

Nutritive value of maize silage in relation to dairy cow performance and milk quality

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Abstract

Maize silage has become the major forage component in the ration of dairy cows over the last few decades. This review provides information on the mean content and variability in chemical composition, fatty acid (FA) profile and ensiling quality of maize silages, and discusses the major factors which cause these variations. In addition, the effect of the broad range in chemical composition of maize silages on the total tract digestibility of dietary nutrients, milk production and milk composition of dairy cows is quantified and discussed. Finally, the optimum inclusion level of maize silage in the ration of dairy cows for milk production and composition is reviewed. The data showed that the nutritive value of maize silages is highly variable and that most of this variation is caused by large differences in maturity at harvest. Maize silages ensiled at a very early stage (dry matter (DM) < 250 g kg⁻¹) were particularly low in starch content and starch/neutral detergent fibre (NDF) ratio, and resulted in a lower DM intake (DMI), milk yield and milk protein content. The DMI, milk yield and milk protein content increased with advancing maturity, reaching an optimum level for maize silages ensiled at DM contents of 300–350 g kg⁻¹, and then declined slightly at further maturity beyond 350 g kg⁻¹. The increases in milk ($R^2 = 0.599$) and protein ($R^2 = 0.605$) yields with maturity of maize silages were positively related to the increase in starch/NDF ratio of the maize silages. On average, the inclusion of maize silage in grass silage-based diets improved the forage DMI by 2 kg d⁻¹, milk yield by 1.9 kg d⁻¹ and milk protein content by 1.2 g kg⁻¹. Further comparisons showed that, in terms of milk and milk constituent yields, the optimum grass/maize silage ratio depends on the quality of both the grass and maize silages. Replacement of grass silage with maize silage in the ration, as well as an increasing maturity of the maize silages, altered the milk FA profile of the dairy cows, notably, the concentration of the *cis*-unsaturated FAs, C18:3n-3 and n-3/n-6 ratio decreased in milk fat. Despite variation in nutritive value, maize silage is rich in metabolizable energy and supports higher DMI and milk yield. Harvesting maize silages at a DM content between 300 and 350 g kg⁻¹ and feeding in combination with grass silage results in a higher milk yield of dairy cows.

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Supporting information may be found in the online version of this article.

Keywords: maize silage; maturity; nutritive value; fatty acids; dairy cow

INTRODUCTION

Silage maize (*Zea mays* L.) is widely grown in many parts of the world. The crop has a relatively stable yield under a wide variety of environmental and agronomical conditions, high energy content and good ensiling characteristics. In addition, the inclusion of maize silage in grass or grass silage-based diets of dairy cows increases feed intake, milk yield and milk protein content.^{1–6} As a result, the cultivation of silage maize has increased significantly in many parts of the world over the past few decades and, next to grass, maize silage has become the major forage component in the ration of dairy cows under most dietary regimes.^{6,7} Because of the increasing reliance on maize silage as a dairy cow feed, it is important to quantify the variation in its nutritive value and identify the causes of this variation, as well as to understand the effect of maize silage quality on the production performance of dairy cows.

Traditionally, grass silage was the major forage component in the ration of dairy cows during the winter period in many countries. However, grass silage dry matter (DM) yield, its nutritive value and ensiling quality are highly variable. Moreover, grass silage results in a relatively lower DM and energy intake potential, which reduces its usefulness in the diets of high-producing dairy cattle.^{2,3,8} As

a result, over the past few decades the incorporation of maize silages in grass silage-based rations has been increased to improve productivity of dairy cows.^{1–5,8–14} The second part of this review summarizes published data on the effect of replacing grass silage with maize silage on DM intake (DMI), milk production and milk composition, and discusses the optimum grass/maize silage ratio in the ration of dairy cows.

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In Europe,^{2,15} but also in other parts of the world,¹⁶ silage maize is harvested at a wide range of maturities, with the whole-crop DM content ranging from 250 to 450 g kg⁻¹ fresh weight. The variation in maturity at ensiling during the grain filling period results in major changes in the content and composition of the carbohydrates (starch/neutral detergent fibre (NDF) ratio) in maize silages,^{2,16} affecting silage DMI, milk yield and milk composition of dairy cows.^{16–21} We summarized literature data to quantify the effect of silage maize harvest maturity on silage nutrient composition, digestibility and dairy cows' performance.

Forages in fresh or ensiled form are often the major sources of polyunsaturated fatty acids (PUFA) in the ration of dairy cows. Over the last one and half decade, extensive research has been conducted to quantify the fatty acid (FA) content and composition of forages,^{22,23} in an effort to identify high-PUFA (C18:3n-3, C18:2n-6) containing forages to improve the milk FA composition of dairy cows.²⁴ The last objective of this review was to summarize recent data on the FA content of maize silages, and to evaluate the effect of maize silage quality and inclusion level in the diet on the milk FA composition of dairy cows.

MATERIALS AND METHODS

Database building

The database was built from scientific publications obtained through systematic web searches, examination of bibliographic references and from the data collected as part of three PhD projects. The studies selected for the database were investigating: (i) the causes of variation in maize silage nutrient and fatty acid composition, ensilage quality and digestive kinetics of nutrients in the rumen and post-ruminal tract; (ii) the effect of replacing grass silage with maize silage in the diets on DMI, milk yield and composition of dairy cows; and (iii) the effect of maize silage harvest maturity (chemical composition and ensiling quality) on milk yield and milk composition of dairy cows. All data were obtained from published work between 1992 and 2013, except harvest maturity, for which data were obtained from all available studies that could be found online (i.e. also before 1992) in order to obtain a more compressive database. To estimate the effect of replacing grass silage with maize silage on DMI, milk yield and composition of dairy cows, 13 studies with 37 direct comparisons were selected. These studies compared the effects of replacing grass silages with different proportions of maize silage and with different qualities of maize silage (such as low starch vs. high starch; differences in maturity) or evaluated the effect of replacing different qualities of grass silage (such as low feed value vs. high feed value; low vs. medium and high metabolizable energy values) with maize silage. To evaluate the effect of maize silage harvest maturity on milk yield and composition, 10 studies with 51 direct comparisons were selected. Each of these studies evaluated at least three maize silages harvested at different stages of maturity during grain filling. In addition to the quantitative work, literature studies on the factors affecting the content, composition and digestion of starches, NDF, protein and FA were reviewed.

Calculations

Mean values and variability in chemical composition, ensiling quality and FA content of maize silages were obtained from the overall database (supporting information, Appendix 1) using the statistics procedure of the Statistical Analysis System (SAS).²⁵ The overall data were then sorted into four categories:

very wet, DM < 250 g kg⁻¹; wet, DM = 250–300 g kg⁻¹; normal, DM = 300–350 g kg⁻¹; and dry, DM > 350 g kg⁻¹. For each category, the mean values and variability in chemical composition, ensiling quality, FA content and total tract digestibility of dietary nutrients were calculated using the descriptive statistics procedure of SAS.²⁵ The statistical methods used to adjust the data for the random effect of experiment and unequal variance among experiments have been described by St-Pierre.²⁶ The PROC MIXED model of SAS²⁵ with a random experiment effect (to account for the variance between experiments) was used to estimate the effect of replacing grass with maize silages on DMI, milk and milk component yield and milk composition. To summarize the effects of harvest maturity on milk yield and composition data from 10 studies with 51 direct comparisons were sorted into four categories based on the DM content of maize silages: very wet, wet, normal and dry. The mean values and variability in DMI, milk and milk component yield and composition were quantified using descriptive statistics procedure in SAS.

NUTRITIVE VALUE OF MAIZE SILAGES FOR DAIRY COWS

Data on the mean contents and variability in chemical composition, FA profile and silage quality parameters are summarized in Table 1. The results showed a large variation in the content of all chemical components, FAs and silage quality parameters. The nutritive value of maize silages is influenced by a number of factors such as genotype (maturity type, cell wall or starch type and endosperm type) agronomic (soil type, fertilization etc.) and growth conditions (temperature, irradiation, etc.), maturity at harvest, harvesting practices (chop length, kernel processing, etc.) and ensiling conditions.^{7,27–31} Khan *et al.*⁷ performed multivariate analyses to identify the major factors that cause the variation in the nutritive value of maize silages. Data on the nutrient contents of maize silages ($n = 96$) were correlated with a large number of variables related to agronomic practices, maize genotypes, harvest maturity and ensiling conditions. The results showed that the large variation in the nutrient content of maize silages was predominantly caused by the (large) differences in maturity at harvest.⁷

In the literature reviewed here, the maturity of maize silages has been defined by variables, such as kernel milk lines and number of frosts, which are not well-defined characteristics. A more precise criterion is the DM content as this increases with advancing maturity, and as such can be used to mark the harvest maturity.^{15,27} Therefore, to allow comparison across studies, the DM content of the silages will be used here to describe the harvest maturity at ensiling. On the basis of DM content, we characterized the maize silages as very wet, DM < 250 g kg⁻¹; wet, DM = 250–290 g kg⁻¹; normal, DM = 300–350 g kg⁻¹ and dry, DM > 350 g kg⁻¹. Indirect comparisons of mean nutrient composition, ensiling quality and total tract digestibility of the very wet, wet, normal and dry silages (Table 2) showed that the harvest maturity of the maize crop not only affects the chemical composition of the maize silages but also the total tract digestibility of the dietary nutrients. The progressing maturity of the maize crop during the grain-filling period increases the content of DM and starch, and decreases the content of NDF and CP.^{27,32,33} The increase in starch content is related to the growth of the kernels and the deposition of starch in the kernels during the grain-filling period. The starch content of the maize silages increases up to a DM content of approximately 380–400 g kg⁻¹ (Fig. 1), indicating that the current recommended harvest practices at a DM content between 300 and 350 g kg⁻¹ is a

Table 1. Average chemical composition, ensiling quality parameters and fatty acid content of maize silages as reported by various studies

	N ^a	Mean	SD ^b	Minimum	Maximum
<i>Chemical composition^c</i>					
Dry matter (g kg ⁻¹ fresh matter)	193	338	52.8	202	568
Crude protein	189	73.7	9.91	57.0	124
Crude fat	153	34.4	4.46	22.0	47.0
Sugar	134	12.6	3.40	6.00	39.0
Starch	176	333	66.3	66.3	591
Neutral detergent fibre	170	399	61.3	207	659
Acid detergent fibre	176	220	30.3	152.0	334
Lignin	93.0	18.3	2.76	12.0	26.0
<i>Silage quality parameters</i>					
pH	149	3.9	0.15	3.5	4.4
NH ₃ -nitrogen (g N kg ⁻¹ N)	77.0	7.83	3.82	3.64	17.0
<i>Fatty acids (g kg⁻¹ DM)</i>					
C16:0	98	3.01	0.485	2.03	4.82
C18:1	98	4.55	1.21	2.15	8.83
C18:2	98	10.6	2.13	6.89	22.4
C18:3	98	1.10	0.417	0.432	2.56
Total fatty acids	98	16.9	3.80	6.05	35.2

^a Number of observations; ^b SD, standard deviation; ^c g kg⁻¹ DM unless otherwise stated.

compromise regarding the starch content of the maize silages. On the other hand, harvesting at this maturity avoids excessive losses of stover DM due to senescence of leaves and ensures good

fermentation during ensiling. The NDF content of the stover increases as maturity advances. However, the NDF content of the whole crop decreases because the proportion of grains in the whole-crop DM increases proportionally faster than that of NDF in the stover.^{30,34} As a result, a negative relationship ($R^2 = 0.669$) between the starch and NDF content of maize silages is observed (Fig. 2). Delaying harvesting time to obtain a high starch content in the maize silages therefore compromises the NDF, particularly the digestible NDF, content of the maize silages. Table 2 shows a marked increase in starch content and a marked decrease in NDF content when the DM content of the maize silages increases from 'very wet' to 'wet' (Table 2). Ear growth and accumulation of nutrients in the kernels is very rapid during the early grain-filling period and the rate declines with progressing maturity, indicating that silage maize ensiled at very early maturity (<250 g kg⁻¹ DM) will result in a markedly lower starch/NDF ratio. In summary, the harvest maturity not only influences the content of important nutrients but also their digestibility and silage fermentation quality.

Factors affecting the nutritive value of starches in maize silages

Starch is the major source of metabolizable energy (ME) in maize silages, and has traditionally been considered the most important characteristic of maize silages. Starch is also one of the main sources of rumen fermentable energy in maize silages, and fuels microbial activities in the rumen. Despite a large decrease in NDF degradability during maturity from very wet to dry (523 vs. 388 g kg⁻¹), maize silages maintained a relatively high whole-tract organic matter degradability (714 vs. 652 g kg⁻¹), which is predominantly related to the increasing content of starch and its high degradability (>950 g kg⁻¹) in the whole digestive tract (Tables 2

Table 2. Effect of harvest maturity on chemical composition, ensiling quality and total tract digestibility of dietary nutrients of maize silages

	Harvest maturity ^a			
	Very wet	Wet	Normal	Dry
<i>Chemical composition (g kg⁻¹ DM)</i>				
Dry matter (g kg ⁻¹)	229 ± 19.6 (14)	291 ± 10.0 (37)	331 ± 14.1 (75)	391 ± 38.9 (67)
Crude protein	87.4 ± 15.9 (12)	74.7 ± 8.41 (37)	73.2 ± 9.24 (74)	71.8 ± 7.95 (65)
Crude fat	24.0 ± 1.73 (3)	34.4 ± 5.12 (28)	34.8 ± 3.67 (65)	34.4 ± 4.43 (57)
Starch	134 ± 79.6 (10)	301 ± 41.3 (32)	339 ± 32.5 (70)	374 ± 63.4 (63)
Neutral detergent fibre	545 ± 50.3 (9)	421 ± 45.5 (30)	386 ± 47.4 (72)	377 ± 52.2 (58)
Acid detergent fibre	290 ± 33.5 (10)	232 ± 23.1 (33)	213 ± 31.3 (71)	207 ± 24.8 (61)
<i>Silage quality parameters</i>				
pH	3.7 ± 0.17 (9)	3.8 ± 0.17 (34)	4.0 ± 0.15 (52)	4.0 ± 0.12 (51)
Ammonia	5.80 ± 7.71 (4)	8.54 ± 3.30 (28)	9.04 ± 3.6 (42)	12.5 ± 8.38 (43)
<i>Fatty acids (g kg⁻¹ DM)</i>				
C16:0	–	2.69 ± 0.71 (20)	2.95 ± 0.59 (47)	3.12 ± 0.65 (31)
C18:1	–	3.72 ± 1.21 (20)	4.27 ± 1.19 (47)	5.19 ± 1.42 (31)
C18:2	–	8.98 ± 3.69 (20)	9.98 ± 1.95 (47)	11.7 ± 2.76 (31)
C18:3	–	1.32 ± 0.539 (20)	1.14 ± 0.39 (47)	0.82 ± 0.305 (31)
Total fatty acids	–	18.5 ± 1.92 (20)	18.7 ± 3.84 (47)	21.3 ± 4.49 (31)
<i>Total tract digestibility (g kg⁻¹)^b</i>				
Dry matter	653 ± 73.0 (3)	–	602 ± 78.3 (5)	571 ± 99.1 (5)
Organic matter	714 ± 8.14 (4)	–	691 ± 37.1 (5)	652 ± 57.0 (3)
Starch	988 ± 7.21 (4)	–	979 ± 25.3 (14)	966 ± 44.2 (13)
Crude protein	887 ± 11.1 (4)	–	826 ± 39.4 (13)	804 ± 59.0 (11)
Neutral detergent fibre	523 ± 41.0 (5)	–	444 ± 66.1 (13)	388 ± 68.3 (8)

Values reported are means ± standard deviation. Number of observations is shown in parentheses. Only data with three or more observation are reported.

^a Very wet, DM ≤ 250; wet, DM = 250–290 g kg⁻¹; normal, DM = 300–350 g kg⁻¹; dry, DM > 350 g kg⁻¹.

^b Determined using mobile Nylon bag technique.

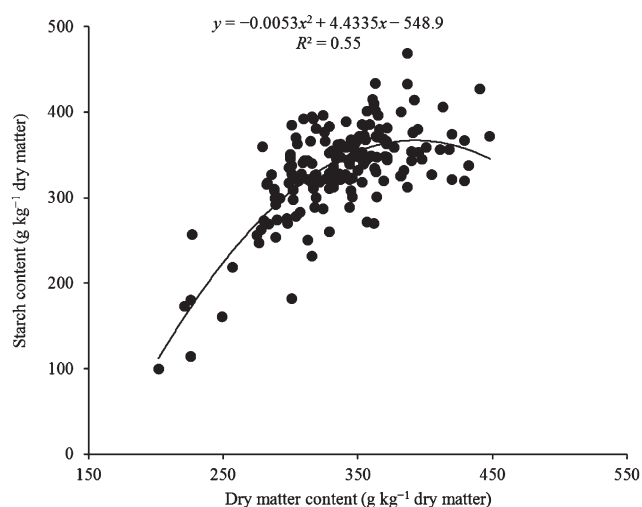


Figure 1. Relationship between dry matter content and starch content of maize silages.

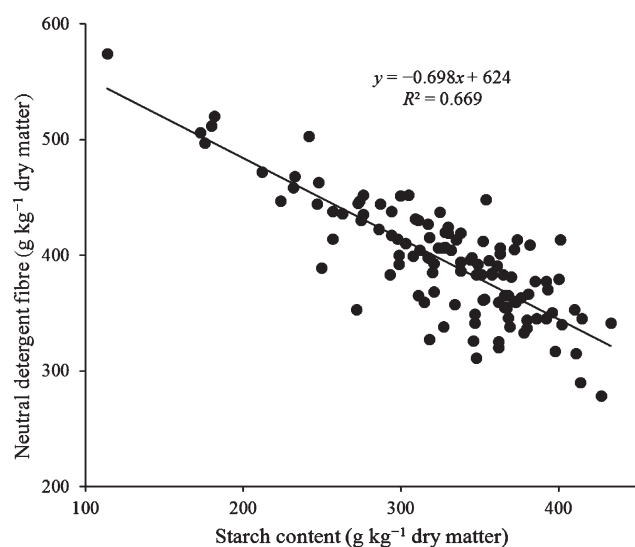


Figure 2. Relationship between starch content and neutral detergent fibre content of maize silages ($n = 118$).

and 3) of dairy cows. Therefore, to understand the true feeding value of maize in dairy rations, it is important to have a good understanding of the overall nutritional value of maize starch.

The starch in ensiled maize grains is almost completely digested at the end of the digestive tract.^{16,29,35–38} However, the site of digestion (rumen vs. intestines) varies, depending on the starch composition (amylose/amylopectin ratio), endosperm type (dent vs. flint) and texture (vitreousness) of the grains. These variables depend on the maize genotype, growing conditions and maturity stage. Moreover, mechanical processing and ensiling can modify the ruminal degradation characteristics, and the site and total digestion of starch. The site of digestion of the starch fraction influences the nature of the end products of digestion (volatile fatty acids vs. glucose), rumen fermentation efficiency, composition of fermentation products, and losses of microbial matter when starch is digested in the hindgut.³⁸ Moreover, the rate and extent of starch digestion in the rumen affect the rumen health (pH), and the content and composition of milk fat.^{6,39}

Maize starch is composed of two distinct types of glucose polymers: amylose, a tightly packed linear chain molecule; and amylopectin, a loosely packed, highly branched chain molecule. The glucose units of the primary chain of amylose and amylopectin are linked by α -(1–4) bonds. In amylopectin additional α -(1–6) linkages are present, which result in branch points. In normal maize genotypes starch is composed of 20–30% amylose and 70–80% amylopectin. However, there is a large genetic variation in starch composition (amylose/amylopectin ratio) of maize kernels, ranging from waxy to high-amylose cultivars. Waxy maize is a generic name of a starch variant of normal maize cultivars which contains almost 100% amylopectin. Amylose maize or amylomaize is the generic name used for maize cultivars that have amylose content higher than 50%. Because of its tightly packed structure, amylose is more resistant to enzymatic hydrolysis than amylopectin.⁴⁰ A number of studies have shown that the ruminal degradability of starch in cereal grains such as barely is negatively correlated with the proportion of amylose in the total starch.^{40–43} Hibberd *et al.*⁴⁴ isolated purified starch from four normal maize cultivars and eight sorghum cultivars differing in amylose:amylopectin ratio. Isolated waxy starch generally gave a higher *in vitro* gas production than non-waxy starches. However, the differences in gas production were quantitatively small and were different for different types of endosperm. Only a few studies have evaluated the effect of starch composition of maize silages on ruminal degradation characteristics⁴³ and milk production. Philippeau *et al.*⁴⁵ observed a higher *in situ* ruminal starch degradability for waxy genotypes compared to amylomaize in only flint cultivars of maize with a vitreous endosperm, whereas in dent cultivars with a floury endosperm, waxy cultivars showed no differences in starch degradation with its isogenic normal control. Across the flint and dent genotypes, ruminal starch degradation was independent of the amylose:amylopectin ratio in starch. In support of these *in vitro* studies, Schroeder *et al.*⁴⁶ found no difference in milk production and composition of dairy cows fed maize silage prepared from dent cultivar or its isogenic waxy counterpart. In contrast, Akay *et al.*⁴⁷ observed higher maize silage starch degradation (0.985 vs. 0.869 g g⁻¹ starch) in the rumen of lambs from waxy compared to the normal starch cultivar. Recent studies in our laboratory also showed a lower rate and extent of starch degradability in rumen fluid from high-amylose cultivars compared to waxy cultivars.⁴³ Moreover, Akay and Jackson⁴⁸ and Moreira *et al.*⁴⁹ observed higher milk yields when lactating cows were fed diets based on waxy maize silage compared to normal starch maize silage. However, Barlow *et al.*⁵⁰ found no differences in yields of milk when lactating cows were fed diets based on waxy maize silage compared with diets based on normal starch maize silage. Overall, these findings indicate that starch composition (amylose:amylopectin ratio) can affect ruminal starch degradation and milk production. However, the effects appear to be inconsistent and other factors such as endosperm type (dent vs. flint) can modify these effects.

Based on the kernel texture, maize cultivars can be distinguished as dent (floury) or flint (vitreous) type.⁵¹ Dent-type (*Zea mays indentata*) kernels contain a large floury endosperm in the central part of the grains, where starch granules are more loosely bounded by a thin, discontinuous protein matrix. The sides and back of the kernels, however, contain the vitreous (horny/corneous) endosperm. Flint maize (*Zea mays indurata*) kernels have a thick, hard, vitreous endosperm. Moreover, the starch granules in flint maize are encapsulated by a dense protein matrix. The protein mixture degrades slowly in the rumen. The protection

Table 3. Effect of maize maturity (dry matter content) on starch intake and digestion in the rumen and post-ruminal digestive tract

Reference	Dry matter (DM) (g kg ⁻¹)	Content (g kg ⁻¹ DM)	Intake (kg d ⁻¹)	Duodenal flow (kg d ⁻¹)	Rumen degradability (g kg ⁻¹)	Total tract digestibility (g kg ⁻¹)	Undigested (g kg ⁻¹)
Sutton <i>et al.</i> ³⁵	221	173	3.11	0.40	870	980	20.0
	372	328	5.04	0.89	820	970	30.0
Jochmann <i>et al.</i> ³⁷	230	250	4.10	0.54	870	990	10.0
	360	340	4.84	0.75	840	980	20.0
Harrison <i>et al.</i> ^{36a}	360	320	4.23	1.20	–	960	40.0
	450	350	4.44	2.10	–	870	130
Bal <i>et al.</i> ^{16a}	301	180	7.34	–	–	940	60.0
	420	370	9.01	–	–	880	120
Jensen <i>et al.</i> ³⁸	257	195	2.10	0.130	930	1000	0.00
	400	334	3.72	0.290	910	980	20.0
Johnson <i>et al.</i> ^{29a}							
Experiment 1	253	152	3.90	1.23	655	974	26.0
	279	196	4.20	1.28	695	979	21.0
Experiment 2	271	200	6.60	1.87	712	981	19.0
	382	253	7.00	2.56	626	955	45.0
Experiment 3	341	306	6.00	1.98	732	973	27.0
	475	365	7.80	2.42	697	968	32.0

Only values for minimum and maximum DM content for the experiments are shown.

^a Kernels were not processed.

by the slowly degradable protein matrix and the hard texture of the starch itself result in a lower rate and extent of ruminal starch degradation in flint compared to dent cultivars. The relative amounts of vitreous (hard) and floury (soft) starch, however, vary among different cultivars of dent and flint maize. Owing to a high DM yield and starch content, most of the maize cultivars grown for silages in Europe and North America are of the dent type. Flint cultivars are used for silage production in the cooler temperate environment zones because of their cold tolerance.

Despite genetic (dent vs. flint) variation, the vitreousness of maize kernels increases during maturation, with a consequent decrease in ruminal starch degradation. The vitreousness is the proportion of vitreous in the total endosperm, and is used to assess the hardness of the maize endosperm. Philippeau and Michalet-Doreau⁵¹ observed that ruminal starch degradation of unensiled maize kernels linearly decreased with increasing whole-crop DM of maize in both dent ($R^2 = 0.854$) and flint ($R^2 = 0.931$) cultivars. However, starch in dent-type maize kernels showed a higher rate and extent of starch degradation than flint-type kernels. Philippeau and Michalet-Doreau⁴² further observed that ensiling increases the ruminal starch degradation in both flint and dent genotypes. However, the differences in ruminal degradation of dent and flint genotypes were similar to the pre-ensiled grains, with dent being more degraded. The increase in starch degradation with ensiling could be related to the softening of the kernels during ensiling. Moreover, the in-silo fermentation (partly) solubilizes the protein matrix around the starch granules, making it more accessible for rumen microbial fermentation. The lower rate and extent of ruminal degradation of starch in flint cultivars are caused by higher vitreousness of the maize kernels.^{45,52} Ngonyamo-Majee *et al.*⁵³ observed a strong negative relationship ($R^2 = 0.822$) between vitreousness of a diverse range of maize kernels and ruminal DM degradation (Fig. 3a). In addition, Philippeau and Michalet-Doreau,⁵¹ characterized the vitreousness of pre-ensiled maize grains from dent and flint

genotypes, harvested at various stages of maturity, and related it to the *in situ* ruminal starch degradability. The degree of vitreousness explained 86% of the variation in ruminal starch digestibility (Fig. 3b). The increasing resistance to degradation with increasing vitreousness of the kernel can be related to increasing hardness (physical barrier) and increasing concentration of insoluble zein proteins (chemical barrier) in the protein matrix that encapsulate the endosperm.⁵⁴ The slowly degradable zein proteins limit the accessibility of starch granules to ruminal microbes.⁵⁴ Moreover, with advancing maturity (vitreousness), sugars in the kernels are converted into starch and the moisture concentration decreases, allowing the starch granules to become more tightly packed and the kernels become highly vitreous.⁵⁵ The vitreousness adversely affects microbial colonization of the grains.⁵⁶ Overall, these findings suggest that vitreousness explains most of the variation in ruminal starch degradation of maize silages.

Although significant variation has been shown in the rate and extent of ruminal starch degradation by a number of *in vitro* and *in situ* studies. *In vivo* results from dairy cows fed maize silages with wide variation in starch content show that the changes in starch supply to the duodenum, although significant, are quantitatively small (on average 0.4 kg d⁻¹; Table 3). Moreover, the starch that leaves the rumen is almost completely digested in the small intestine, and only a small amount (on average 40 g kg⁻¹) of undigested starch is excreted in the faeces (Table 3). Apart of the inherent difference in the *in vivo* and *in vitro/in situ* environments and fermentation dynamics, this could also be related to the fact that most of the *in vitro* and *in situ* studies evaluated very contrasting types (dent vs. flint; waxy vs. high amylose) or pre-ensiled maize starches. The *in vivo* studies evaluated mostly starch from dent type maize, which is grown widely for silage production. The studies of Harrison *et al.*³⁶ and Bal *et al.*¹⁶ reported higher starch excretion of 130 and 120 g kg⁻¹, respectively (Table 3). However, in those studies the kernels were not mechanically processed and the high starch excretion was mainly caused by the passage of whole kernels in

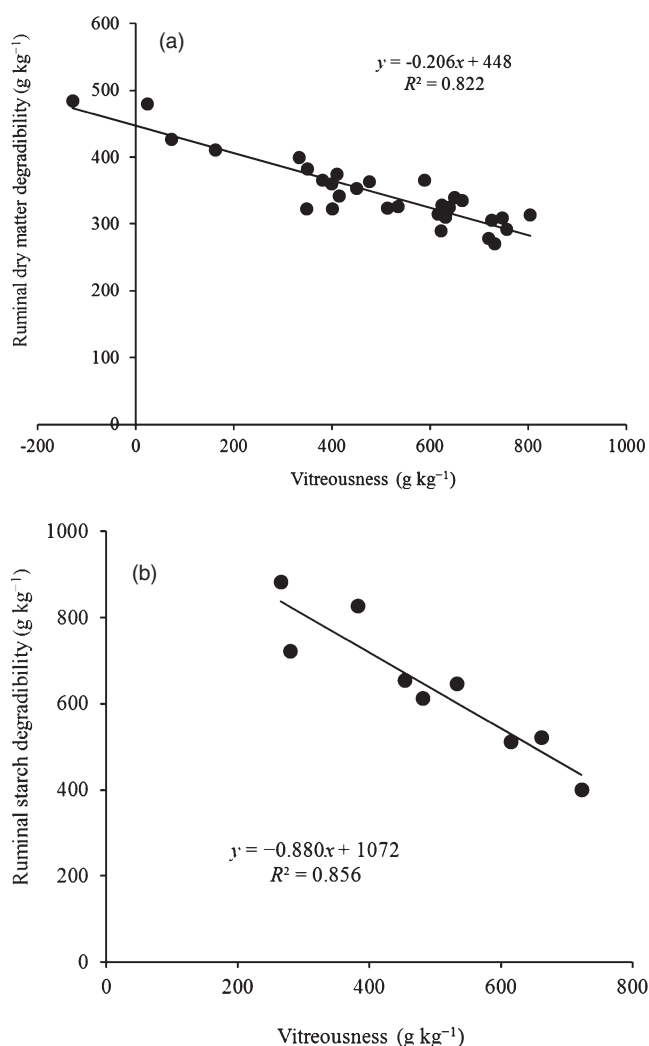


Figure 3. Effect of vitreousness of maize grains on *in situ* dry matter (a)⁵³ and starch degradation (b).⁵¹

the faeces. This shows that kernels need to be processed, particularly, at the later stage of maturity. Recently, kernel processing has been commonly used, and as such we speculate that the passage of undigested starch in the faeces will be quantitatively very small. As starch is relatively inert during the ensiling process, very little starch is lost in the silage, in contrast to, for example, water-soluble carbohydrates. The latter components may be lost through fermentation processes or through seepage during storage. As such, the process of starch formation, whether it is based on ongoing photosynthesis or on reallocation of water-soluble carbohydrates from the stem, greatly contributes to the production of storable dry matter. Moreover, starch availability from silage is markedly increased by kernel processing as well as by the fermentation process. With only a small range in the amount of whole-tract indigestible starch from maize silages, particularly in those that are kernel processed, the nutritive value of maize silage appears to be much more dependent on the starch content than on starch availability or digestibility. However, the high availability of starch from maize silage needs to be in balance with physically effective fibre, especially when fed as a sole diet to dairy cows. A combination of maize silages (with a high starch content) with high amounts or

highly degradable concentrates can decrease the rumen pH and affect rumen health and milk fat content and composition.

Factors affecting the NDF content of maize silages

Our dataset showed that the NDF content ($399 \pm 61.3 \text{ g kg}^{-1} \text{ DM}$) of maize silages was highly variable (Table 1). NRC-2001⁵⁷ reported a higher content but a similar wide range ($451 \pm 47.2 \text{ g kg}^{-1} \text{ DM}$) in NDF content of maize silages. The primary factors affecting NDF content and composition of maize silages are harvest maturity and genotype. Other minor factors include growth temperature, irradiation, population density, harvest height and fertilization. Kruse *et al.*⁵⁸ conducted a 3-year field experiment to evaluate differences in whole-crop and stover fibre content among a set of commercial cultivars covering three maturity groups (early, mid and late) and different maturation types (dry-down, normal, stay-green). The study showed that harvest maturity explained most of the variation in NDF content and composition, followed by maturity type and environmental conditions, respectively. Khan *et al.*⁷ performed multivariate analyses on a large number of variables related to agronomic practices, maize genotypes, harvest maturity and ensiling conditions to identify the major factors that cause variation in the nutritive value of maize silages. The multivariate analyses showed that the large variation in the NDF content of maize silages was predominantly caused by the large differences in maturity at harvest.⁷ Data in Table 2 show that the mean content of NDF decreases from 545 to 377 g kg⁻¹ DM with an increasing DM content from very wet (DM < 250 g kg⁻¹) to dry (DM > 350 g kg⁻¹). However, much of the decrease in NDF content from 545 to 421 g kg⁻¹ DM occurred when the DM content of maize silages increased from very wet (<250 g kg⁻¹) to wet (250–290 g kg⁻¹; Table 2). Although the NDF content continues to decrease with increasing DM content from wet to dry silages, the magnitude of this decrease (from 421 to 377 g kg⁻¹) was relatively small. A number of direct comparisons^{2,20,35} also reported a large decrease in NDF content (68–117 g kg⁻¹ DM) during the early part of grain filling (DM, 230–280 g kg⁻¹) and a much more gradual and relatively small (16–31 g kg⁻¹) decline during prolonged ripening (DM 280 to >350 g kg⁻¹). The relatively high SD values (Table 2) show that within each maturity category there was a large variation in NDF content. This could be due to the fact that each category represents a range of DM contents. This variation can originate from intrinsic differences in the maize plants or may be due to the fact that environmental and ensiling conditions can influence the DM content of the maize silages during ensiling. Moreover, the variation in NDF methodologies between labs can also result in systematic differences in NDF content.

Factors affecting the digestibility of NDF in maize silages

From a series of systematic research studies aimed at exploring the variation in NDF (cell walls) degradability of silage maize due to harvest maturity, genotypes and growth conditions, Cone *et al.*^{34,59–62} and Bonn *et al.*^{63–66} concluded that the lignin content, cross-linkage of lignin with fibre and secondary cell wall thickness explain most but not all the variation in NDF degradability of maize silages. The lignin fraction of plant cell walls has long been considered as the primary barrier for the microbial fermentation of fibre, as a negative correlation exists between lignin content and the cell wall degradability of maize stover. However, Cone *et al.*⁶⁰ showed that lignin content explains variation in NDF degradability within a particular maize cultivar but not across all cultivars. Maize silages with a lower lignin content, such as those harvested early

in the grain-filling period or those genetically modified for a lower lignin content (brown midrib (BMR), degrade rapidly in the rumen with a consequent increase in DMI. However, the BMR cultivars are not commonly used for silage production because of negative pleiotropic effects on the agronomical values such as stalk lodging and yield.

The indirect comparison in Table 2 shows that NDF degradability markedly decreased from 523 to 388 g kg⁻¹ with increasing DM content of the maize silages from 'very wet' to 'dry'. However, parallel to the NDF content, most of this decrease occurred when the DM content of maize silages increased from 'very wet' to 'wet'. Data from *in vivo* trials on the effect of maize DM content on NDF intake and degradation in the rumen and the post-ruminal tract are summarized in Table 4. On average, 42% of the NDF is digested in the rumen and 7% post-ruinally, while 51% is excreted in the faeces. Ali *et al.*⁶⁷ evaluated the whole-tract NDF degradability of 20 maize silages with a broad range in chemical composition, using the mobile Nylon bag technique. Their study reported an average ruminal NDF degradation of 32%, and another 7% was digested in the post-ruminal tract. The lower ruminal NDF degradability in their study could be partly explained by the short (24 h) rumen incubation period. The study further reported that hindgut fermentation made up 9–35% of the whole-tract NDF digestion. Tamminga⁶⁸ reported that post-ruminal digestion made up 0–20% of the whole-tract NDF digestion. The lignification, maturation and thickness (hardness) of cell walls can all contribute to the decreasing degradation of NDF with increasing maturity. Moreover, with increasing maturity of maize silages the starch content increases, which negatively affects ruminal fibre degradation.^{16,35}

Genetic variation in NDF degradability

There is considerable interest in quantifying the genetic differences in NDF content, composition and digestibility among maize cultivars in an effort to harvest more energy from it. Cone *et al.*³⁴ studied the effects of maize genotypes harvested at various stages of maturity on *in vitro* rumen fermentation characteristics. The maize types included early- and late-maturing cultivars of stay-green and dry-down genotypes. The stems and leaves of the stay-green types are supposed not to senesce rapidly and stay green during the grain filling period, whereas the stems and leaves of the dry-down types senesce faster, turning brown at silage maturity. Consequently, at the same harvest date the stay-green types are believed to have a higher NDF degradability than the dry-down types. However, the results of their trial showed that maize type had no systematic effect on NDF content, composition or ruminal degradation characteristics.³⁴ Kruse *et al.*⁵⁸ evaluated the genetic differences in whole-crop and stover NDF content and composition among a set of commercial hybrids covering three maturity groups (early, mid and late) and different maturation types (dry-down, normal, stay-green). The study showed that varietal differences within the maize cultivars were marginal, with only a few significant differences observed in the early stages of development. The differences in commercially grown maize genotype in the content, composition and digestibility of NDF are marginal. However, large difference in digestibility have been reported among a BMR mutant and its isogenic normal control, ranging from 14.9% for late to 19% for early hybrids.⁶⁹ Although the NDF degradation of BMR cultivars is much higher within the rumen, the effects of BMR on the total tract (*in vivo*) NDF digestibility are equivocal.^{69,70} This inconsistency could be partly related to the opposing effect of rapid degradation and rumen

passage/retention. Thus the increased DMI, in turn, often increases the level, but often not the efficiency, of milk production.^{71,72}

Improving the NDF degradability through breeding is a challenging goal. Among the factors involved for selecting an ideal cultivar for silage production, the selection for high DM and starch yield is of prime interest to the breeders. On the other hand, selection for a lower lignin content and higher NDF degradability, such as the BMR cultivars, is negatively associated with a lower agronomic value of the crop, such as lower yield and stalk lodging. A lower lignin content of maize silage can also reduce its physical effectiveness. From a practical point of view, at present silage producers are advised to select maize cultivars for proper maturity and yield, and then they can maximize their efforts to obtain high yields of digestible NDF. These include the choice of the most appropriate harvest stage, chop length, kernel processing, silage packing and storage management to avoid DM losses and ensure good ensiling conditions.

Effect of length of cut and kernel processing on NDF digestibility

The physical effectiveness of fibre depends not only on fibre degradation rate but also on particle size. Longer particles are needed in the diet to stimulate chewing, salivation and rumination. On the other hand, a longer particle size can decrease the DMI due to rumen fill. Reduction of chop length may improve digestibility because of increased microbial attachment sites, but if cut too short it may decrease digestibility due to an increased rate of passage of the digesta. Moreover, a short length of cut (LOC) may also reduce chewing time and ruminal pH. An optimal LOC must be determined for maize silage to stimulate chewing and rumination, without decreasing the DMI and affecting animal health and production levels.

The influence of LOC of ensiled maize on the total-tract digestibility of NDF is equivocal in the literature, with reports of similar^{62,73–78} or increased^{31,79,80} NDF digestibility, with longer LOC of ensiled maize. In a recent study,⁷³ an indirect comparison of 24 published studies and 106 treatment means showed no significant influence of LOC on the total-tract NDF digestibility, DMI, milk production and composition. The total-tract NDF digestibility numerically decreased with increasing LOC, with the highest value of 465 g kg⁻¹ recorded with the lowest LOC (0.48–0.64 cm) and the lowest value 449 g kg⁻¹ recorded with the highest LOC (>3.2 cm).

Content and composition of protein in maize silages

Maize silages are relatively low in crude protein (CP). Our data set showed a mean CP content of 74 g kg⁻¹ DM, with a broad range of 57–124 g kg⁻¹ (Table 1). The CP content and its digestibility decrease with maturity of the maize silages. Indirect comparison shows that the mean content of CP decreased from 87 ± 15.9 g kg⁻¹ in the 'very wet' to 72 ± 7.9 g kg⁻¹ in the 'dry' silages (Table 2). Despite late harvesting, the apparent digestibility of CP in maize silages in the whole tract is high (827 ± 41 g kg⁻¹). The digestibility, however, decreased from 887 to 804 g kg⁻¹ with an increasing DM content of the maize silages from 'very wet' to 'dry' (Table 2). Ali *et al.*⁶⁷ evaluated the whole-tract CP degradability of 20 maize silages with a broad range of chemical composition, using the mobile Nylon bag technique. Their study reported an average ruminal CP degradation of 555 g kg⁻¹, and another 353 g kg⁻¹ was digested in the post-ruminal tract. However, there was wide range in rumen (420–672 g kg⁻¹) and

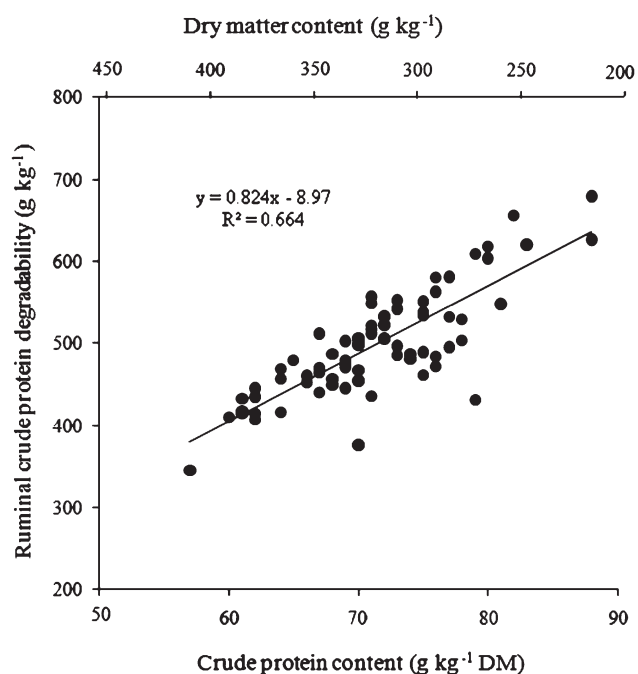
Table 4. Effect of maize maturity on neutral detergent fibre (NDF) intake and digestion in the rumen and post-ruminal tract

Reference	Dry matter (g kg ⁻¹)	Content (g kg ⁻¹ DM)	Intake (kg d ⁻¹)	Duodenal flow (kg d ⁻¹)	Rumen degradability (g kg ⁻¹)	Total tract digestibility (g kg ⁻¹)	Undigested (g kg ⁻¹)
Sutton <i>et al.</i> ³⁵	221	506	7.82	3.95	500	590	410
	227	438	7.97	4.07	499	537	463
	308	407	7.37	4.37	413	531	469
	372	409	7.84	4.75	400	530	470
Jochmann <i>et al.</i> ³⁷	230	459	6.3	–	–	670	330
	298	502	5.72	–	–	622	378
	305	486	5.60	–	–	624	376
	360	492	6.01	–	–	601	399
Bal <i>et al.</i> ¹⁶	301	520	–	–	–	460	540
	324	444	–	–	–	380	620
	351	405	–	–	–	340	660
	420	413	–	–	–	029	710
Jensen <i>et al.</i> ³⁸	257	458	5.80	2.30	470	560	440
	350	401	5.78	2.80	430	510	490
	400	381	5.29	2.68	360	430	570
Experiment 1	264	549	8.60	4.13	518	504	496
	284	544	8.50	4.02	531	491	509
	280	558	8.50	3.96	574	546	454
Experiment 2	284	468	8.00	4.90	377	385	615
	331	414	7.90	4.70	390	400	600
	384	449	7.90	4.65	417	384	616
Experiment 3	357	427	7.10	5.13	280	424	576
	418	403	7.40	4.93	330	470	530
	503	437	7.20	4.69	322	430	570

post-rumen (250–503 g kg⁻¹) degradation. Our unpublished data showed a strong positive relationship between the CP content of maize silage and *in situ* rumen degradation (Fig. 4). Abeysekara *et al.*⁸¹ reported a significant genetic variation (62–89 g kg⁻¹ DM) in CP content and CP subfractions, mainly soluble protein (425–511 g kg⁻¹ CP), neutral detergent-insoluble protein (156–220 g kg⁻¹ CP) and acid detergent-insoluble protein (50–67 g kg⁻¹ CP). Maize cultivars also differed in protein molecular structures which were correlated with protein degradation in the rumen. The inherent protein molecular structures affect protein degradation in the rumen by changing the protein solubility and the access of microbes and microbial enzymes in the rumen.^{82,83} Abeysekara *et al.* (unpublished data) used the NRC-2001 and DVE/OEB models to estimate the protein supply from various cool-season cultivars of silage maize using data from *in situ* trials. The two models showed large negative values (–55 to –80 g kg⁻¹ DM) for the degraded protein balance in the rumen, which shows a large deficiency of degraded N in the rumen compared to degraded energy when maize silages are fed as a sole diet.

Content and composition of fatty acids in maize silages

Data on the FA content of maize silages reported in the literature are summarized in Table 1. C18:1 (4.6 g kg⁻¹ DM; 27% of total FA) and C18:2 (10.6 g kg⁻¹ DM; 63% of total FA) are the major FAs in maize silages. Compared to grass (11.17 g kg⁻¹ DM; 58% of total FA) the content of C18:3n-3 is much smaller in maize silages (1.1 g kg⁻¹ DM; 7% of total FA).⁷ The FA content and composition of maize silages appear to be highly variable. The content of C18:2n-6 (16 g kg⁻¹ DM) showed the largest variation, followed by

**Figure 4.** Relationship between crude protein content and effective rumen degradability of crude protein of maize silages ($n = 75$).

C18:1n-9 (7 g kg⁻¹ DM) and C16:0 (2.8 g kg⁻¹ DM). The large variation in the FA content in maize silages was predominantly caused by differences in maturity at harvest.⁷ Khan *et al.*¹⁵ studied the changes in FA content and composition in stover (leaves + stem)

and cobs of maize plants during maturity from 14 to 84 days after flowering (whole-crop DM content of 220–380 g kg⁻¹). The study revealed that C18:3n-3 was the major FA of the stover part of maize plants, whereas C18:1n-9 and C18:2n-6 were the major FAs of the grains/cobs. With the progressive maturity of maize plants from a DM content of 220–380 g kg⁻¹, the content of C18:3n-3 and total FAs decreased in the stover.¹⁵ The decline in C18:3n-3 content in the stover could be related to the decrease in leaf:stem ratio, and maturation and senescence of the leaves during the grain filling period.¹⁵ In contrast, the content of C18:1n-9, C18:2n-6 and total FA increased in the ear.¹⁵ The maximum FA content in the ear was reached at a whole-crop DM content of 295 g kg⁻¹, and then remained more or less constant. Weber *et al.*⁸⁴ reported that the deposition of FAs in the grains occurs only during a brief period after flowering. In the whole crop, the content of C18:3n-3 decreased linearly during maturation, while the content of C18:2n-6 and the total FA increased up to a whole crop DM content of 295 g kg⁻¹ and then remained constant.¹⁵ The consistent decrease in C18:3n-3 content in the whole plant is caused by the decreasing content of C18:3 in the stover, and by the decreasing proportion of stover in the whole plant, due to the substantial increase of the ears. At the whole plant level, the maximum amount of PUFAs can be harvested at a DM content of 295 g kg⁻¹ DM, which is before the onset of the rapid senescence. Moreover, a delay in harvesting maize at the end of the grain-filling period needs to be avoided in order to minimize the losses of green leaves and with it that of C18:3n-3.¹⁵ Alternatively, maize hybrids with a high green leaf area index, which stay greener towards the end of the grain-filling period, can be expected to maintain a higher content of C18:3n-3.

MAIZE SILAGE AND DAIRY COW PERFORMANCE

Effect of replacing grass silage with maize silages on dairy cow performance

Summarizing data from 13 published studies with 37 direct comparisons showed that the inclusion of maize silage in grass silage-based diets improved the forage DMI by 2 kg d⁻¹, the milk yield by 1.9 kg d⁻¹ and the milk protein content by 1.2 g kg⁻¹ (Table 5). These comparisons further show that the inclusion of maize silages in grass-based diets significantly increased the yield of milk protein, fat and lactose. The increase in protein yield was caused by both the increase in protein content and milk yield. However, the fat and lactose contents of milk did not change significantly with the replacement of grass silage with maize silage, and the increase in yield of fat and lactose was due to the large increase in milk yield.

Although the forage DMI always increased with the inclusion of maize silages in grass silage-based diets, there was a large variation in the intake response, ranging from 0.1 to 4.5 kg d⁻¹. Similarly, there was a large variation in the milk yield (–1.1 to 6.7 kg d⁻¹) and milk protein content (–0.5 to 3.5 g kg⁻¹ milk). This variability could be related to the quality of both the grass and maize silages, as well as to the inclusion level of maize silage in the diets. Keady *et al.*⁴ stated that the feed value of grass silage, and not that of maize silage, had the greatest effect on the overall forage intake. For example, including maize silage with low-ME (9.8) or high-ME (12.0) grass silages had a mean response on the DMI of +2.25 and +0.51 kg DM per cow, respectively. Phipps *et al.*⁸ replaced 0%, 25%, 50% or 75% of grass silage with a low energy value (ME, 9.9) or an average energy value (ME, 10.6) with maize silage (ME,

10.9) in the diet of dairy cows. With the low energy value grass silage, the higher the inclusion level of the maize silage, the higher were the DMI and milk yield. However, peak DMI and milk yield were achieved when 50% of the average energy grass silage was replaced with maize silage.⁸ It should be noted that, in this study, the same concentrate (containing a CP level of 202 g kg⁻¹ DM) was fed with all the diets, and consequently the total dietary CP was reduced as the inclusion rate of the maize silage increased. This may have limited the DMI and milk production of the dairy cows fed diets containing 75% and 100% of the maize silages. When diets were balanced for CP, maximum DMI and milk yield were achieved when 75% (vs. 33, 0%) of a good-quality grass silage (ME, 10.9) was replaced with a high-quality maize silage (DM, 354 g kg⁻¹, ME, 11.1).¹ Feeding iso-nitrogenous diets, O'Mara *et al.*³ reported that 67% of high-quality grass silages (dry matter digestibility (DMD), 759 g kg⁻¹) can be successfully replaced with a moderate-quality (257 g DM kg⁻¹; 219 g starch kg⁻¹ DM) maize silage. Moreover, forage DMI increased when the grass silage was completely replaced by maize silage. However, the milk yield and milk protein content decreased numerically. Kliem *et al.*⁵ observed a linear increase in DMI, milk yield and milk protein content with a gradual (0%, 12%, 33% and 50%) replacement of grass with maize silage. Summarizing these findings, it can be concluded that a mixture of grass and maize silage improves animal performance compared to grass or maize silage as a sole forage. Although in practice a 50:50 ratio of grass and maize silage is generally recommended, in terms of animal performance this ratio will depend on the quality of both the grass and maize silages.

The high intake of maize silage is important for high-yielding dairy cows to achieve a high milk production, particularly during early lactation. Multiple mechanisms regulate the forage DMI, such as forage NDF content, rate of rumen degradability and rate of rumen passage.⁸⁵ The higher intake characteristics of maize silage can be attributed to lower NDF and higher starch or energy content,^{2,4,39} and to a faster degradation in the rumen.^{4,11,86} The DMI generally declines with increasing NDF content of the diet, especially forage NDF.^{85,87} The high DMI of maize silage is, however, not supported by the lower digestibility of maize silages as compared to grass silages. In general, a positive relationship exists between forage intake and forage digestibility.^{87–89} However, despite a lower DM and NDF digestibility, the inclusion of maize silage in grass silage-based diets increases the DMI.^{3,9,10,13} This suggests that, compared to grass silages, the rate of digestion and the passage of digesta from the rumen is faster with maize silages. The high starch content and smaller particle size of maize silages could partly explain the faster degradation and clearance from the rumen.^{85,86,90,91} The decreased retention time in the rumen results in less distension and a higher DMI. On the other hand, the large particle size, higher NDF content and slower rate of fermentation of grass silages extend the duration of particles buoyant in the rumen, reduce the rate of passage and increase the filling effect with NDF over time.^{88,92} The lower DMI observed for grass silages compared to maize silages suggests that the increased filling effect of grass NDF is a potential limitation of perennial grasses.

The increased milk yield with the replacement of grass silage with maize silage is primarily caused by the increase in ME intake.^{4,20,35,86} However, the efficiency of milk production is not improved.²⁰ Combining data from 13 studies (Table 5), the average efficiency of feed conversion to milk yield was found to be reduced by 10% with the replacement of grass silage by maize silage. While it is desirable to increase the forage intake in order

Table 5. The effect of including maize silage in grass silage-based diet on the performance of dairy cows

	n	Grass silage (GS)		Grass + maize silage (GMS)		Difference (GMS – GS)		
		Mean	SD ^a	Mean	SD	Mean	Minimum	Maximum
Maize silage ratio ^b	36	0	0	51.0	21.0	–	–	–
Intake (kg d ⁻¹)								
Forage dry matter	45	10.6	3.64	12.6	3.65	1.99**	0.100	4.50
Total dry matter	22	16.7	2.22	19.3	2.34	1.55**	0.301	4.80
Milk yield (kg d ⁻¹)	36	25.7	3.85	27.9	4.53	1.91**	–1.13	6.70
Milk composition (g kg ⁻¹)								
Fat	36	40.3	2.84	40.4	2.94	0.083	–3.80	7.00
Protein	36	30.2	2.29	31.4	1.90	1.20**	–0.500	3.50
Lactose	28	47.7	2.65	46.5	2.87	–0.906	–9.60	2.60
Yield (g d ⁻¹)								
Fat	36	1.04	0.183	1.11	0.188	0.071**	–0.049	2.50
Protein	45	0.83	0.197	0.920	0.212	0.088*	–0.042	0.250
Lactose	28	1.21	0.169	1.29	0.189	0.075**	–0.140	0.350
Fat + protein	36	1.85	0.354	2.02a	0.373	0.160**	–0.143	0.519

Adapted from the data of Burke *et al.*,¹³ Cooke *et al.*,¹⁴ Fitzgerald *et al.*,⁹ Hamleer,¹⁰ Keady *et al.*,⁴ Kliem *et al.*,⁵ Mulligan *et al.*,¹¹ Murphy *et al.*,¹² O'Mara *et al.*,³ Phipps *et al.*,¹ Phipps *et al.*² and Phipps *et al.*⁸

^a standard deviation. ^b The proportion of maize silage in the mixture of grass and maize silage. * $P < 0.01$; ** $P < 0.001$.

to increase milk production or to reduce concentrate supplementation, the efficiency with which the additional forage is utilized for milk production is an important criterion. A lower efficiency could be related to the lower digestibility of maize silages. The increase in milk protein content could be related to high starch and so high ME intakes.⁴ An increase in milk protein concentration may also be attributed to the high efficiency of microbial protein synthesis on maize silage as compared to grass silage-based diets.⁹³

Effect of harvest maturity of maize silages on the performance of dairy cows

A number of studies have shown that an increasing maturity of silage maize at harvest has a major effect on the DMI,^{9,19,85,88,94} milk yield and milk protein content of dairy cows.^{6, 20,35,87,88} Summarizing data from 10 studies with 51 direct comparisons of maize silage, ensiled at different harvest maturity, on milk production and milk composition of dairy cows showed that the silage maize harvest maturity has a marked influence on the DMI, milk yield and milk protein content (Table 6). The lowest DMI, milk yield and milk protein content were obtained when maize silages were harvested and ensiled at a very early stage (DM < 250 g kg⁻¹). The DMI, and milk and protein yield increased with advancing maturity, reaching an optimum level for silages, ensiled at a DM content of 300–350 g kg⁻¹, and then declined slightly at further maturity, beyond 350 g kg⁻¹ (Table 6). The lower DMI of maize silages, ensiled at a very early maturity, could be related to the high content of NDF and very low content of starch in these silages. The data from these studies were further analysed and it was found that the starch content of maize silage significantly increased ($R^2 = 0.701$), and the NDF content decreased ($R^2 = 0.522$), with increasing maturity. Phipps *et al.*² found a significant positive relationship between silage starch content and DMI, and a significant negative relationship between NDF and DMI. Remarkably, most of the change in starch/NDF ratio occurred early in the grain-filling period,³⁵ because the growth of the kernels and the accumulation of nutrients in the kernels are very rapid during the early grain-filling period, and the rate declines with progressing

maturity. Moreover, the DMI generally decreases with increasing moisture content of the forages.^{19,85,89} Erdman⁹⁵ suggested that the DMI of high-moisture silages is more likely limited by the fermentation end products, a lower pH and high NH₃ levels. The lower starch/NDF ratio and the high moisture content could explain the lower DMI of very wet maize silages. The DMI slightly declines when the (ensiled) crop matures from beyond a DM content of 350 g kg⁻¹, despite a decrease in NDF content and an increase in starch content. This relationship can be explained by the decline in fibre and starch digestibility in the more mature maize silages. The decline in fibre digestibility could be related to negative associative effects of higher starch diets on the ruminal fibre digestion and to the lower digestibility of stover as maize matures.^{16,96} The decline in starch digestibility could be related to the lower efficiency of post-ruminal starch digestion in cows fed higher-starch diets,⁹⁷ and to a more whole kernel passage from the very mature maize silages.³⁶

The responses in milk and protein yields with increasing maturity of silage maize were more or less parallel to that of the DMI. The lowest yields of milk and protein were associated with the feeding of very low DM silages (Table 6), predominantly due to a lower starch/NDF ratio, and a subsequent decrease in DMI. Based on the reviewed dataset,^{2,6,16,20,21,35} the differences in milk yield ($R^2 = 0.599$; Fig. 5a) and protein content ($R^2 = 0.605$; Fig. 5b) were strongly related to changes in the starch/NDF ratio during maturation of the maize. Parallel to the increase in the starch/NDF ratio, the milk and protein yield increased with the maize silage harvest maturity, with a maximum yield being recorded for DM content of 300–350 g kg⁻¹, with some flexibility. Upon a further increase in DM content (beyond 350 g kg⁻¹), the milk and protein yield declined in most studies, with significant differences observed at a DM content of 380 g kg⁻¹² and 450 g kg⁻¹.¹⁹ The decrease in milk and protein yield by harvested maize silages towards the end of growing season (>350 g kg⁻¹) is mainly caused by a decrease in NDF and starch digestibility. When the maturity of maize silage increases from 2/3 milkline to black layer (>350 g kg⁻¹) there is a significant decrease in digestibility of organic matter, NDF and

Table 6. Effect of the maize silage dry matter (DM) content on the DM intake (DMI) of dairy cows and the milk yield and milk composition. The values are presented as means \pm standard deviation, and number of observations are shown in parentheses

	Maize silage DM content ^a			
	Very wet	Wet	Normal	Dry
DM (g kg ⁻¹)	223 \pm 16.40 (7)	284 \pm 12.2 (15)	328 \pm 15.4 (13)	402 \pm 36.70 (16)
DMI (kg d ⁻¹)	17.8 \pm 2.98 (7)	18.8 \pm 3.23 (15)	22.2 \pm 3.49 (13)	20.5 \pm 3.72 (16)
Milk				
Yield (kg d ⁻¹)	25.1 \pm 4.76 (7)	27.7 \pm 6.29 (15)	32.5 \pm 6.94 (13)	30.4 \pm 7.13 (16)
Protein (g kg ⁻¹)	32.3 \pm 1.03 (5)	32.5 \pm 1.43 (14)	33.3 \pm 1.67 (11)	32.5 \pm 1.52 (12)
Protein (kg d ⁻¹)	0.996 \pm 0.218 (5)	1.07 \pm 0.206 (11)	1.16 \pm 0.102 (11)	1.11 \pm 0.156 (12)
Fat (g kg ⁻¹)	40.7 \pm 3.64 (7)	40.0 \pm 3.45 (14)	38.2 \pm 3.88 (13)	37.8 \pm 5.03 (14)
Fat (kg d ⁻¹)	1.04 \pm 0.273 (7)	1.14 \pm 0.315 (14)	1.25 \pm 0.325 (13)	1.19 \pm 0.348 (14)

Adapted from: Bal *et al.*,¹⁶ Buck *et al.*,¹⁸ Cammell *et al.*,²⁰ Johnson *et al.*,¹¹⁰ Huber *et al.*,¹⁷ Keady *et al.*,⁴ Khan *et al.*,⁶ Phipps *et al.*,² Pierre *et al.*¹⁹ and Warner *et al.*²¹

^a Very wet, DM < 250 g kg⁻¹; wet, DM = 250–300 g kg⁻¹; normal, DM = 300–350 g kg⁻¹; Dry, DM > 350 g kg⁻¹.

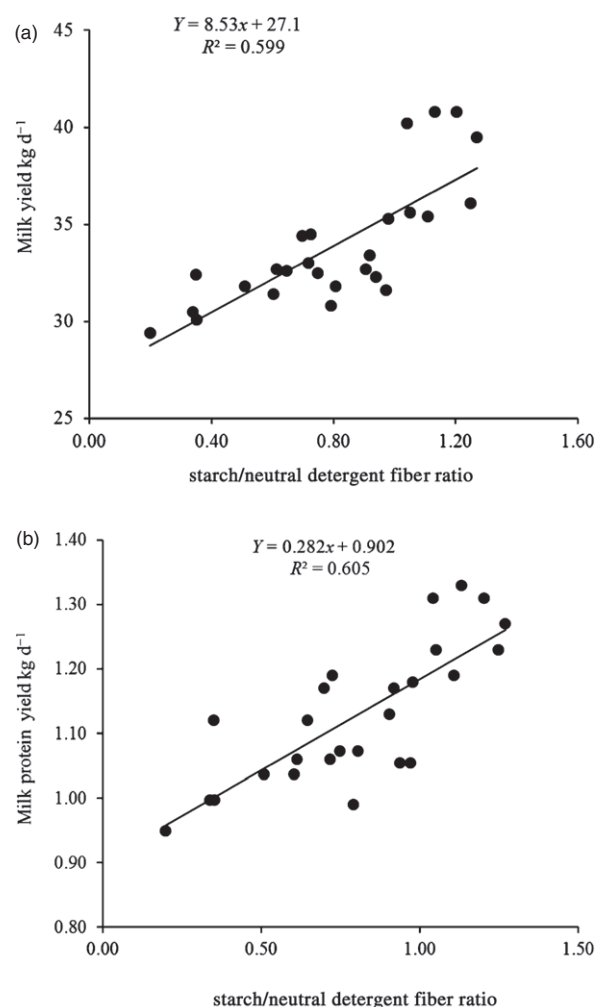
starch,^{16,36} with a concomitant decrease in ME content.²⁰ As a consequence, a decrease in milk yield is observed with the feeding of very mature/black layer maize silages (DM > 350 g kg⁻¹), despite a high starch:NDF ratio. Overall, these findings indicate that in terms of animal performance the best stage of maturity for harvesting silage maize is when the whole-crop DM content is between 300 and 350 g kg⁻¹.

MILK FATTY ACID COMPOSITION

Effect of replacing grass silage on milk fatty acid composition

Replacing grass silages in a ration with maize silages increases the concentration of medium-chain saturated FAs (C6:0 to C14:0),^{5,98} and C18:2n-6, and decreases the concentration of C16:0, C18:0 and C18:3n-3 in milk fat.^{5,39,98–100} Moreover, replacing grass silage with maize silage decreases the concentration of total n-3 PUFA and increases the concentration of n-6 PUFA in milk, leading to an elevated n-6/n-3 PUFA ratio. This shift in FA composition of milk fat is related to the inherent difference in content and composition of carbohydrates (starch/NDF ratio) and FAs in grass and maize silages.^{6,99} The increase in short- and medium-chain saturated FAs is related to the high starch and lower NDF content of maize silages,⁷ which leads to the overall higher production of volatile FAs. The volatile FAs, acetic acid and β -hydroxybutyric acid are used for the *de novo* synthesis of saturated FAs (<16:0) in the mammary gland.⁹⁹ Moreover, maize silages are particularly rich in C18:2n-6 (10.5 \pm 2.01 vs. 3.3 \pm 0.54 g kg⁻¹ DM in grass silage), whereas grass silages show a high content of C18:3n-3 (11.2 \pm 3.10 vs. 1.1 \pm 0.39 g kg⁻¹ DM in maize silage), which can explain the decreases in n-6/n-3 ratio with the replacement of grass by maize silages.⁷

The effect of replacement of grass with maize silage on the milk conjugated linoleic acid (CLA) content is equivocal. Some studies showed that maize silage-based rations increase the *cis*-9,*trans*-11 C18:2 content of milk fat compared with grass-based diets.^{100,101} Others showed no differences in the *cis*-9,*trans*-11 C18:2 content of milk fat from cows offered grass or maize silage-based diets.^{5,99,102} However, it has been established that the replacement of grass silage with maize silage in the diet increases the milk *trans*-10 C18:1 and the total *trans* C18:1.^{39,99–101} Sterk *et al.*³⁹ observed that the proportion of *trans*-10 C18:1 in milk fat linearly increased during the transition of dairy cows from an 80% grass silage ration

**Figure 5.** Relationship between the starch:neutral detergent fibre (NDF) ratio of maize silages and milk (a) and protein (b) yield of dairy cows.

to an 80% maize silage ration. Some studies showed a significant interaction between maize silage and concentrate (type and proportion in the diet) on the concentration of *cis*-9,*trans*-11 C18:2; *trans*-10, *cis*-12 C18:2; *trans*-11 C18:1 and *trans*-10 C18:1. Maize

silage combined with a low level of concentrate ($\leq 350 \text{ g kg}^{-1}$ DM) in the diet resulted in a significantly higher concentration of *cis*-9,*trans*-11 C18:2 and *trans*-11 C18:1.^{99,100} This means that under normal conditions in the rumen the hydrogenation of C18:2n-6 mainly results in an increased concentration of *cis*-9,*trans*-11 C18:2 and *trans*-11 C18:1, which are considered to be potentially beneficial to human health. However, a combination of maize silage with a higher level of concentrate ($\geq 47.3\%$ ration) or highly degradable carbohydrate concentrates mainly increase the concentration of *trans*-10,*cis*-12 C18:2 and *trans*-10 C18:1.^{6,99,100} The increased proportion of *trans*-10,*cis*-12 C18:2 and *trans*-10 C18:1 in milk fat reduces the milk fat content.^{39,100,102,103} Sterk *et al.*³⁹ showed that an increase in starch content in the diet, by increasing the proportion of maize silage and concentrate, increased ($R^2 = 0.50$) the *trans*-10 C18:1 proportion in milk fat, which was strongly related to a decrease ($R^2 = 0.81$) in milk fat content. The increase in *trans*-10,*cis*-12 C18:2 and *trans*-10 C18:1 proportion in relation to high-starch diets may be related to changes in the bacterial population in the rumen. High-grain diets promote the growth of the bacterial strain *Megasphaera elsdenii* YJ-4^{91,104} and decrease the main cellulose-degrading bacterial strain *Butyrivibrio fibrisolvens*.¹⁰⁵ These different bacterial strains convert C18:2n-6 and C18:3n-3 through different biohydrogenation pathways. *Megasphaera elsdenii* YJ-4 can convert C18:2n-6 to *trans*-10,*cis*-12 C18:2 and *trans*-10 C18:1,¹⁰⁶ whereas *Butyrivibrio fibrisolvens* produces *cis*-9,*trans*-11 C18:2 and *trans*-11 C18:1 as intermediates in the hydrogenation of C18:2n-6.¹⁰⁷ Moreover, increasing the starch/NDF ratio in the diet decreases ($P < 0.05$) the content of iso-C13:0, iso-C15:0, iso-C17:0 and the total odd- and branched-chain FAs, and increased the anteiso-C17:0 in milk fat.⁶ The decrease in odd-chain iso-FA and total odd- and branched-chain FA content in milk fat with rations with a high starch/NDF ratio can be related to the decrease in relative abundance of cellulolytic bacteria in the rumen containing large amounts of iso-FA, compared to amylolytic bacteria.¹⁰⁸ This suggests that the starch content and starch/NDF ratio in the diet is an important determinant of the *trans*-C18:1 isomer profile, as well as to the odd- and branched-chain FAs in milk, due to their effects on the rumen environment and relative abundance and activity of specific bacterial populations in the rumen.

The medium-chain saturated FAs (C12:0–C16:0) are traditionally regarded as hypercholesterolaemic.¹⁰⁹ The contents of C12:0 and C14:0 increase with the replacement of grass silage by maize silage in the dairy cows' ration. However, the major medium-chain saturated FA, C16:0, decreases with the replacement of grass silages by maize silages. This favourable change in milk fat composition with increasing inclusion levels of maize silage in the ration of dairy cows may be counterbalanced by the observed decrease in the total *cis*-monounsaturated and n-3 PUFA in the milk, which is against human dietary recommendations.⁵ Despite some beneficial changes associated with the replacement of grass silage by maize silage, the overall effects on milk FA composition would not be expected to improve long-term human health. However, the effect of maize silage on milk fat composition needs to be balanced against the large increase in DMI, and yields of milk, milk protein and milk fat.

Effect of harvest maturity on milk fatty acid composition

The variation in maturity of maize at harvest during the grain-filling period produces major changes in the content and composition (starch/NDF ratio) of carbohydrates² and FAs,¹⁵ altering the FA profile of milk fat in dairy cows.⁶ The starch/NDF ratio increases and

the content of C18:3n-3 decreased with maturity of the maize silages. Increasing harvest maturity of the maize silages from 319 to 387 g kg^{-1} decreases the content of C18:3n-3 and total n-3 and increased the n-6/n-3 ratio in milk fat. This shift in milk fat composition is caused by a decrease in C18:3n-3 and an increase in C18:2n-6 during the maturation of maize. Increased maturity of maize decreases the content of iso-C13:0, iso-C15:0, iso-C17:0 and total odd- and branched-chain FAs and increases the anteiso-C17:0 in milk fat.⁶ The variation in odd- and branched-chain FAs in milk indicates a shift in the rumen microbial population, as these FAs are predominantly of bacterial origin. The decrease in odd-chain iso-FA and total odd- and branched-chain FA content in milk fat at an increasing maturity (high starch/NDF ratio) can be related to the decrease in the relative abundance of cellulolytic bacteria, containing large amounts of iso-FA, compared to amylolytic bacteria.¹⁰⁸ These findings suggest that increasing maize harvest maturity at ensiling did not affect the medium-chain saturated FAs, but decreased the contents of C18:3n-3 and total n-3 and increased the n-6/n-3 ratio in the milk fat of dairy cows.

CONCLUSIONS

This review summarizes literature data on the nutritional value of maize silages for dairy cows, as well as the effect of maize silage on dairy cow performance and milk quality. Nutrient and FA composition, ensiling quality and total tract digestibility of dietary nutrients of maize silages are quantified, and the major factors that cause this variation are discussed. The nutritive value of maize silages is highly variable. A number of factors cause variation in the nutritive value of maize silages, but most of the variation in the nutrient composition and the total tract digestibility originates from large differences in the maturity of the maize at harvest. Maize ensiled at a very early stage ($\text{DM} < 250 \text{ g kg}^{-1}$) is relatively low in starch/NDF ratio, and this results in a lower DMI, and yields of milk and milk protein. The DMI and yields of milk and protein increase with advancing maturity, reaching an optimum for maize ensiled at DM contents of 300–350 g kg^{-1} , and declines slightly at maturities beyond 350 g kg^{-1} . The changes in milk ($R^2 = 0.599$) and milk protein ($R^2 = 0.605$) yields with maize silage maturity are positively related to changes in starch/NDF ratio. Inclusion of maize silage in grass silage based diets improves the forage DMI by, on average, 2 kg d^{-1} , milk yield by 1.9 kg d^{-1} and milk protein content by 1.2 g kg^{-1} . Maize silage maturity and an increasing proportion of maize silage in grass-based diets change the milk FA profile of dairy cows – notably, the concentration of *cis*-unsaturated FA, C18:3n-3 and n-3/n-6 FA ratio decreased in the milk fat.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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