$$GRA = 26.5 + 1.7159 STA - 0.00098 STA^2$$

$$\pm 40; R = 0.935; N = 234 \text{ (fig 6)}$$

$$STA = 838 - 2.8921 CF \pm 47; R = 0.816;$$

$$N = 234$$

$$STA = 862 - 2.7365 ADF \pm 43;$$

$$R = 0.847; N = 234$$

$$ADF = 10.7 + 1.0480 CF \pm 7.4;$$

$$R = 0.957; N = 234$$

More generally, the ratio of total cytoplasmic carbohydrates (starch + soluble carbohydrates) and cell walls (*NDF*) increases from 0.4 to 0.9 during grain development.

For the 53 comparisons, the starch content measured by the methods of Thivend *et al* (1965) (*Y* in g/kg DM) was, on average, 14.7 g higher than that obtained with Ewers' method. As the following equation shows, the difference between the 2 methods is reduced when the starch content is high, that is, at later harvest dates:

$$Y = 37.05 + 0.9131 X \pm 14.4; R = 0.987;$$

$$N = 53$$

In general, age is a poor predictor of plant composition since the latter depends mainly on grain development and thus on temperature. For a given age, the sums of temperatures after flowering (base 6°C) varied significantly between locations. This is the reason why DM content and sum of temperatures which are quite closely correlated in normal growing conditions provide a better prediction of plant composition. Of the 2 growth stage criteria, neither of which is entirely satisfactory, DM content appears preferable due to its nutritional significance and to its frequent use in publications on this subject.

Influence of other factors

For a given location and a given DM content, there are significant year and genotype effects on chemical composition (*Appendix 2, 3*).

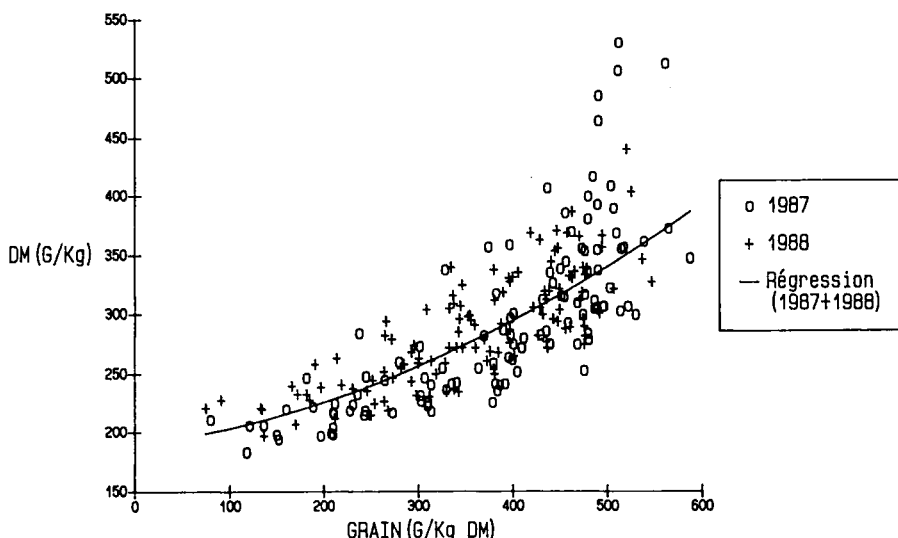


Fig 3. Relationship between DM and grain content of maize plant.

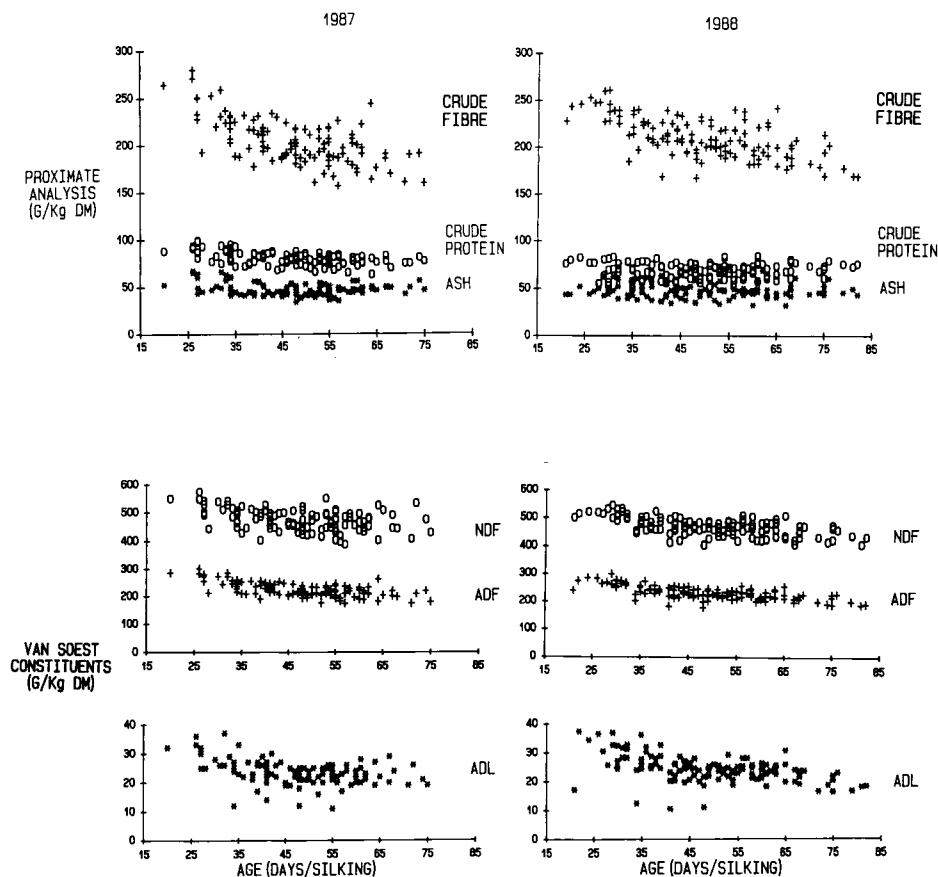


Fig 4. Relationship between chemical composition of maize plant and its age during 2 yr.

However, the appearance, in most locations, of interactions between year and hybrid (eg at Lusignan) or between year and DM content (Rennes and La Jaillière) makes it difficult to analyse these effects. Of the chemical composition parameters, protein content is the most affected by year; it was always lower in 1988 (mean of 69 g) than in 1987 (mean 80 g) except at Rennes, where greater fertilisation in 1988 may have masked the effect (table III).

Genotypic effects, when significant, mainly concern crude protein and cell-wall contents, but have very little effect on WSC. These effects were particularly noticeable at Clermont-Ferrand, where, in the absence of any significant interactions, it was possible to distinguish hybrid 13 from hybrid 3 (table V) by its higher grain and starch contents and lower cell-wall contents (crude fibre and ADL). If in order to analyse effects at the usual stage for si-

Table IV. Composition and nutritive value of maize hybrids studied: means, range of variation, coefficient of variation (CV) observed for the 234 samples and the bm3 hybrid.

A. The 234 samples (N = 234)	Abbreviation	Means	Variation range	CV (%)
1 Age at harvest (d after silking)	AGE	49	20–82	27
2 Summed temperatures at harvest ^a	ST6	558	270–913	23
Morphological composition (g/kg DM)				
3 Grain	GRA	370	75–590	31
4 Ear (with husks)	EAR	510	270–680	19
Chemical composition ^b				
5 Dry matter	DM	291	183–531	21
6 Ash	ASH	48	33–80	17
7 Crude protein	CP	74	50–99	12
8 Crude fibre	CF	208	157–280	11
9 NDF	NDF	473	389–575	7
10 ADF	ADF	229	174–302	11
11 ADL	ADL	24	11–37	21
12 Starch	STA	236	29–404	34
13 Water-soluble carbohydrates	WSC	119	36–226	34
Enzymatic solubility (% DM)				
14 Aufrère method	AUF	71.0	61.2–83.1	4
15 Limagrain method	LGS	78.8	70.3–88.7	4
16 Lila method	APC	79.6	70.6–90.3	4
In vivo digestibility (%)				
17 Organic matter	OMD	71.9	66.5–80.6	4
18 Crude fibre	CFD	56.7	41.9–76.3	10
<hr/>				
B. The bm3 hybrid (N = 8)				
1 Age at harvest (d after silking)	AGE	40	21–55	26
2 Summed temperatures at harvest ^a	ST6	492	270–706	27
Morphological composition (g/kg DM)				
3 Grain	GRA	348	170–490	27
4 Ear (with husks)	EAR	515	374–604	15
Chemical composition ^b				
5 Dry matter	DM	279	207–355	18
6 Ash	ASH	44	35–52	13
7 Crude protein	CP	80	73–86	6
8 Crude fibre	CF	190	168–228	11
9 NDF	NDF	449	406–501	7
10 ADF	ADF	204	179–239	10
11 ADL	ADL	13	10–17	17
12 Starch	STA	206	35–301	40
13 Water-soluble carbohydrates	WSC	148	121–170	12
Enzymatic solubility (% DM)				
14 Aufrère method	AUF	79.7	77.6–83.1	3
15 Limgrain method	LGS	87.7	85.5–88.7	1
16 Lila method	APC	88.6	86.4–90.3	2
In vivo digestibility (%)				
17 Organic matter	OMD	78.5	75.1–80.6	4
18 Crude fibre	CFD	70.0	64.0–76.3	6

^a Calculated from silking with a base temperature of 6 °C; ^b in g/kg DM except for DM content (g/gross kg).

Table V. Increase or decrease in chemical composition and nutritive value of maizes grown at Clermont-Ferrand, due to the effect of year and hybrid at the same DM content.

Year effects ³	Contents (g/kg DM)				In vivo digestibility (points)			Contents (g/kg DM)		Solubility (points)		
	GRA ¹	STA	WSC	CF	ADL	OM	CF	NDF	UNDF ²	AUF	LGS	APC
1987	+22 ^a	+26 ^a	-16 ^b	NS	-0.8 ^b	+1.4 ^a	+1.9 ^a	+1.9 ^a	-11 ^b	+0.6 ^a	+0.4 ^a	NS
1988	-22 ^b	-26 ^b	+16 ^a	NS	+0.8 ^a	-1.4 ^b	-1.9 ^b	-1.9 ^b	+11 ^a	-0.6 ^b	-0.4 ^b	NS
<i>Hybrid effect³</i>												
1	+30 ^a	+15 ^a	-4 ^b	-7 ^b	+0.2 ^{ab}	-0.8 ^{bc}	-2.9 ^{bc}	-2.5 ^b	+5 ^a	+0.1 ^b	+0.4 ^{ab}	+1.8 ^a
3	-19 ^{bc}	-23 ^b	+7 ^a	+13 ^a	+2.3 ^a	-1.5 ^c	-0.9 ^b	-1.2 ^b	+12 ^a	-2.1 ^c	-2.0 ^b	-2.2 ^c
4	-30 ^c	-22 ^b	+5 ^a	+2 ^{ab}	+1.2 ^a	0.0 ^b	+0.7 ^b	-0.3 ^b	+3 ^a	-0.2 ^b	+0.3 ^{ab}	+0.1 ^b
11	+7 ^{ab}	+19 ^a	-2 ^{ab}	-6 ^b	-1.8 ^b	-0.8 ^{bc}	-3.4 ^{bc}	-1.1 ^b	+7 ^a	+0.6 ^{ab}	+0.2 ^{ab}	-0.2 ^b
13	+12 ^a	+11 ^a	-5 ^b	-2 ^b	-1.9 ^b	+3.2 ^a	+6.6 ^a	+5.2 ^a	-27 ^b	+1.6 ^a	+1.2 ^a	+0.5 ^{ab}

¹ For abbreviations see table IV; ² undigested NDF content (g/kg DM); ³ values with different letters are significantly different ($P = 0.05$).

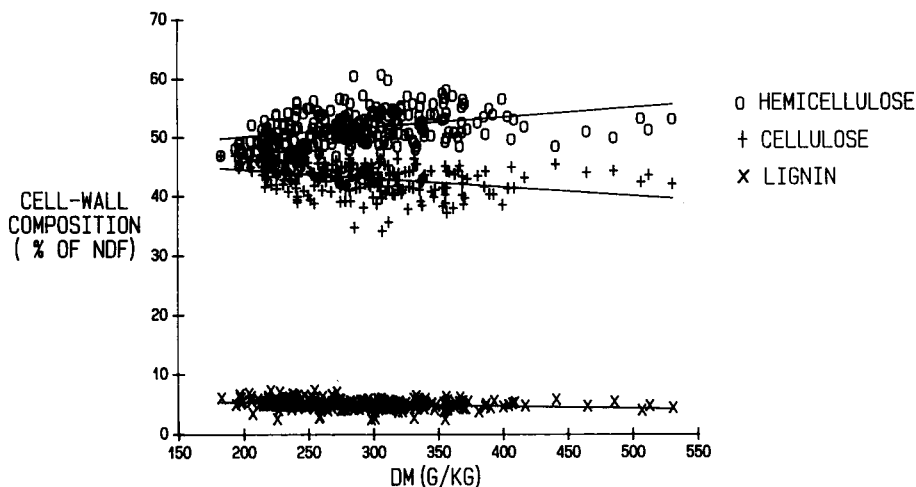


Fig 5. Relationship between cell-wall composition and DM content of maize plant after silking.

lage production, only the samples with a DM content > 27.5% are taken into account, the growth stage \times genotype interactions remain significant.

Analyses of location effects were limited by the experimental design (*Appendix 3, 4*). Overall, this factor appears as important as year and genotype. Ash content is one of the constituents most affected by trial location.

In vivo digestibility

Mean organic matter digestibility (OMD) was 71.9%, varying from 67 to 81%. Discounting results obtained with the hybrid bm3, the mean value (71.7%) and the range of variation (67 to 78%) were comparable with earlier results (Demarquilly and Andrieu, 1973).

Generally, digestibility showed little variation according to growth stage at harvest, in particular measured by DM content ($R =$

$+ 0.182^{**}$ [significant at $P = 0.01$; $N = 234$): from a mean of 70.8% at 20% DM, there was an increase to a maximum of 72.5% at 36% DM and thereafter a slow reduction. This variation with stage was, however, different according to location (*Appendix 3, fig 7*): it was considerable and significant at Clermont-Ferrand, Lusignan, Dijon and Toulouse, and negligible at Rennes, Le Pin and La Jaillière.

For all locations at a given DM content there was a significant year effect (*Appendix 2*): in 1987 digestibility was higher than in 1988, in all sites except Rennes, where the opposite trend was observed. In the latter site, for a DM content of 23%, digestibility of the 3 hybrids studied was lower in 1987 than in 1988 by 4 points. The size of the difference between years varied with stage at harvest (interaction) in 4 locations (Clermont-Ferrand, Rennes, Le Pin and La Jaillière).

Genotypic effects were significant ($P < 0.01$) only in 2 locations: Clermont-Ferrand and Lusignan (*Appendix 2*). Since year \times

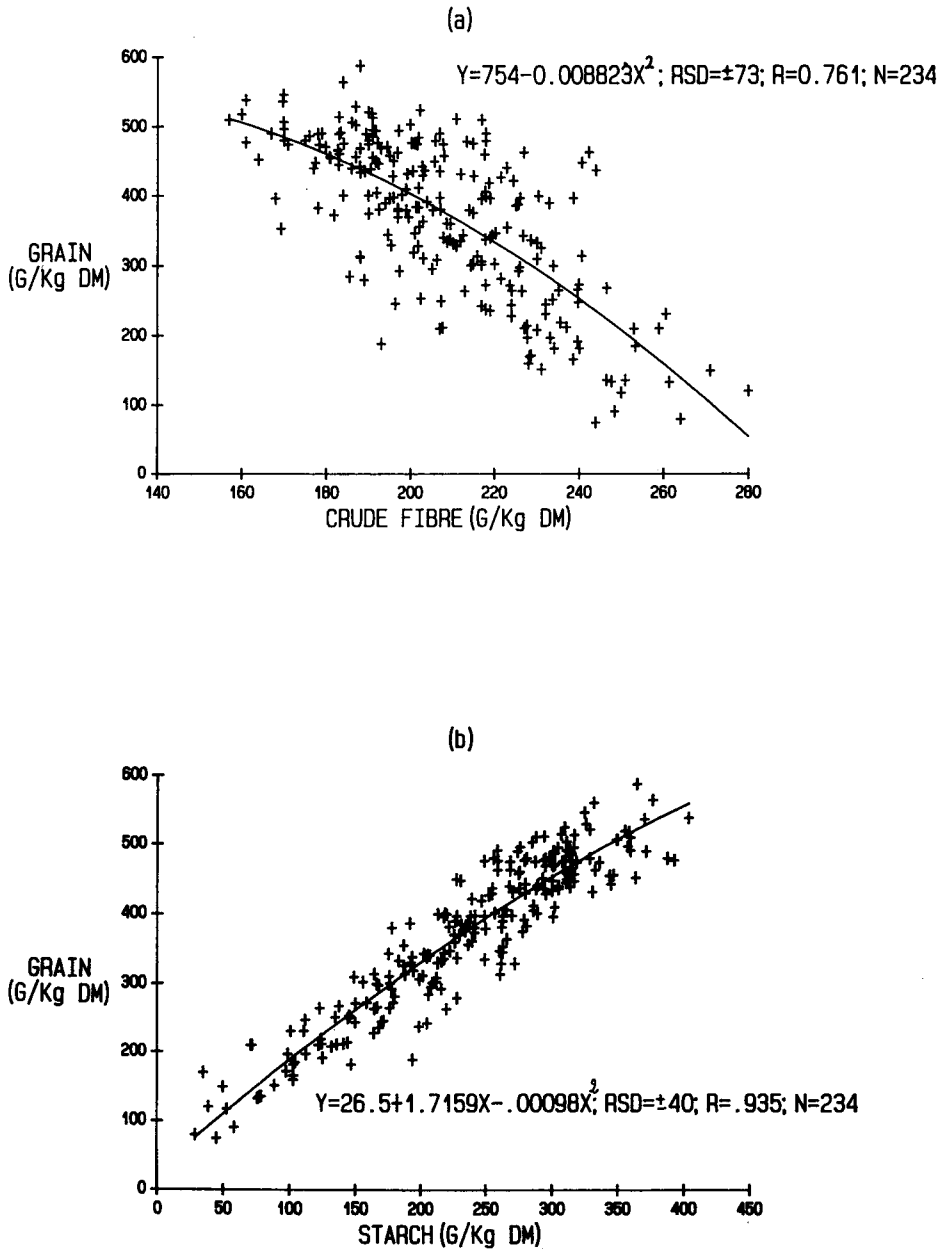


Fig 6. Relationship between grain content of maize plant and its crude fibre (a) or starch content (b).

hybrid interactions were not significant at Clermont-Ferrand, mean effects independent of stage and year appeared: hybrid 13 was much more digestible (+ 4.7 points) than hybrid 3 (table V). However, it should be noted that compared with 4 other hybrids at La Jaillière in 1988, hybrid 13 was not distinguished by its digestibility. There were also significant genotypic effects at Lusignan, but the year \times hybrid interactions made it impossible to determine mean effects, when either all samples or only those with $> 27.5\%$ DM were considered. In contrast, for a given year, in particular 1988, the hybrid bm3 was much more digestible (+ 5 points) than the other genotypes.

The other more incomplete comparisons permitted by the experimental plan

indicate that location effects are comparable with year effects and more important than those due to genotype (*Appendix 2, 3*).

Since urea was fed, the digestibility of proteins will not be considered. The digestibility of crude fibre was rather low (a mean of 56.7%) and varied between wide limits (42 to 76%). Both overall and for single hybrids, it varied independently of stage at harvest (*Appendix 2*). In contrast, for single locations, it was sometimes related to genotype (Clermont-Ferrand, Lusignan in 1988). From the more complete measurements of digestibility carried out at Clermont-Ferrand and at Lusignan (table VI), the following regressions were calculated between *NDF* or *ADF* digestibilities (*NDFD* or *ADFD* in percent) and crude fibre (*CFD* in percent):

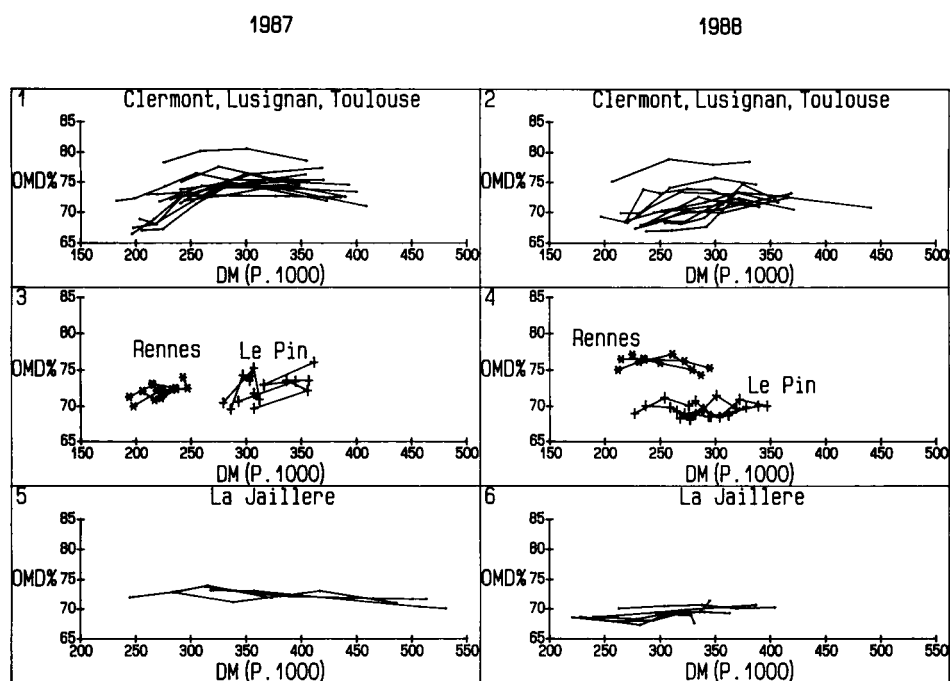


Fig 7. Relationship according to years and locations between *OMD* of maize plant and its *DM* content.

Table VI. Main constituents of DM in maize: contents and *in vivo* digestibility (crops from Clermont-Ferrand and Lusignan).

Parameters	Normal hybrids (N = 91)		Experimental bm3 hybrids (N = 8)	
	Mean	CV % ^b	Mean	CV % ^b
Contents (g/kg DM)				
S ^a	527	7.2	551	5.7
NDF	473	8.0	449	7.0
NDF-ADF	242	7.5	245	4.8
ADF	231	11.9	204	9.7
ADF-ADL	206	11.6	192	9.7
ADL	25	17.2	13	17.4
<i>In vivo</i> digestibility (%)				
OM	71.9	3.6	78.5	2.1
S	80.5	2.5	81.4	2.4
NDF	56.6	7.1	69.0	4.1
NDF-ADF	61.0	7.1	71.2	4.4
ADF	51.7	9.7	66.5	4.1
ADF-ADL	57.1	8.6	70.1	4.0

^a S = 1 000 - NDF; ^b coefficient of variation.

$$NDFD = 14.30 + 0.7643 \text{ CFD} \pm 2.1;$$

$$R = 0.920; N = 99$$

$$ADFD = -2.02 + 0.9693 \text{ CFD} \pm 1.7;$$

$$R = 0.964; N = 99$$

Relations between digestibility of the whole plant and of its principal constituents

The relations were studied using the measurements mentioned above.

The cell content (proteins, soluble carbohydrates, starch, lipids) that is considered as the fraction of dry matter soluble in neutral detergent (S = 1 000 - NDF in g/kg

DM) have a high apparent digestibility (*SD* in percent = 81 ± 2), which increases linearly with *S* content:

$$SD = 55.2 + 0.04778 \text{ S} \pm 1.0; R = 0.882;$$

$$N = 99$$

As in the case of crude protein, there is thus a close relation between the digestible "S" content (*SD* in g/kg DM) and the plant "S" content:

$$DS = 1.0535 \text{ S} - 131 \pm 5; R = 0.992;$$

$$N = 99$$

This regression shows that the true digestibility of the soluble fraction is almost 100% but that the apparent digestion is rather

less, due to faecal excretion of 131 g/kg DM intake of soluble constituents of microbial and endogenous (metabolic) origin.

The fact that the cell content has an almost complete true digestibility and that metabolic faecal excretion is almost constant explains why the quantity of undigested OM excreted per kg DM intake and thus the OMD, depends largely on the undigested cell-wall content (UNDF in g/kg DM):

$$\text{OMD} = 92.94 - 0.1028 \text{ UNDF} \pm 0.66;$$

$$R = 0.981; N = 99; \text{fig 8}$$

As a result, methods of prediction only give a correct idea of *in vivo* OMD if they take into account variations in undigested cell wall contents.

The equations relating *in vivo* OMD with chemical composition or enzymatic solubility will not be given here (see Dardenne *et al*, 1993). However, it appeared of interest to use the limited but complete data to compare correlations between digestibility (*in vivo* or enzymatic) and the main explanatory or predictive variables (fig 9). For the reasons mentioned above, the cor-

relations between *in vivo* OMD with grain contents and cytoplasmic constituent contents considered separately (proteins, starch) are weaker than those between the same OMD and the different cell-wall constituents (in particular lignin) or the *in vivo* digestibility of cell-wall constituents (in particular NDFD). For chemical methods, the best correlation ($R = 0.804$; $N = 99$) is obtained by associating, in the same equation, total cell-wall content (NDF) and the degree of lignification (ADL/NDF). This correlation is, however, lower than that involving the undigested cell wall content ($R = 0.981$) for 2 reasons: first, because the digestibility of total cell walls, which was $58\% \pm 5$ on average, is independent of their content in the plant and, more especially, because the correlation between total cell wall digestibility and their degree of lignification is much weaker ($R = 0.391$ or 0.681 , according to whether the hybrids carrying the gene *bm3* are eliminated or not – table VII) than that generally observed with forage crops (Van Soest, 1967).

Similarly, enzymatic solubility, by whatever method used, provides a poor reflection of *in vivo* OMD (see Appendix 2 and 3;

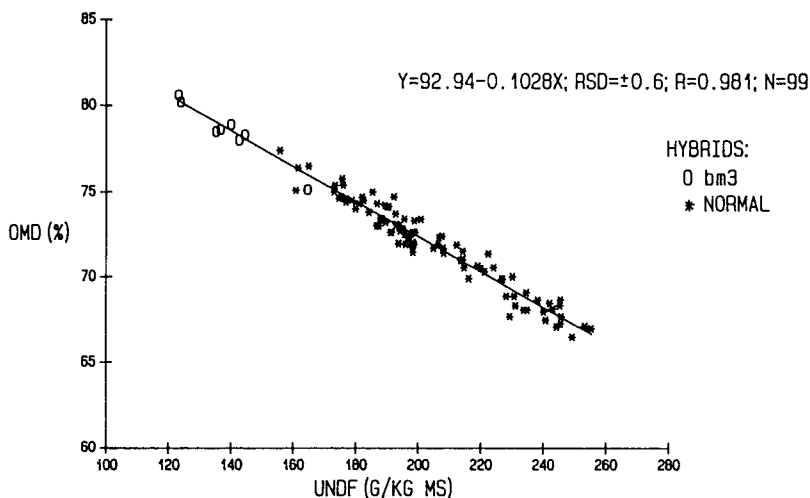
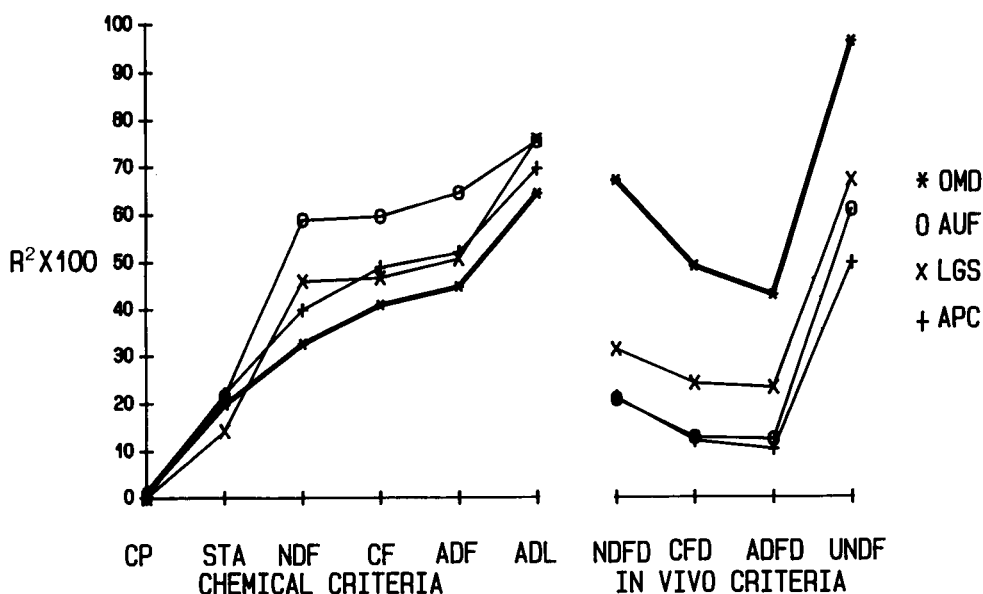


Fig 8. Relationship between OMD of maize plant and its undigested cell-wall content (UNDF).

Table VII. Correlation coefficients between apparent digestibility of the main plant constituents and the extent of cell wall lignification.

Y	X	ADL/NDF			ADL/ADF			Log ADL/ADF		
		Maize *		Other plants**	Maize		Other plants	Maize		Other plants
		-bm3	+bm3		-bm3	+bm3		-bm3	+bm3	
Apparent digestibility										
S ****		0.34 ^b ***	0.32 ^b	NS	0.20 ^a	0.23 ^a	NS	NS	NS	NS
NDF		0.39 ^b	0.68 ^b	0.90 ^b	0.34 ^b	0.68 ^b	0.95 ^b	0.35 ^b	0.69 ^b	0.98 ^b
NDF-ADF		0.56 ^b	0.71 ^b	0.87 ^b	0.32 ^b	0.60 ^b	0.93 ^b	0.32 ^b	0.60 ^b	0.96 ^b
ADF		NS	0.51 ^b	0.86 ^b	0.25 ^a	0.63 ^b	0.93 ^b	0.26 ^a	0.65 ^b	0.95 ^b
CF		NS	0.56 ^b	0.83 ^b	0.31 ^b	0.65 ^b	0.91 ^b	0.32 ^b	0.67 ^b	0.93 ^b
ADF-ADL		NS	0.54 ^b	0.87 ^b	0.28 ^b	0.62 ^b	0.93 ^b	0.29 ^b	0.63 ^b	0.96 ^b

* Without or with the bm3 maize hybrid; ** Van Soest, 1967; *** a significant $P = 0.05$, ^b significant $P = 0.01$; NS: non significant; **** S = cell content.

**Fig 9.** Correlations (R squared $\times 100$) between OMD or enzymatic solubilities and chemical composition, digestibility of NDF, CF, ADF (NDFD, CFD, ADFD) or undigested NDF content (UNDF).

and Barrière *et al*, 1991; Dardenne *et al*, 1993). This results mainly from the fact that it is more closely correlated with cell wall contents (R between 0.63 and 0.77, according to method) than with their digestibility (R between 0.46 and 0.56).

DISCUSSION

After flowering, the digestibility of a maize plant may increase, decrease or remain constant, according to growing conditions (Struik, 1983). When the latter are favorable (water and temperature not limiting factors), the rapid and considerable development of grain results, as at Clermont-Ferrand, Lusignan and Toulouse, in a considerable increase in the ratio of cytoplasmic carbohydrates cell wall constituents, and thus of digestibility (fig 10). However, as the results obtained at Clermont-Ferrand in 1987 show, this increase is all the greater when the digestibility is low at

the beginning of grain formation. This change, which had not been observed in earlier studies in comparable conditions (Demarquilly and Andrieu, 1973) had perhaps been covered by greater digestive interactions, due to *ad libitum* feeding without any nitrogen and mineral supplement. In contrast, when grain maturation is slower (as at Rennes, Le Pin and La Jaillière) due to less favorable climatic conditions (insufficient temperature, drought), digestibility does not change according to age, since the ratio of cytoplasmic and cell wall constituents varies to a much smaller extent (fig 10). Even if some starch accumulates in the grain, this accumulation is much slower and is based on transformation of carbohydrates synthesized before flowering and stored in the stem bases. In still more extreme conditions, particularly when photosynthesis stops due to destruction of leaves by an early frost (Andrieu, 1976), the digestibility of the plant decreases with age.

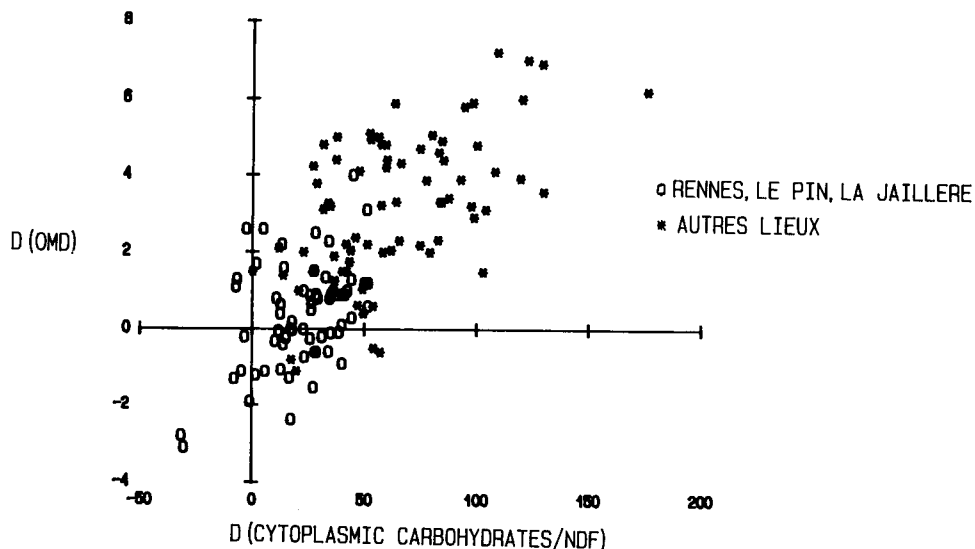


Fig 10. Relationship between increase in organic matter digestibility ($D(OMD)$ in points) and relative increase in % of cytoplasmic carbohydrate/NDF ratio (the first crop of each maize variety is considered as base).

However, climatic conditions after flowering do not provide a complete explanation of differences in digestibility observed at silage-making for maize genotypes grown in different environments (location, year). As shown by Struik (1983), the effect of climatic factors may induce large differences in digestibility at flowering, differences which remain, more or less, until harvest, according to later growing conditions. As indicated by the large differences in digestibility observed between years for crops when little change occurred after flowering (Rennes), the year factor may induce, at flowering, large differences in the undigestible cell wall content of the plant. However, it should be noted, without any evident explanation, that the year effect was not in the same direction at Rennes as in the other locations. The relation (cause or effect) with the lodging observed at Rennes in 1988 has not been clearly established.

Of climatic factors, temperature is certainly one of the most important since it affects the content of cell walls and its digestibility (Dirven and Deinum, 1977) and grain development (Ragland *et al.*, 1965). Temperature can have a very variable effect according to plant physiological stage and to the duration of particular temperature levels. However, according to Struik *et al.* (1985) the depressive effect of high temperatures on digestibility is of particular importance during the growth phase from 7 to 8 leaves to grain filling.

By not taking into account the hybrid bm3, the digestibility of the commercial hybrids was very similar to that observed 20 yr earlier for different hybrids. For single locations and years, there are significant differences in digestibility between hybrids, but these result from differences in undigested cell wall contents which may not be found the following year in the same location or the same year in a different loca-

tion. This is due to the fact that demonstration of a genotype effect was not the main objective of the experimental design. In addition, the differences, when they exist, are small in relation to the precision of measurements, which is poorer for maize than for other forage crops (Deinum, 1984). For enzymatic solubilities, the significant differences that appear between hybrids are not necessarily found *in vivo* (Appendix 2, 3). Their use in breeding work thus needs confirmation by measurements on animals.

The present results confirm that maize (Dirven et Deinum, 1977) and other forage crops (Jarrige and Minson, 1964; Van Soest and Moore, 1965) show a number of common characteristics, in particular the complete true digestion of cell content, and the close correlation which results from this between OM digestibility and undigested cell-wall content. However, the present results indicate that in other aspects, maize and other forage crops are considerably different at the growth stages where they are usually harvested for conservation. In particular, maize cell walls, which constitute a smaller part of plant DM have a composition which is not only different (lower cellulose content, higher mean hemicellulose/cellulose ratio), but also less variable with age. Their degree of lignification remains almost constant due to the effect of grain dilution. In addition, the digestibility of maize cell walls is, in contrast with that of other forage crops, almost independent of their content in the plant, and, more especially much less related to their degree of lignification (table VII). Such a result explains why enzymatic methods, which depend largely on cell-wall content, are much less satisfactory for maize than for other forage species. Finally, and more particularly, the digestibility of maize cell walls is, for a given lignification (*ADL/ADF* ratio) much less (by a mean of at least 10 points) than that of other species (fig 11). This results mainly from the fact that cellulose di-

gestibility is on average 4 points lower than that of hemicellulose. Several hypotheses have been put forward to explain the lower digestibility of maize cell walls, in particular the possible negative influence of high contents in cytoplasmic carbohydrates on the cellulolytic activity of the rumen liquid. However, the fact that *ADL* contains only part of the lignin may also be important: according to Engels and Cones (1989), *ADL* may be constituted by core lignin and certain authors (Buritt *et al*, 1974; Jung and Fahey, 1984) have shown that other less elaborated forms (non-core lignin) may reduce cell-wall digestibility.

CONCLUSION

During the vegetation phase considered in this study, the differences in digestibility between maize crops are relatively low and often of the same magnitude of accuracy as the *in vivo* measurement method.

In fact, it is difficult to identify the sources of variation, for example the influence of the hybrid. In the context of the present study, similar conclusions were obtained as those found 15 yr ago with different vegetative material, for the hybrid effect is seldom significant for a given location. If so, it is of the same magnitude as those of location and year of the hybrid given.

This study illustrates the importance of cell walls and especially their digestibility, which is indicative of the digestibility of the whole plant.

A study on the factors that determine the variability in *in vivo* digestibility of the plant cell wall at the silage stage is of interest, but is a complex undertaking. Measurements of digestibility have to be carried out with taking into account the interactions between digestibility of cell walls and cell contents (soluble sugars and starch); and an applicable *in vitro* method to measure this digestibility is also required.

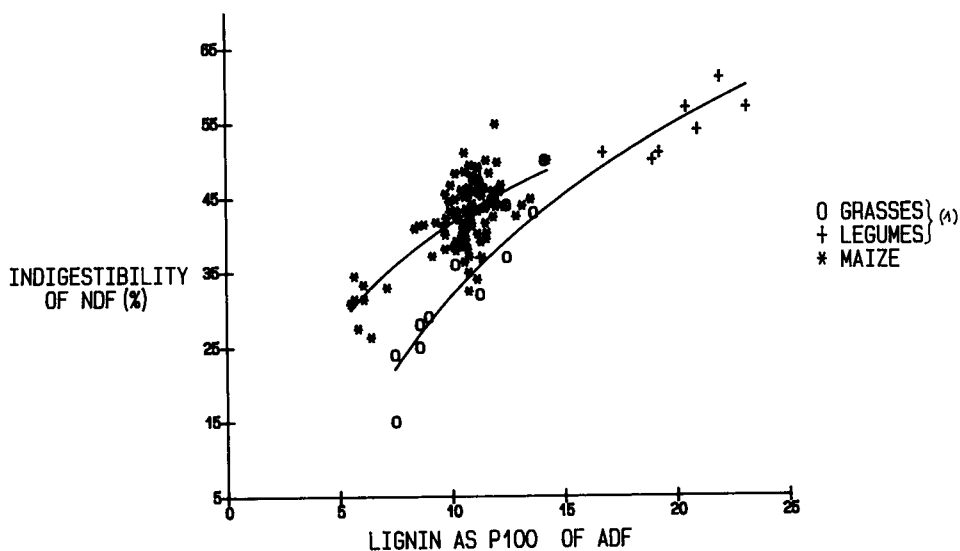


Fig 11. Relationship between indigestibility (fecal *NDF*: % forage intake *NDF*) and lignin concentration in *ADF*.

Appendix 2a. Effect (F values) of year (Y), hybrid (H), and dry matter content (DM) on chemical composition and nutritive value of maize grown at Clermond-Ferrand.

Variates *	Factorials		Interactions			Covariates	
	Y	H	Y x H	Y x DM	H x DM	DM	DM ²
ASH	NS	2.7 ^a	NS	NS	NS	125.2 ^b	NS
CP	216.3 ^b	NS	NS	37.7 ^b	NS	9.6 ^b	NS
GRA	19.1 ^b	9.6 ^b	NS	NS	NS	60.2 ^b	38.2 ^b
STA	47.1 ^b	8.0 ^b	NS	NS	NS	79.1 ^b	53.7 ^b
WSC	89.8 ^b	2.9 ^a	NS	NS	NS	43.2 ^b	26.3 ^b
NDF	NS	NS	NS	NS	NS	54.6 ^b	NS
ADF	9.8 ^b	3.4 ^a	NS	NS	NS	83.3 ^b	NS
CF	NS	3.7 ^a	NS	NS	NS	74.4 ^b	NS
ADL	5.7 ^a	5.4 ^b	NS	NS	NS	64.1 ^b	NS
Solubility							
AUF	10.3 ^b	11.1 ^b	NS	NS	NS	26.2 ^b	19.5 ^b
LGS	6.6 ^a	11.2 ^b	NS	NS	NS	21.1 ^b	16.3 ^b
APC	NS	6.9 ^b	NS	NS	NS	8.6 ^b	5.6 ^a
Digestibility							
OM	51.3 ^b	20.7 ^b	NS	NS	NS	37.3 ^b	29.6 ^b
CF	18.1 ^b	16.4 ^b	NS	NS	NS	NS	NS

* For abbreviations see table IV. NS: non significant; ^a significant at $P = 0.05$; ^b significant at $P = 0.01$.

Appendix 2b. Effect (F values) of year (Y), hybrid (H), and dry matter content (DM) on chemical composition and nutritive value of maize grown at Rennes.

Variates *	Factorials		Interactions			Covariates	
	Y	H	Y x H	Y x DM	H x DM	DM	DM ²
ASH	108.2 ^b	NS	NS	NS	NS	11.7 ^b	NS
CP	NS	11.5 ^b	NS	NS	NS	NS	NS
GRA	NS	5.1 ^a	NS	9.6 ^b	NS	58.7 ^b	NS
STA	NS	NS	NS	11.0 ^b	NS	52.7 ^b	NS
WSC	NS	NS	NS	NS	NS	21.9 ^b	NS
NDF	9.7 ^b	6.7 ^b	NS	12.0 ^b	NS	20.3 ^b	NS
ADF	NS	NS	NS	11.8 ^b	NS	37.5 ^b	NS
CF	6.4 ^a	NS	NS	8.6 ^b	NS	11.3 ^b	NS
ADL	NS	NS	NS	6.1 ^b	NS	19.1 ^b	NS
Solubility							
AUF	9.4 ^b	NS	NS	NS	NS	8.1 ^a	7.0 ^a
LGS	22.5 ^b	8.5 ^b	NS	NS	NS	9.4 ^b	7.9 ^a
APC	21.0 ^b	NS	NS	NS	NS	7.1 ^a	NS
Digestibility							
OM	88.6 ^b	NS	NS	11.1 ^b	NS	NS	NS
CF	43.7 ^b	NS	NS	NS	NS	NS	NS

* For abbreviations, see table IV. NS: non significant; ^a significant at $P = 0.05$; ^b significant at $P = 0.01$.

Appendix 2c. Effect (F values) of year (Y), hybrid (H) and dry matter content (DM) on chemical composition and nutritive value of maize grown at Lusignan.

Variates *	Factorials		Interactions			Covariates	
	Y	H	Y x H	Y x DM	H x DM	DM	DM ²
ASH	22.9 ^b	10.0 ^b	5.1 ^b	NS	NS	60.6 ^b	NS
CP	126.4 ^b	23.0 ^b	7.1 ^b	NS	NS	34.0 ^b	NS
GRA	65.0 ^b	NS	5.6 ^b	NS	4.5 ^b	97.6 ^b	63.4 ^b
STA	32.9 ^b	NS	3.6 ^a	NS	NS	36.4 ^b	24.2 ^b
WSC	8.9 ^b	NS	NS	7.0 ^b	4.4 ^b	84.5 ^b	NS
NDF	4.9 ^a	3.4 ^a	3.0 ^a	NS	NS	72.9 ^b	NS
ADF	10.1 ^b	8.4 ^b	3.8 ^a	NS	NS	65.3 ^b	NS
CF	12.1 ^b	7.2 ^b	2.9 ^a	NS	NS	51.5 ^b	NS
ADL	13.0 ^b	55.0 ^b	4.9 ^b	NS	NS	49.5 ^b	NS
Solubility							
AUF	NS	65.2 ^b	10.1 ^b	NS	NS	14.6 ^b	11.3 ^b
LGS	23.2 ^b	88.2 ^b	5.1 ^b	NS	NS	18.3 ^b	14.9 ^b
APC	NS	72.5 ^b	NS	NS	NS	9.5 ^b	7.1 ^a
Digestibility							
OM	82.2 ^b	82.5 ^b	3.7 ^a	NS	NS	20.0 ^b	14.4 ^b
CF	24.6 ^b	43.6 ^b	NS	4.8 ^a	NS	NS	NS

* For abbreviations, see table IV. NS: non significant; ^a significant at $P = 0.05$; ^b significant at $P = 0.01$.

Appendix 2d. Effect (F values) of year (Y), hybrid (H), and dry matter content (DM) on chemical composition and nutritive value of maize grown at Le Pin-au-Haras.

Variates *	Factorials		Interactions			Covariates	
	Y	H	Y x H	Y x DM	H x DM	DM	DM ²
ASH	NS	5.0 ^b	NS	NS	3.0 ^a	NS	NS
CP	25.8 ^b	24.9 ^b	3.3 ^a	NS	NS	NS	NS
GRA	NS	NS	NS	4.7 ^a	NS	24.3 ^b	NS
STA	NS	NS	4.6 ^a	NS	NS	19.6 ^b	NS
WSC	24.7 ^b	NS	NS	8.9 ^b	NS	8.3 ^b	NS
NDF	15.4 ^b	NS	NS	NS	NS	7.5 ^b	NS
ADF	NS	NS	5.4 ^b	NS	NS	13.2 ^b	NS
CF	NS	4.9 ^b	9.2 ^b	NS	NS	21.5 ^b	NS
ADL	18.9 ^b	NS	NS	NS	NS	NS	NS
Solubility							
AUF	10.7 ^b	NS	10.5 ^b	NS	NS	NS	NS
LGS	21.5 ^b	4.7 ^b	4.2 ^a	NS	NS	17.8 ^b	NS
APC	17.6 ^b	NS	NS	NS	NS	NS	NS
Digestibility							
OM	14.3 ^b	3.6 ^a	NS	11.8 ^b	NS	19.4 ^b	NS
CF	NS	3.0 ^a	9.5 ^b	9.1 ^b	NS	NS	NS

* For abbreviations see table IV. NS: non significant; ^a significant at $P = 0.05$; ^b significant at $P = 0.01$.

Appendix 2e. Effect (F values) of hybrid (H) and dry matter content (DM) on chemical composition and nutritive value of maize grown at Dijon.

Variates *	H	Interactions		Covariates	
		H x DM	DM	DM ²	
ASH	5.2 ^a	5.9 ^a	16.1 ^b	NS	
CP	15.5 ^b	NS	12.1 ^a	NS	
GRA	8.7 ^a	NS	48.0 ^b	NS	
STA	NS	10.5 ^a	146.7 ^b	NS	
WSC	13.2 ^b	7.6 ^a	200.0 ^b	NS	
NDF	NS	7.2 ^a	73.8 ^b	NS	
ADF	6.7 ^a	15.4 ^b	100.2 ^b	NS	
CF	NS	6.0 ^a	42.5 ^b	NS	
ADL	30.3 ^b	17.4 ^b	76.3 ^b	NS	
Solubility					
AUF	NS	7.0 ^a	12.8 ^a	NS	
LGS	24.6 ^b	17.5 ^b	140.8 ^b	NS	
APC	NS	NS	27.0 ^b	NS	
Digestibility					
OM	NS	NS	13.3 ^b	12.0 ^a	
CF	NS	NS	NS	NS	

* For abbreviations see table IV. NS : non significant;
^a significant at $P = 0.05$; ^b significant at $P = 0.01$.

Appendix 2g. Effect (F values) of hybrid (H) and dry matter content (DM) on chemical composition and nutritive value of maize grown at Toulouse.

Variates *	H	Interactions		Covariates	
		H x DM	DM	DM ²	
ASH	76.1 ^b	NS	33.0 ^b	NS	
CP	NS	18.5 ^b	93.1 ^b	NS	
GRA	8.8 ^a	38.3 ^b	276.9 ^b	188.8 ^b	
STA	NS	8.0 ^a	55.8 ^b	34.3 ^b	
WSC	10.2 ^b	NS	31.9 ^b	NS	
NDF	6.7 ^a	NS	34.7 ^b	NS	
ADF	7.8 ^a	NS	33.8 ^b	NS	
CF	11.3 ^b	NS	43.0 ^b	NS	
ADL	20.3 ^b	NS	40.6 ^b	NS	
Solubility					
AUF	6.9 ^a	NS	18.1 ^b	NS	
LGS	NS	5.7 ^a	38.0 ^b	25.7 ^b	
APC	NS	NS	NS	NS	
Digestibility					
OM	NS	NS	17.4 ^b	15.1 ^b	
CF	6.7 ^a	NS	NS	NS	

* For abbreviations, see table IV. NS: non significant; ^a significant at $P = 0.05$; ^b significant at $P = 0.01$.

Appendix 2f. Effect (F values) of year (Y), hybrid (H) and dry matter content (DM) on chemical composition and nutritive value of maize grown at La Jaillière.

Variates *	Factorials		Interactions			Covariates	
	Y	H	Y x H	Y x DM	H x DM	DM	DM ²
ASH	NS	NS	NS	NS	NS	NS	NS
CP	291.4 ^b	NS	NS	NS	NS	NS	NS
GRA	3.3 ^a	6.2 ^b	NS	36.2 ^b	8.5 ^b	328.4 ^b	NS
STA	5.2 ^a	NS	6.8 ^b	56.4 ^b	10.4 ^b	152.7 ^b	NS
WSC	NS	4.3 ^a	NS	30.8 ^b	5.0 ^b	143.7 ^b	NS
NDF	5.6 ^a	5.6 ^a	NS	7.2 ^b	NS	NS	NS
ADF	6.4 ^a	9.1 ^b	3.4 ^a	12.0 ^b	NS	NS	NS
CF	7.3 ^a	15.0 ^b	3.9 ^a	11.9 ^b	NS	NS	NS
ADL	14.2 ^b	8.9 ^b	4.7 ^a	NS	NS	NS	NS
Solubility							
AUF	NS	20.4 ^b	NS	NS	3.6 ^a	NS	NS
LGS	NS	14.4 ^b	NS	NS	NS	NS	NS
APC	NS	8.2 ^b	NS	6.8 ^b	NS	NS	NS
Digestibility							
OM	94.4 ^b	NS	NS	21.5 ^b	5.4 ^b	NS	NS
CF	13.3 ^b	NS	NS	NS	NS	NS	NS

* For abbreviations see table IV. NS: non significant; ^a significant at $P = 0.05$; ^b significant at $P = 0.01$.

Appendix 3a. Effect (F values) of year (Y), location (L) (Clermont and Lusignan), hybrid (H) (1,4) and dry matter (DM) on chemical composition and nutritive value.

Variates *	Factorials			Interactions						Covariate
	Y	L	H	Y x L	Y x H	L x H	Y x DM	L x DM	H x DM	DM
ASH	NS	176.3 ^b	11.3 ^b	NS	NS	NS	NS	NS	NS	36.3 ^b
CP	77.1 ^b	33.6 ^b	NS ^a	NS	NS	NS	6.7 ^a	NS	NS	14.0 ^b
GRA	4.8 ^a	NS	6.0 ^a	NS	NS	NS	NS	NS	NS	102.0 ^b
STA	10.6 ^b	NS	6.0 ^a	5.8 ^a	NS	NS	NS	NS	NS	82.7 ^b
WSC	30.2 ^b	19.3 ^b	7.1 ^a	NS	NS	NS	NS	NS	NS	112.2 ^b
NDF	5.1 ^a	16.6 ^b	4.2	5.8 ^a	NS	NS	NS	NS	NS	46.9 ^b
ADF	13.7 ^b	5.6 ^a	NS	5.1 ^a	NS	NS	NS	NS	NS	39.9 ^b
CF	7.4 ^a	NS	NS	9.5 ^b	NS	NS	NS	NS	NS	30.7 ^b
ADL	19.2 ^b	5.3 ^a	NS	4.2 ^a	NS	NS	NS	NS	6.2 ^a	44.6 ^b
Solubility										
AUF	NS	30.5 ^b	NS	6.4 ^b	NS	NS	NS	NS	NS	17.4 ^b
LGS	10.7 ^b	37.7 ^b	NS	13.5 ^b	NS	NS	NS	NS	NS	19.5 ^b
APC	NS	NS	10.4 ^b	NS	NS	NS	NS	NS	NS	21.8 ^b
Digestibility										
OM	15.2 ^b	11.2 ^b	NS	NS	NS	4.3 ^a	NS	NS	NS	24.7 ^b
CF	8.6 ^b	10.0 ^b	4.7 ^a	NS	NS	NS	NS	NS	NS	NS

* For abbreviations, see table IV. NS: non significant; ^a significant at $P = 0.05$; ^b significant at $P = 0.01$.

Appendix 3b. Effect (F values) of year (Y), location (L) (Rennes and La Jaillière), hybrid (H) (2,10) and dry matter (DM) on chemical composition and nutritive value.

Variates *	Factorials			Interactions						Covariate
	Y	L	H	Y x L	Y x H	L x H	Y x DM	L x DM	H x DM	DM
ASH	18.2 ^b	NS	NS	16.8 ^b	NS	NS	NS	15.8 ^b	NS	19.7 ^b
CP	66.4 ^b	NS	24.6 ^b	95.7 ^b	NS	NS	8.5 ^b	NS	NS	NS
GRA	NS	19.6 ^b	7.5 ^a	NS	NS	NS	NS	7.8 ^b	6.2 ^a	75.3 ^b
STA	NS	5.9 ^a	NS	4.9 ^a	NS	NS	5.4 ^a	9.3 ^b	4.5 ^a	40.4
WSC	NS	NS	NS	NS	NS	NS	4.6 ^a	NS	NS	30.3 ^b
ADF	NS	NS	5.9 ^a	14.7 ^b	NS	4.2 ^a	5.7 ^a	12.3 ^b	4.5 ^a	14.0 ^b
CF	NS	NS	NS	9.1 ^b	NS	NS	NS	NS	NS	NS
ADL	NS	NS	9.3 ^b	5.5 ^a	NS	6.0 ^a	NS	7.2 ^b	NS	4.4 ^a
Solubility										
AUF	NS	NS	NS	4.2 ^a	NS	4.5 ^a	NS	NS	NS	NS
LGS	26.1 ^b	NS	29.1 ^b	NS	NS	NS	NS	7.2 ^a	NS	5.9 ^a
APC	14.9 ^b	NS	8.0 ^b	11.6 ^b	NS	NS	NS	NS	NS	NS
Digestibility										
OM	NS	11.1 ^b	NS	47.7 ^b	NS	NS	NS	NS	NS	NS
CF	4.9 ^a	NS	NS	11.0 ^b	NS	NS	NS	NS	NS	NS

* For abbreviations, see table IV. NS non significant; ^a significant at $P = 0.05$; ^b significant at $P = 0.01$.

Appendix 3c. Effect (F values) of year (Y), location (L) (Lusignan and La Jaillière), hybrid (H) (1,5) and dry matter (DM) on chemical composition and nutritive value.

Variates *	Factorials			Interactions						Covariate
	Y	L	H	Y x L	Y x H	L x H	Y x DM	L x DM	H x DM	DM
ASH	NS	35.3 ^b	NS	5.1 ^a	NS	NS	NS	9.1 ^b	NS	16.1 ^b
CP	130.3 ^b	12.3 ^b	12.6 ^b	38.2 ^b	NS	NS	NS	NS	NS	8.1 ^b
GRA	8.7 ^b	14.7 ^b	NS	NS	4.5 ^a	6.9 ^a	18.0 ^b	5.1 ^a	7.1 ^a	227.4 ^b
STA	11.0 ^b	10.4 ^b	NS	NS	6.1 ^a	NS	11.3 ^a	8.2 ^b	NS	91.5 ^b
WSC	NS	NS	NS	NS	NS	NS	6.4 ^a	NS	8.3 ^b	45.4 ^b
NDF	6.2 ^a	60.8 ^b	4.9 ^a	NS	NS	NS	NS	23.9 ^b	NS	23.5 ^b
ADF	10.3 ^b	37.1 ^b	NS	NS	7.9 ^b	NS	NS	16.5 ^b	NS	25.0 ^b
CF	10.1 ^b	66.9 ^b	9.4 ^b	NS	NS	NS	NS	19.0 ^b	NS	27.0 ^b
ADL	20.7 ^b	NS	NS	NS	17.9 ^b	NS	4.4 ^a	17.1 ^b	NS	15.4 ^b
Solubility										
AUF	NS	72.2 ^b	NS	5.0 ^a	NS	NS	NS	171.1 ^b	NS	14.4 ^b
LGS	NS	33.9 ^b	NS	5.9 ^a	NS	NS	NS	10.4 ^b	NS	12.7 ^b
APC	NS	7.4 ^a	5.6 ^a	NS	NS	NS	4.7 ^a	7.5 ^a	NS	9.1 ^b
Digestibility										
OM	34.4 ^b	45.5 ^b	15.6 ^b	NS	NS	NS	12.7 ^b	8.1 ^b	NS	22.3 ^b
CF	10.9 ^b	6.4 ^a	NS	NS	NS	NS	NS	NS	NS	NS

* For abbreviations, see table IV. NS: non significant; ^a significant at $P = 0.05$; ^b significant at $P = 0.01$.

Appendix 4. Effect (F values) of year (Y), location (L) (Clermont-Ferrand, Lusignan, le Pin-au-Haras, La Jaillière) and dry matter content (DM) on chemical composition and nutritive value of hybrid 1.

Variates *	Factorials		Interactions			Covariates	
	Y	L	Y x L	Y x DM	L x DM	DM	DM ²
ASH	NS	25.3 ^b	NS	NS	3.6 ^a	11.5 ^b	NS
CP	74.1 ^b	4.4 ^a	8.5 ^b	NS	NS	NS	NS
GRA	21.4 ^b	NS	NS	NS	4.0 ^a	13.8 ^b	8.8 ^b
STA	25.8 ^b	NS	NS	NS	6.5 ^b	8.9 ^b	5.9 ^a
WSC	NS	NS	4.5 ^a	9.8 ^b	NS	28.5 ^b	NS
NDF	NS	4.7 ^b	7.2 ^b	NS	6.3 ^b	16.3 ^b	NS
ADF	8.3 ^b	3.0 ^a	NS	NS	5.3 ^b	18.6 ^b	NS
CF	4.8 ^a	8.4 ^b	NS	NS	5.5 ^b	20.9 ^b	NS
ADL	7.3 ^a	3.1 ^a	6.4 ^b	NS	5.5 ^b	11.2 ^b	NS
Solubility							
AUF	NS	9.3 ^b	NS	NS	NS	8.6 ^b	NS
LGS	NS	11.2 ^b	6.4 ^b	NS	NS	15.3 ^b	NS
APC	NS	NS	3.7 ^a	NS	NS	10.2 ^b	NS
Digestibility							
OM	21.7 ^b	8.2 ^b	NS	NS	4.4 ^a	10.1 ^b	NS
CF	8.3 ^b	3.2 ^a	NS	NS	NS	NS	NS

* For abbreviations, see table IV. NS: non significant; ^a significant at $P = 0.05$; ^b significant at $P = 0.01$.

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