Effects of free air carbon dioxide enrichment and drought stress on the rumen in sacco degradability of corn silage harvested at various times

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Abstract

The present study investigated the effects of increased atmospheric CO_2 concentration, drought stress and harvest date on the rumen in sacco dry matter degradability of corn silage. A free air carbon dioxide enrichment facility (FACE) was operated in a field to generate a CO_2 concentration of 550 ppm in three treatment plots. Three plots served as control. All plots were divided into two semicircles to produce drought stress by the exclusion of precipitation in one half each. Corn plants were harvested at three dates (26 August, 12 September, 29 September 2008), chopped, ensiled, dried and ground. The in sacco degradability after 2, 4, 8, 16, 24, 48 and 96 h was evaluated using six non-lactating rumen cannuled Holstein cows. The potential dry matter degradability, the sum of water soluble and degradable unsoluble fraction, was not affected by CO_2 elevation. A low CO_2 effect below 1 % unit was found on the effective degradability, which is calculated in consideration of an assumed rate of passage from the rumen. Drought did not alter the potential degradability, but the kinetics of dry matter degradation and decreased the effective degradability by 2 % units. Harvest date affected all degradation parameters. Later harvest was related to an increased potential but reduced effective degradability. The potential degradability had close inverse relationships to neutral detergent fibre concentration ($r = -0.74$, $P < 0.01$) but was positively correlated to starch ($r = 0.80$, $P < 0.01$) and DM ($r = 0.80$, $P < 0.01$). The correlations between effective degradability and crude nutrients were generally not significant. Harvest date will remain an important factor influencing the feed value of corn silage, but the effects of elevated CO_2 concentration and drought stress did not indicate considerable impacts.

Keywords: CO_2 concentration, drought stress, in sacco degradability, corn silage, harvest date

Zusammenfassung

Einfluss von erhöhter CO_2-Konzentration, Trockenstress und Erntezeitpunkt auf die in sacco Abbaubarkeit von Maissilage

Die Effekte von erhöhter atmosphärischer CO_2-Konzentration, Trockenstress und Erntezeitpunkt auf die in sacco Abbaubarkeit der Trockensubstanz von Maissilage wurden untersucht. Unter Verwendung von Freiluft CO_2-Expositionstechnik wurde in einem Maisfeld an drei Stellen eine erhöhte CO_2-Konzentration von 550 ppm generiert. Drei weitere Flächen dienten als Kontrolle. In der Hälfte jeder Stelle erfolgte die Erzeugung von Trockenstress durch Niederschlagsausschluss. Maispflanzen wurden an drei Zeitpunkten geerntet, siliert und vermahlen. Zur Ermittlung der in sacco Abbaubarkeit der Trockensubstanz nach 2, 4, 8, 16, 24, 48 und 96 Stunden wurden sechs am Pansen fistulierte Kühe verwendet. Die potentielle Abbaubarkeit, die Summe aus wasserlöslicher und unlöslicher Fraktion, wurde nicht durch die CO_2-Konzentration beeinflusst. Allerdings konnte ein geringer CO_2 Effekt von unter 1 %-Punkt auf die effektive Abbaubarkeit, welche unter Berücksichtigung einer angenommenen Passagerate aus dem Pansen errechnet wird, festgestellt werden. Trockenstress veränderte die potentielle Abbaubarkeit nicht, beeinflusste jedoch die Kinetik des Abbaues und reduzierte die effektive Abbaubarkeit um 2 %-Punkte. Der Erntezeitpunkt beeinflusste alle untersuchten Abbauparameter. Spätere Ernte induzierte eine erhöhte potentielle, aber verminderte effektive Abbaubarkeit. Die potentielle Abbaubarkeit war negativ mit den Gehalten an neutraler Detergenzienfaser ($r = -0{,}74$, $P < 0{,}01$) sowie negativ mit den Gehalten an Stärke ($r = 0{,}80$, $P < 0{,}01$) und Trockensubstanz ($r = 0{,}80$, $P < 0{,}01$) korreliert. Der Erntezeitpunkt wird ein bestimmender Faktor für den Futterwert von Maissilage bleiben. Die Effekte von steigender atmosphärischer CO_2-Konzentration und Trockenstress lassen nicht auf nennenswerte Veränderungen schließen.

Schlüsselwörter: CO_2 Konzentration, Trockenstress, in sacco Abbaubarkeit, Maissilage, Erntezeitpunkt

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1 Introduction

Changing climatic conditions will likely affect both crop and livestock production with considerable regional differences. Since the beginning of human industrialisation, the atmospheric CO_2 concentration has risen from about 280 ppm to a current value of approximately 390 ppm and may exceed 700 ppm by the middle and 1000 ppm by the end of the century, depending on the prospective greenhouse emission scenario (IPCC, 2007). According to the same survey, many regions in different parts of the world may be affected by a higher incidence of drought.

Various effects of elevated atmospheric CO_2 concentrations on photosynthesis, yield and chemical composition of C_3 plants such as decreased forage and grain protein contents were reported (Schenk et al., 1997; Wu et al., 2004; Weigel and Manderscheid, 2005; Yang. et al., 2007; Manderscheid et al., 2009). In contrast, C_4 plants do not respond to increasing CO_2 concentrations with an increase of photosynthesis and biomass production due to their CO_2 concentration mechanism in the leaves which serves to saturate photosynthesis in ambient air (Ghannoum, 2009). However, in both C_3 and C_4 plants decreased stomatal water loss can be observed under elevated CO_2 concentrations. For example, decreased stomatal plant water loss of corn (*Zea mays L.*) was observed using free air carbon dioxide enrichment (FACE) technology (Leakey et al., 2006). Consequently, positive CO_2 effects on C_4 crops like corn may only be observed under water shortage potentially reducing the negative effects of drought. While the physiological mechanisms of CO_2 x drought interactions are basically known there is little evidence from field scale studies under true agronomic growth conditions testing the consequences of changes of these important climate change factors on crop growth and food quality (DaMatta et al., 2010).

More information about possible impacts of rising CO_2 and its interactions with water supply on corn are necessary as besides the immense importance for human food supply whole plant corn silage is used prevalently as a main component of dairy and beef cattle diets to meet the requirements of high-yielding animals. Both chemical composition and feed value of corn silage strongly depend on plant maturity. Later harvest date was reported to reduce the in sacco degradability of cob-free corn plants (Flachowsky et al., 1993; Akbar et al., 2002). Nevertheless, within the process of starch deposition in the cob later harvest results in a decreased cell wall but increased starch content in whole corn plants indicating an improved ruminal degradability, though the proportion of bypass-starch that is not degradable in the rumen may rise with advanced maturity (Johnson et al., 2003; Filya, I., 2004).

The aim of the present study was to investigate effects of elevated atmospheric CO_2 concentration and drought stress on the ruminal in sacco degradability of whole plant corn silage harvested at different harvest dates.

2 Materials and methods

2.1 FACE experiment and sampling

In 2008, the corn variety "Romario" (S 240, K 240) was planted on an experimental field of the Institute of Biodiversity, Johann Heinrich von Thünen-Institut, Federal Research Institute for Rural Areas, Forestry and Fisheries, Braunschweig, Germany (52°18´N, 10°26´E, 79 m a.s.l.), according to local farm practices. A FACE (Free air carbon dioxide enrichment) system was operated as described by Lewin et al. (1992). Treatments included three rings with blowers and CO_2 enrichment to meet a target CO_2 concentration of 550 ppm during daylight hours (FACE) and three control rings operated with blowers and ambient air of approximately 380 ppm (Control), respectively. The rings had an outer diameter of 20 m and were divided into 2 semicircles. A facility for the exclusion of precipitation in a rain-laden summer was designed to generate drought stress in one semicircle each (drought stress). Water was provided continuously via drip-irrigation in the other semicircles to exceed 50 % field capacity (well watered).

Five whole plants per semicircle were harvested manually within an inner diameter of 16 m at three sampling dates each (26 August (1), 12 September (2) and 29 September (3)). The corn plants were chopped and stored at -18 °C. After defrosting, the samples from all semicircles per treatment and harvest were pooled. Ensiling was performed for 28 consecutive days in airtight glass laboratory jars containing a volume of 2.5 l each. The jars were kept at a constant temperature of 25 °C. Afterwards, the samples were freeze dried for 48 h (Epsilon I/15, Martin Christ Gefriertrocknungsanlagen GmbH, Osterode, Germany) and ground to pass through a 3 mm sieve for further analyses (DR 100/15-40, Retsch GmbH, Haan, Germany).

2.2 In sacco degradability

The in sacco experiment was conducted at the experimental station of the Institute of Animal Nutrition, Friedrich-Loeffler-Institute (FLI), Federal Research Institute for Animal Health, Braunschweig, Germany. Six non-lactating German Holstein cows with a mean initial bodyweight of 663 ± 69 kg equipped with large rubber cannulas in the dorsal rumen sac were used. The animals were kept in a tethered barn with individual troughs and free access to water. The cows were fed on 8.2 kg dry matter (DM) silage mixture, consisting of 60 % corn and 40 % grass silage, 2 kg concentrate mixture and 100 g mineral and vitamin premix per day. The diet was presented twice daily in equal portions at 5:30 h and 15:30 h. 4 ± 0.1 g of ground corn silage samples were weighed in nylon bags (100 x 200 mm, pore size 50 ± 15 µm, Ankom Technology, New York, USA). Two samples of every treatment were incubated in the rumen of each cow 30 minutes before morning feeding for 2, 4, 8, 16, 24, 48 and 96 hours. Immediately after removal from the rumen the bags were transferred into iced water to inhibit microbial activity followed by a cleaning in cold water using a washing machine. Subsequently the samples were oven-dried at 60 °C for 24 hours and weighed. For the determination of the water soluble fraction four bags of each treatment were subjected to the same procedure except the incubation in the rumen.

2.3 Chemical analyses

Water soluble carbohydrates (WSC) in fresh whole corn plants were determined via colorimetry using anthrone as described by Laws and Oldenburg (1993). Fermentation acids and ethanol in corn silages were measured following Canale et al. (1984) and Siegfried et al. (1984). The composition of the corn silages (DM, crude ash, crude protein, ether extract, starch, neutral detergent fibre (NDF) and acid detergent fibre (ADF)) was determined according to the methods of the Association of German Agricultural Analysis and Research Centres (VDLUFA, 1976). NDF and ADF were expressed without residual ash.

2.4 Calculations

The content of DM in the examined silages was corrected for potential substance losses during drying following the equation for corn silages given by Weissbach and Kuhla (1995).

The ruminal in sacco degradability was determined according to Ørskov and McDonald (1979). Dry matter degradability data were fitted to the non-linear degradation equation $p = a + b\,(1 - e^{-ct})$, where p is the DM degradation (%) at time t, a represents the intercept of the degradation curve at time zero or the water soluble fraction including small but insoluble particels, b is the insoluble, but degradable fraction, c is the rate of degradation of b (% h^{-1}) and a + b represents the potential degradability.

The effective degradability was calculated by the equation $P = a + bc / (c + k)$ (McDonald, 1981), where k is the assumed fractional rate of passage of 0.05 h^{-1} from the rumen following Tothi et al. (2003).

2.5 Statistical Analysis

Statistical analyses were performed using the software package SAS version 9.1. DM degradation parameters were analyzed by the GLM procedure. CO_2 concentration (CO_2), irrigation (I) and harvest date (H) were used as the class variables in the model. Pearson correlation coefficients were calculated using the procedure "CORR". The content of water soluble carbohydrates in fresh corn plants and the chemical composition of the generated corn silages could not be subjected to statistical analysis since the samples from all plots per treatment were pooled before ensiling. Differences were considered to be significant at P < 0.05. Trends were declared at P < 0.1.

3 Results

3.1 Chemical composition

The pH values and the concentration of fermentation acids and ethanol of the investigated corn silages are given in Table 1. pH was found to be generally below 4.0 and the contents of butyric acid were below 0.05 % of DM in all samples. Water soluble carbohydrates in fresh plants and the crude nutrient contents of the experimental corn silages are presented in Table 2. The nominal effects of both atmospheric CO_2 concentration and irrigation on the chemical composition were low or not existent. Later harvest was accompanied by a considerable decline of WSC in fresh samples. Furthermore, progressing maturity resulted in nominally increased silage DM and starch but decreased fibre content. However the CO_2 control sample grown under drought stress and harvested at 29 September showed a reduced starch concentration and an increase of WSC compared to all other treatments at the third harvest. Moreover, the increase of WSC was already visible at the first harvest date.

Table 1:
Fermentation acids, ethanol and pH in corn silages (% dry matter).

Treatment[a]			Parameter					
CO_2	I	H	Acetic acid	Propionic acid	Butyric acid	Lactic acid	Ethanol	pH
FACE	WW	1	0.3	0.02	0.00	7.6	0.5	3.6
		2	0.5	0.03	0.03	6.5	0.3	3.6
		3	0.4	0.14	0.02	5.9	0.4	3.7
	DS	1	0.3	0.05	0.00	7.7	1.0	3.6
		2	0.2	0.06	0.00	6.4	0.4	3.7
		3	0.5	0.05	0.00	5.6	0.3	3.8
Control	WW	1	0.4	0.02	0.00	7.9	0.3	3.5
		2	0.3	0.09	0.01	6.1	0.8	3.7
		3	0.3	0.09	0.01	5.6	0.4	3.7
	DS	1	0.3	0.04	0.00	7.9	1.5	3.6
		2	0.2	0.08	0.00	5.9	0.3	3.7
		3	0.6	0.00	0.00	6.3	0.4	3.8

[a] Treatments were CO2 concentration (CO2, FACE vs. Control), irrigation (I, Well Watered (WW) vs.
Drought Stress (DS)) and harvest date (H, 26 August (1), 12 September (2) and 29 September (3)).

Table 2:

Water soluble carbohydrates in fresh corn plants (% DM) as well as DM (% fresh matter) and crude nutrient content of corn silages (% DM).

Treatment[a]			Parameter[b]							
CO_2	I	H	WSC	DM	Ash	CP	EE	NDFom	ADFom	Starch
FACE	WW	1	15.2	27.3	4.5	5.8	1.8	51.3	26.7	21.7
		2	9.4	31.8	3.9	6.0	2.7	44.4	24.6	30.0
		3	8.1	35.5	4.2	5.1	2.5	42.9	22.8	32.6
	DS	1	16.8	28.1	4.3	5.8	2.0	51.3	26.2	17.4
		2	10.9	33.5	3.8	5.6	2.5	47.2	24.0	26.6
		3	6.5	41.2	3.7	5.1	2.5	45.3	23.3	31.9
Control	WW	1	15.7	26.3	4.1	5.9	1.9	49.4	25.8	18.6
		2	9.2	32.5	3.8	5.1	2.4	48.4	25.0	28.3
		3	8.5	37.1	3.9	5.0	2.4	40.9	20.9	35.7
	DS	1	21.1	28.9	4.1	6.3	1.8	52.1	26.1	15.2
		2	11.2	34.8	3.6	5.5	2.4	48.6	24.1	27.3
		3	9.8	39.7	4.1	6.3	2.1	47.3	24.3	26.7

[a] Treatments were CO_2 concentration (CO_2, FACE vs. Control), irrigation (I, Well Watered (WW) vs. Drought Stress (DS)) and harvest date (H, 26 August (1), 12 September (2) and 29 September (3)).

[b] WSC, water soluble carbohydrates; DM, dry matter; Ash, crude ash; CP, crude protein; EE, ether extract; NDFom, neutral detergent fibre expressed without residual ash; ADFom, acid detergent fibre expressed without residual ash.

Table 3:

Effects of atmospheric CO_2 concentration, irrigation and harvest date on degradation parameters (%) of corn silage DM (Means ± SD, n=6).

Treatment[a]			Parameter[b]				
CO_2	I	H	a	b	c	a + b	P
FACE	WW	1	35.9 ± 1.1	32.1 ± 1.0	0.035 ± 0.003	68.0 ± 1.0	49.1 ± 0.6
		2	35.0 ± 0.8	37.3 ± 2.1	0.032 ± 0.007	72.3 ± 2.2	49.5 ± 1.3
		3	34.2 ± 1.0	39.2 ± 1.7	0.032 ± 0.006	73.4 ± 1.2	49.4 ± 1.5
	DS	1	34.0 ± 0.4	33.3 ± 1.2	0.037 ± 0.006	67.3 ± 1.2	48.1 ± 1.1
		2	33.0 ± 1.4	39.4 ± 1.8	0.030 ± 0.005	72.3 ± 2.0	47.6 ± 1.0
		3	29.7 ± 0.7	46.6 ± 0.7	0.028 ± 0.002	76.3 ± 1.0	46.2 ± 1.0
Control	WW	1	36.4 ± 0.5	32.9 ± 1.3	0.033 ± 0.006	69.6 ± 1.3	49.7 ± 1.2
		2	32.4 ± 0.8	40.1 ± 2.2	0.030 ± 0.004	72.5 ± 2.0	47.5 ± 1.4
		3	33.9 ± 0.9	40.9 ± 1.3	0.030 ± 0.005	74.8 ± 1.9	49.0 ± 1.1
	DS	1	35.6 ± 0.8	32.7 ± 1.8	0.033 ± 0.007	68.3 ± 1.9	48.4 ± 1.3
		2	32.7 ± 0.7	39.7 ± 0.8	0.032 ± 0.005	72.4 ± 0.8	48.1 ± 1.3
		3	27.3 ± 1.1	45.7 ± 1.6	0.027 ± 0.004	73.0 ± 1.4	43.3 ± 1.1
P-value							
CO_2			0.020	0.072	0.251	0.647	0.027
I			<0.001	<0.001	0.461	0.610	<0.001
H			<0.001	<0.001	0.002	<0.001	<0.001
$CO_2 \times I$			0.388	0.004	0.592	0.017	0.926
$CO_2 \times H$			<0.001	0.226	0.592	0.050	0.011
I × H			<0.001	<0.001	0.306	0.223	<0.001
$CO^2 \times I \times H$			<0.001	0.765	0.560	0.027	0.003

[a] Treatments were CO_2 concentration (CO_2, FACE vs. Control), irrigation (I, Well Watered (WW) vs. Drought Stress (DS)) and harvest date (H, 26 August (1), 12 September (2) and 29 September (3)).

[b] a = water soluble fraction, b = insoluble, but degradable fraction, c = rate of degradation of b (% h^{-1}), a+b = potential degradability, P = effective degradability.

3.2 *In sacco degradability*

The potential ruminal DM degradability (a + b) of the investigated silages was found to be generally below 80 % (Table 3). Assuming a rate of passage of 0.05 h^{-1} from the rumen, the estimated effective DM degradability (P) did not exceed 50 %. The lowest values of both water soluble fraction (a) and effective degradability were observed for the CO_2 control sample grown under drought stress and harvested at 29 September which was characterized by a low starch but high fibre content, compared to the other treatments.

Though the atmospheric CO_2 concentration had significant effects on water soluble fraction and effective degradability, the nominal impacts on both parameters were below 1 % unit and the other degradation parameters were not influenced by CO_2 enrichment. Drought stress decreased the water soluble fraction and the effective degradability of the incubated samples by 2.5 and 2 % units, respectively. However the insoluble, but degradable fraction (b) was increased by 2.5 % units resulting in a lack of impacts of drought stress on the potential degradability of silage DM. Harvest date had a significant effect on all calculated degradation parameters and altered both DM degradation kinetics and degradability. Later harvest resulted in a decreased water soluble fraction and effective degradability as well as a slower rate of DM degradation. However, the rising insoluble, but degradable fraction overcompensated these effects and the potential degradability increased with later harvest. The pooled potential degradabilities were 71.6 ± 3.4 % for FACE and 71.8 ± 2.7 % for CO_2 Control treatment, 71.8 ± 2.9 % for well watered and 71.6 ± 3.3 % for drought stress treatment as well as 68.3 ± 1.5 %, 72.4 ± 1.7 % and 74.4 ± 1.9 % for harvest 1, 2 and 3, respectively.

Though various interactions were found to influence the kinetics of DM degradation significantly, the nominal differences were mostly low or undirected. Interestingly, CO_2 elevation resulted in a slightly higher potential degradability during drought stress (1 % unit) but lower a + b (0.7 % unit) during sufficient water supply (CO_2 x I. P = 0.017). Furthermore, the CO_2 x I x H interaction was found to be significant for the potential degradability (P = 0.027). For harvest 3, the CO_2 control samples showed a reduced a + b when grown under drought stress (3 % units).

WSC in fresh samples and the cell wall contents of the produced silages were found to have close inverse relationships to the insoluble, but degradable fraction and the potential degradability, respectively, however ADFom was closer negatively correlated to the fraction b than NDFom (Table 4). Furthermore, positive relationships of WSC and ADFom to both water soluble fraction and rate of DM degradation were observed. Both silage DM and starch content were positively correlated to the insoluble, but degradable fraction and the potential degradability, respectively, but had negative relationships to the other degradation parameters. Except for DM, the correlations between the examined nutrients and the effective degradability were generally not significant.

Table 4:

Correlation coefficients between degradation parameters and water soluble carbohydrates in fresh corn plants (% DM), silage DM (% fresh matter) as well as silage crude nutrient contents (% DM).

Parameter[a]	Fraction[b]				
	WSC	DM	ADFom	NDFom	Starch
a	0.54**	-0.79**	0.43**	0.22	-0.39**
b	-0.79**	0.93**	-0.71**	-0.58**	0.71**
c	0.35**	-0.43**	0.35**	0.28**	-0.32**
a + b	-0.81**	0.80**	-0.77**	-0.74**	0.80**
P	0.23	-0.53**	0.17	-0.04	-0.08

[a] a = water soluble fraction, b = insoluble, but degradable fraction, c = rate of degradation of b (% h^{-1}), a + b = potential degradability, P = effective degradability.
[b] WSC, water soluble carbohydrates; DM, dry matter; Ash, crude ash; NDFom, neutral detergent fibre expressed without residual ash; ADFom, acid detergent fibre expressed without residual ash.
*: P < 0.05, ** P < 0.01.

4 Discussion

In a recent study, Porteaus et al. (2009) investigated the responses of the nutritive value of wheat (*Triticum aestivum L.*) straw and grain to an increased atmospheric CO_2 concentration of 550 ppm and reported the quality to be altered in a potentially adverse fashion. Though the composition of wheat straw was generally not affected by CO_2 enrichment, significant reductions of crude protein and NDF in grain DM were reported to be accompanied by increased starch concentrations. In C_4 plants, CO_2 is concentrated in the leaves {Ghannoum, 2009) and the effect of elevated atmospheric CO_2 will therefore likely be limited. Leakey et al. (2006) demonstrated in a FACE experiment that increased atmospheric CO_2 did not stimulate corn photosynthesis, yield, the activity of key photosynthetic enzymes or metabolic markers of carbon and nitrogen status in the absence of drought. In a recent FACE trial CO_2 enrichment did not increase corn growth and yield under sufficient water supply but under drought stress (Manderscheid et al., 2011). Accordingly, the effects of increased CO_2 on both water soluble fraction and effective ruminal degradability of the investigated corn silages did not indicate relevant alterations of the feed value in the present experiment as for both parameters the nominal differences between the CO_2 treatments were below 1 % unit.

Drought stress can decrease biomass and grain yield of corn (Bolanos and Edmeades, 1993; Azeez et al., 2005;

Efeoglu et al., 2009), kernel number per ear (Otegui et al., 1995; Zinselmeier et al., 1999; Boyer and Westgate, 2004) as well as thousand kernel weight (Weerathaworn et al., 1992) and hence potentially impact the feed value of corn silage since starch as a major constituent is primarily located in the grains. However, restricted irrigation did not affect the potential DM degradability of the incubated samples and, though significant, only low nominal effects on the kinetics of DM degradation and the estimated effective degradability were found. Furthermore, a slightly decreased effective ruminal DM degradability of corn silage, a feedstuff containing relatively slowly rumen degradable starch (Tothi et al., 2003; Matthe et al., 2003), does not necessarily indicate a reduced feed value. A potentially increased flooding of starch into the small intestine may result in a more efficient use of starch for milk synthesis than that digested in the rumen (Nocek and Tamminga, 1991). However, within the limits of the conducted analyses it is unknown which compounds contributed to the decreased effective degradability of the investigated silages grown under drought stress.

In corn, atmospheric CO_2 enrichment was reported to result in decreased plant water loss via stomatal conductance (Leakey et al., 2006) and an increase of the water use efficiency of biomass production (Manderscheid et al., 2011). That may lead to the hypothesis that atmospheric CO_2 elevation may reduce the negative effects of drought stress on corn growth and composition and hence indirectly improve the feed value of corn silage during periods of drought. However, this was not reflected in the examined parameters of DM degradation in the present experiment. No significant CO_2 x I interaction was observed for the effective degradability of silage DM and though significance was calculated for the potential degradability, the nominal effects were below 1 % unit. However, due to elevated CO_2 a slightly higher potential degradability was found during drought stress but it decreased if the plants were grown well watered. For harvest 3, the CO_2 control sample grown under drought stress was characterized by an unexplainable low starch but high fibre content in comparison to the other treatments and the previous harvest. These differences were not clearly explainable within the performed analyses and therefore incorrect sampling may have contributed to this effect.

Advancing maturity is accompanied by substantial changes in the chemical composition of corn since WSC levels in fresh whole plants were reported to decrease (Johnson et al., 2003; Filya et al., 2006), whereas starch concentration and DM percentage increase up to a certain limit (Browne et al., 2004; Browne et al., 2005; Mc Geough et al., 2010). In the present experiment, these alterations were reflected in significant effects on both kinetics and extent of ruminal degradability. Insoluble, but degradable fraction and potential degradability increased gradually with later harvest. Both parameters were found to have close positive relationships to DM and starch content and were negatively correlated to silage fibre concentration, which is known to decrease with later harvest (Filya, 2004). These observations were consistent because increasing starch, but decreasing fibre contents will likely enhance the ruminal DM degradability of corn silage since ground corn grain was reported to be highly degradable exceeding 90 % after longer periods of incubation in the ovine forestomach (Flachowsky et al., 1992). Though the ruminal DM degradability of cobs does not necessarily increase with later harvest, their percentage of the whole plants rises and they are generally faster and to a greater extent degradable than stover (Akbar et al., 2002), which were shown to contain more fibre and to become less degradable with later harvest (Flachowsky et al., 1993). Nevertheless, these processes do not imperatively lead to an improved DM degradability of ensiled corn. Jochmann et al. (1999) compared both in sacco DM degradability and effective degradability of corn silages harvested at different maturity stages and did not observe significant differences between the incubated samples.

5 Conclusion

In the present experiment, the low effects of rising atmospheric CO_2 concentration and drought stress on the calculated parameters of in sacco DM degradation of corn silage did not indicate considerable alterations of the future feed value of ensiled whole corn plants grown under changed cultivation conditions. In contrast, harvest date influenced all evaluated degradation parameters and will likely remain an important factor determining feed value and ruminal degradability of corn silage.

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References

Akbar MA, Lebzien P, Flachowsky G (2002) Measurement of yield and in situ dry matter degradability of maize varieties harvested at two stages of maturity in sheep. Anim Feed Sci Tech 100(1-2):53-70

Azeez JO, Chikoye D, Kamara AY, Menkir A, Adetunji MT (2005) Effect of drought and weed management on maize genotypes and the tensiometric soil water content of an eutric nitisol in South Western Nigeria. Plant Soil 276:61-68

Bolanos J, Edmeades GO (1993) 8 cycles of selection for drought tolerance in lowland tropical maize : 1. Responses in grain-yield, biomass, and radiation utilization. Field Crop Res 31:233-252

Boyer JS, Westgate ME (2004) Grain yields with limited water. J Exp Bot 55:2385-2394

Browne EM, Juniper DT, Bryant MJ, Beever DE (2005) Apparent digestibility and nitrogen utilization of diets based on maize silage harvested at three stages of maturity and fed to steers. Grass Forage Sci 60:274-282

Browne EM, Juniper DT, Bryant MJ, Beever DE, Fisher AV (2004) Intake, liveweight gain and carcass characteristics of beef cattle given diets based on forage maize silage harvested at different stages of maturity. Anim Sci 79:405-413

Canale A, Valente ME, Ciotti A (1984) Determination of volatile carbolic-acids (C1-C51) and lactic-acid in aqueous acid-extracts of silage by high-performance-liquid-chromatography. J Sci Food Agr 35:1178-1182

DaMatta FM, Grandis A, Arenque BA, Buckeridge MS (2009) Impacts of climate changes on crop physiology and food quality. Food Res Int 43:1814-1823

Efeoglu B, Ekmekci Y, Cicek N (2009) Physiological responses of three maize cultivars to drought stress and recovery. S Afr J Bot 75:34-42

Filya I (2004) Nutritive value and aerobic stability of whole crop maize silage harvested at four stages of maturity. Anim Feed Sci Tech 116:141-150

Filya I, Sucu E, Karabulut A (2006) The effect of Lactobacillus buchneri on the fermentation, aerobic stability and ruminal degradability of maize silage. J Appl Microbiol 101:1216-1223

Flachowsky G, Baldeweg P, Schein G (1992) A note on the in sacco dry-matter degradability of variously processed maize grains and of different maize varieties in sheep. Anim Feed Sci Tech 39:173-181

Flachowsky G, Peyker W, Schneider A, Henkel K (1993) Fiber analyses and in sacco degradability of plant fractions of 2 corn varieties harvested at various times. Anim Feed Sci Tech 43:41-50

Ghannoum O (2009) C4 photosynthesis and water stress. Ann Bot 103:635-644

Forster PV, Ramaswamy P, Artaxo P, Berntsen T, Betts R, Fahey DW, Haywood J, Lean J, Lowe DC, Myhre G, Nganga J, Prinn R (2007) Changes in atmospheric constituents and in radiative forcing. In: Solomon S, Qin D, Mannin M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) Climate change 2007 : the physical science basis : contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge : Cambridge Univ Pr, pp 131-217

Jochmann K, Lebzien P, Dänicke R, Flachowsky G (1999) Zum Einfluß des Reifestadiums von Maispflanzen und des Einsatzes von Milchsäurebakterien bei ihrer Einsilierung auf die Nährstoffumsetzungen im Verdauungstrakt von Milchkühen. J Anim Physiol Anim Nutr 82:178-192

Johnson LM, Harrison JH, Davidson D, Mahanna WC, Shinners K (2003) Corn silage management : effects of hybrid, maturity, inoculation, and mechanical processing on fermentation characteristics. J Dairy Sci 86:287-308

Laws W, Oldenburg E (1993) Zuckergehalte von Wintergerste und Mais : 2. Methodenvergleich HPLC/Anthron. Landbauforsch Völkenrode 43(2/3):60-63

Leakey ADB, Uribelarrea M, Ainsworth E, Naidu SL, Rogers A, Ort DR, Long SP (2006) Photosynthesis, productivity, and yield of maize are not affected by open-air elevation of CO_2 concentration in the absence of drought. Plant Physiol 140:779-790

Lewin KF, Hendrey GR, Kolber Z (1992) Brookhaven National Laboratory free-air carbon-dioxide enrichment facility. Crit Rev Plant Sci 11:135-141

Manderscheid R, Erbs M, Weigel H-J (2012) Interactive effects of free-air CO_2 enrichment and drought stress on maize growth. Eur J Agron [online]. To be found at <http://dx.doi.org/10.1016/j.eja.2011.12.007> [quoted 29.05.2012]

Manderscheid R, Pacholski A, Frühauf C, Weigel H-J (2009) Effects of free air carbon dioxide enrichment and nitrogen supply on growth and yield of winter barley cultivated in a crop rotation. Field Crop Res 110(3):185-196

Matthe A, Lebzien P, Hric I, Flachowsky G (2003) Influence of prolonged adaptation periods on starch degradation in the digestive tract of dairy cows. Anim Feed Sci Technol 103(1):15-27

McGeough EJ, O'Kiely P, Foley PA, Hart KJ, Boland TM, Kenny DA (2010) Methane emissions, feed intake, and performance of finishing beef cattle offered maize silages harvested at 4 different stages of maturity. J Anim Sci 88:1479-1491

McDonald I (1981) A revised model for the estimation of protein degradability in the rumen. J Agr Sci 96:251-252

Nocek JE, Tamminga S (1991) Site of digestion of starch in the gastrointestinal tract of dairy cows and its effect on milk yield and composition. J Dairy Sci 74:3598-3629

Orskov ER, McDonald I (1979) Estimation of protein degradability in the rumen from incubation measurements weighted according to rate of passage. J Agr Sci 92:499-503

Otegui ME, Andrade FH, Suero EE (1995) Growth, water-use and kernel abortion of maize subjected to drought at silking. Field Crop Res 40:87-94

Porteaus F, Hill J, Ball AS, Pinter PJ, Kimball BA, Wall GW, Adamsen FJ, Hunsaker DJ, LaMorte RL, Leavitt SW, Thompson TL, Matthias AD, Brooks TJ, Morris CF (2009) Effect of Free Air Carbon dioxide Enrichment (FACE) on the chemical composition and nutritive value of wheat grain and straw. Anim Feed Sci Technol 149:322-332

Schenk U, Jäger H-J, Weigel H-J (1997) The response of perennial ryegrass/white clover swards to elevated atmospheric CO_2 concentrations : II. Effects on yield, fodder quality and water use. Grass Forage Sci 52:232-241

Siegfried R, Rückemann H, Stumpf G (1984) Eine HPLC-Methode zur Bestimmung organischer Säuren in Silagen. Landwirt Forsch 37:298-304

Tothi R, Lund P, Weisbjerg MR, Hvelplund T (2003) Effect of expander processing on fractional rate of maize and barley starch degradation in the rumen of dairy cows estimated using rumen evacuation and in situ techniques. Anim Feed Sci Technol 104:71-94

Van Soest PJ, Robertson JB, Lewis BA (1991) Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. J Dairy Sci 74:3583-3597

VDLUFA (1976) Die chemische Untersuchung von Futtermitteln. Darmstadt: VDLUFA-Verl

Weerathaworn P, Thiraporn R, Soldati A, Stamp P (1992) Yield and agronomic characters of tropical maize (Zea Mays L.) cultivars under different irrigation regimes. J Agron Crop Sci 168:326-336

Weigel H-J, Manderscheid R (2005) CO_2 enrichment effects on forage and grain nitrogen content of pasture and cereal plants. J Crop Impr 13(1-2):73-89

Weissbach F, Kuhla S (1995) Substance losses in determining the dry matter content of silage and green fodder: arising errors and possibilities of correction. Übers Tierernährg 23:189-214

Wu DX, Wang GX, Bai YF, Liao JX (2004) Effects of elevated CO_2 concentration on growth, water use, yield and grain quality of wheat under two soil water levels. Agric Ecosyst Environ 104:493-507

Yang LX, Wang YL, Dong GC, Gu H, Huang JY, Zhu JG, Yang HJ, Liu G, Han Y (2007) The impact of free-air CO_2 enrichment (FACE) and nitrogen supply on grain quality of rice. Field Crop Res 102:128-140

Zinselmeier C, Jeong BR, Boyer JS (1999) Starch and the control of kernel number in maize at low water potentials. Plant Physiol 121:25-35