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Evaluation of genotype and environmental variation in fibre content of silage maize using a model-assisted approach

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Abstract

High cell wall contents of forage maize may limit digestibility and fodder intake of ruminants, and reduce methane output in biogas plants. However, not too many empirical studies on the impact of hybrid and environment on the content of cell wall constituents of silage maize are found in literature. A 3-year field experiment was conducted in northern Germany to evaluate differences in whole-crop and stover fibre content (neutral detergent fibre, acid detergent fibre, cellulose, hemicellulose, acid detergent lignin) among a set of commercial hybrids covering three maturity groups (early to mid-late) and different maturation types (dry-down, normal, stay-green). The experimental data were used additionally, to calibrate the dynamic FOPROQ model quantifying the relative contributions of individual environmental factors (temperature, radiation, soil water availability) on fibre contents. Statistical analysis showed only few interactions of harvest time × variety within maturity group, all of which occurred at early growth stages only. Differentiation was more evident for maturity groups after grain set, with a maximum difference of 58.1 g NDF, 43.0 g ADF, 37.5 g cellulose, and 15.2 g hemicellulose kg^{-1} dry matter for the whole-crop, but diminished with advancing maturity. The FOPROQ model proved suitable for describing seasonal changes in fibre components. Model calibration revealed quality changes to be driven primarily by temperature and radiation, with negligible impact from soil water availability. A 30-year simulation study documented a moderate effect of environment on variation in fibre components, with coefficients of variation ranging between 2.6% (hemicellulose) and 8.9% (cellulose). For the range of weather conditions and genotypes of this study, the variation in fibre contents was more strongly influenced by environmental than by genotypic factors.

Keywords: Silage maize; Cell wall constituents; Genotype; Environmental conditions; Model; Simulation study

1. Introduction

Silage maize is a key component of ruminant diets due to its high yield and energy content and has also gained importance in recent years as a substrate for biogas production, especially in Germany. For both applications it is essential to harvest the crop at the optimum developmental stage, as both forage quality and methane yield may change with advancing maturity (Filya, 2004; Heiermann and Plöchl, 2004). Cell wall concentration, composition and degradability are thought to limit forage digestibility (Jung and Deetz, 1993; Jensen et al., 2005) and influence anaerobic digestion (Eder et al., 2006). Accordingly, the proportion of cell wall fractions may serve as an indicator of quality changes in silage maize, especially for maize stover (Cone and Engels, 1993; Verbic et al., 1995).

Genotype and weather conditions are known to be potentially influential on the content of cell wall fractions (Struik et al., 1985; Hunt et al., 1993) and on cell wall quality (Struik, 1985; Jung and Buxton, 1994). Efforts to improve stover quality, e.g. by the introduction of stay-green hybrids, have so far made little progress (Ettle and Schwarz, 2003). Brown midrib hybrids, which are characterised by higher cell wall digestibility (Barrière et al., 2003), are of no importance to the European market. Environmental conditions may affect the content of cell wall fractions directly and/or indirectly if plant morphology, e.g. the ear-to-stover ratio, is modified. Struik et al. (1985) documented the impact of temperature on cell wall content in different developmental phases. Lower cell wall concentrations were consistently reported for hot and/or dry growing seasons compared to cool and/or wet conditions (Allen et al., 1991; Wiersma et

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al., 1993; Cox et al., 1994), which may be due to the accumulation of water-soluble carbohydrates (Crasta et al., 1997). As yet little focus was put on investigating the combined importance of genotype and weather factors on the seasonal changes in cell wall fractions.

The use of appropriate models can facilitate quantification of the environmental impact on fibre content and provide tools for predicting cell wall content and composition. Simple regression approaches relating fibre content to weather factors have had limited explanatory power (Crasta et al., 1997; Darby and Lauer, 2002). The dynamic, weather-based FOPROQ model (Kornher et al., 1991), originally developed for grassland, considers the influence of environmental conditions, e.g. temperature, radiation and plant-available soil water, and of crop characteristics and management inputs on the development of yield and forage quality. Recently, the model has been successfully introduced as a harvest time prognosis tool in silage maize for whole-crop dry matter content (Herrmann et al., 2006). Extending the model applicability to the content of cell wall fractions would be useful from a scientific and practical point of view.

The objective of the present study was therefore to investigate the contribution of genotype and weather conditions to seasonal changes in cell wall fractions, characterised by neutral detergent fibre (NDF), acid detergent fibre (ADF), hemicellulose, cellulose, and acid detergent lignin (ADL). Applying the dynamic FOPROQ model allowed us to (i) quantify environmental impact by means of a long-term simulation study and (ii) assess the importance of individual environmental factors (temperature, radiation, soil water availability).

2. Materials and methods

2.1. Experimental design and trial management

The study is based on data collected in a field trial repeated over 3 years (2001–2003) at the experimental farm 'Hohenschulen' (53°18′N, 9°58′E, 32 m altitude) of the University of Kiel in northern Germany. The soil type at Hohenschulen can be classified as pseudogleyic sandy loam. The prevailing climate at the experimental site is humid-temperate, with an average annual precipitation of 759 mm and daily mean temperature of 8.7 °C (1974–2005). Weather conditions differed considerably among the experimental years (see Table 1). While temperatures in 2001 were at average levels, the daily mean temperature during the maize vegetation period (1 May to 30 September) in 2002 and 2003 exceeded the long-term average substantially by up to 2 °C. Precipitation was exceptionally low in 2003, at only 63% of the long-term average, while the previous 2 years had above average amounts of rainfall.

A one-factorial block design with two replicates (plot size: 90 m^2) was used for the field trial, where eight hybrids (Arsenal, Oldham, Symphony, Probat, Attribut, Fuego, Clarica, Benicia), covering a wide range of maturity groups (early to mid-late) and different maturation types (dry-down, normal and stay-green), were investigated. Maize was sown in early May in rows 0.75 m apart, with a final plant density of 9–10 plants m^{-2}. Plots received an annual application of 150 kg N ha^{-1}, split into three dressings: before planting, first-leaf-stage and 6–8-leaf stage. Phosphorous (P_2O_5), potassium (K_2O) and magnesium (MgO) were applied at 40, 250, and 30 kg ha^{-1}, respectively. Plant protection was conducted according to the codes of 'Good Agricultural Practice in Plant Protection and Fertilization'. Crop samples were taken on six dates, which were chosen to be in line with developmental stages of a reference hybrid (Probat, mid-early maturity group), scheduled to phenological stage of BBCH 32 (Meier, 2001) and ear dry matter (DM) contents of 20, 30, 40, 50, and 55%. On each sampling date 10 consecutive plants, randomly assigned to a row section bordered by unharvested rows, were hand-clipped near the soil surface. The plants were weighed, separated into ear and stover (including husks), and chopped. Representative sub-samples of ear and stover were oven-dried at 105 °C until reaching constant weight to obtain DM content and yield. Additional sub-samples of ear and stover were stored at −18 °C for quality determination. After freeze-drying, the samples were first pre-ground in a rotor beater mill to pass a 4 mm sieve (Retsch GmbH, Haan, Germany) and subsequently ground in a Cyclotec mill (Foss Tecator AB, Höganäs, Sweden) to a 1 mm particle size.

2.2. Analysis of cell wall fractions

The contents of cell wall fractions were estimated using near-infrared reflectance spectroscopy (NIRS). Ground samples were scanned on a NIRSystems 5000 scanning monochromator (FOSS GmbH, Rellingen, Germany), and software (ISI-version) for data collection and manipulation was supplied by Infrasoft International® (ISI, Port Matilda, PA, USA). Calibrations were developed separately for ear and stover. Calibration and validation subset samples were analysed for the content of ash-free NDF, ADF, and ADL according to Goering and van Soest

Table 1
Climatic conditions given as annual values and corresponding data for the maize vegetation period (1st May to 30th September) of mean temperature (°C), mean radiation (J cm^{-2} d^{-1}), and precipitation sum (mm) for the experimental years (2001–2003) and the long-term average (1974–2005)

	Precipitation (mm)		Temperature (°C)		Radiation (J cm^{-2} d^{-1})	
	Annual	Vegetation period	Annual	Vegetation period	Annual	Vegetation period
2001	810.3	436.2	8.8	14.8	987.9	1658.0
2002	960.9	445.3	9.7	16.4	1002.4	1651.3
2003	524.1	210.1	9.6	16.7	1070.3	1731.5
1974–2005	759.1	332.4	8.7	14.8	989.1	1632.2

Data were kindly provided for the nearest weather station (Kiel-Holtenau) by the German Weather Service.

(1970, cited in Naumann and Basler, 1976). Ear samples were pre-treated with heat-stable amylase to ensure starch degradation. Standard errors of validation ranged between 0.97 and 1.80 g kg^{-1} DM, depending on plant part and quality parameter. The estimated contents of NDF, ADF, and ADL were then used to calculate the hemicellulose and cellulose concentrations of ear and stover according to the following equations: hemicellulose = NDF − ADF and cellulose = ADF − ADL. Whole-plant contents of cell wall fractions were derived from corresponding values of stover and ear and their weight proportions.

2.3. Statistical analysis

A mixed-model analysis was performed using PROC MIXED of SAS 8.2 (SAS Institute Inc., 2001) by considering year, maturity group, variety within maturity group, harvest date, and block as fixed factors and by assuming a heterogeneous, autoregressive covariance structure for repeated measurements. The resulting model equation for a given cell wall fraction CW was:

$$\begin{aligned}\mathrm{CW}_{ijklm} = {} & M + y_i + \mathrm{mat}_j + \mathrm{var(mat)}_{jk} + \mathrm{har}_l + \mathrm{bl}_m \\ & + (\mathrm{mat} \times \mathrm{har})_{jl} + (\mathrm{var(mat)} \times \mathrm{har})_{jkl} + (y \times \mathrm{mat})_{ij} \\ & + (y \times \mathrm{var(mat)})_{ijk} + (y \times \mathrm{har})_{il} + (y \times \mathrm{mat} \times \mathrm{har})_{ijl} \\ & + (y \times \mathrm{var(mat)} \times \mathrm{har})_{ijkl} + e_{ijklm}\end{aligned}$$

where M is the overall mean, y_i the year i, mat_j the maturity group j, $\mathrm{var(mat)}_{jk}$ the variety k nested in maturity group j, har_l the harvest date l, bl_m the block m, and e_{ijklm} denotes the residual error. Effects were considered significant in all statistical calculations for p-values <0.05. For significant interactions, linear contrasts were calculated using the SLICE procedure in SAS. Comparison of means was performed by t-test with a Bonferroni–Holm adjustment.

2.4. Modelling contents of cell wall constituents

The FOPROQ (FOrage PROduction Quality) model was applied to simulate the contents of NDF, ADF, hemicellulose, and cellulose. Lignin was not considered because of insufficient variation in the whole-crop. Model calibration was based on the 2001–2003 data. FOPROQ consists of two sub-modules, one for DM yield and one for forage quality, see also Appendix A. The model requires as input daily data on average air temperature (°C), precipitation (mm), potential rates of evapotranspiration (mm), and incident global radiation (MJ m^{-2} d^{-1}). Growth calculations are based on weather data as well as plant and soil characteristics. The quality and growth sub-modules are linked via the plant-available soil water, which is calculated by a simple soil water balance in the growth part and serves as input for the quality part. The sub-module for quality prediction assumes the existence of different levels of quality over the entire growing period, with gradual changes from one level to another. The present model, however, allows only for two such levels. The levels and changes in quality depend on input variables reflecting genetics, environment, and management. Environmental factors (temperature, radiation, and plant-available soil water) are converted into corresponding change rates based on exponential or negative exponential functions. These change rates are combined multiplicatively to obtain daily environmental changes rates, which then are accumulated and related to forage quality by appropriate threshold response functions. Genotypic differences were accounted for by parameters t_c and T_{th} (constant and threshold of temperature change function), r_c and R_{th} (constant and threshold of radiation change function), and m_c (constant in soil moisture change function) determining the shape of the functions for temperature, radiation, and soil moisture. Furthermore, genotype-specific values were required for the parameters controlling the threshold response function: Q_n (minimum content of fibre fraction at onset of growth), Q_x (maximum content at maturity), c (determines the inclination), and v (determines the inflexion point of the curve).

Environmental conditions may influence the content of cell wall constituents indirectly by affecting processes such as photosynthesis, respiration, morphological development, and ageing (Deinum et al., 1996; Groot et al., 2003). External factors may also affect chemical composition directly—higher temperatures, for instance, are thought to accelerate lignification of forage species (Deinum, 1984; Wilson et al., 1991). However, the structure of the FOPROQ model cannot differentiate between direct and indirect effects. Taking both effects into account, we assumed temperature, radiation, and water deficit to accelerate changes in fibre components of both whole-crop and stover.

Model calibration was conducted by an integrated parameter optimisation module, which minimises the deviation between simulated and experimental data in terms of the sum of squared residuals. Model parameters were optimised separately for each hybrid, and model performance was assessed by the root mean square error (RMSE) and the coefficient of determination.

2.5. Design of the simulation study

In order to obtain a comprehensive assessment of fibre component variation due to environmental factors, we applied the calibrated model to a complementary long-term simulation study based on 30 years of weather records (1976–2005). The simulation study was conducted using the module FOSIM, which runs FOPROQ with a pre-specified harvest strategy, controlling the harvest time by setting target values of harvest date, DM yield, and/or forage quality. As soon as one of the target values was reached, the simulation run was terminated. We set the harvest time in the study at a whole-crop DM content of 320 g DM kg^{-1} fresh weight. For unfavourable climatic conditions with delayed maturity we set 10 October as the latest possible harvest date if silage maturity had not been reached by then.

3. Results

Samples included in statistical analysis and model calibration covered a wide range of developmental stages, as indicated by the whole-crop DM content (Table 2). Our criterion of 32% DM for silage maturity was met at harvest 5 for the early and mid-early maturity group, and at harvest 6 for the mid-late group. The

Table 2
Whole-plant dry matter content (g kg^{-1} fresh matter) of the tested hybrids provided for the sampling dates as means of the growing periods 2001–2003

Harvest date	Arsenal (early)	Oldham (early)	Symphony (early)	Probat (mid-early)	Attribut (mid-early)	Fuego (mid-early)	Clarica (mid-late)	Benicia (mid-late)
1	108.1	99.4	114.8	103.9	112.2	107.1	109.4	95.7
2	207.5	209.1	223.1	200.9	212.1	218.8	197.7	195.5
3	231.8	224.0	253.0	220.5	233.9	246.7	216.1	222.0
4	293.7	288.7	303.5	270.2	276.2	285.9	256.1	256.2
5	347.7	322.1	335.1	321.9	319.9	316.1	284.7	288.4
6	393.2	407.1	391.4	388.4	385.1	369.1	333.6	327.8

Table 3
F-values and levels of significance for stover contents of neutral detergent fibre (NDF), acid detergent fibre (ADF), hemicellulose, cellulose, and acid detergent lignin (ADL) of eight silage maize hybrids in three maturity groups harvested on six dates between 2001 and 2003

Effect	Num DF	*F*-value				
		NDF	ADF	Hemicellulose	Cellulose	Lignin
Year	2	54.93***	14.93***	59.34***	55.64***	115.49***
Maturity	2	63.76***	21.71***	62.82***	39.75***	1.60n.s.
Var(mat)	5	7.28***	8.44***	4.11**	6.90***	5.11**
Har.date	5	1194.15***	1417.64***	299.35***	1568.70***	280.51***
Block	1	5.85*	4.14n.s.	2.85n.s.	3.60n.s.	5.17*
Maturity × har.date	10	16.13***	10.18***	7.19***	11.19***	3.39**
Var(mat) × har.date	25	2.48**	3.17**	1.68n.s.	2.91**	2.31**
Year × maturity	4	2.72*	1.51n.s.	1.80n.s.	1.75n.s.	1.47n.s.
Year × var(mat)	10	2.15*	1.67n.s.	1.20n.s.	1.52n.s.	0.63n.s.
Year × har.date	10	48.35***	41.03***	23.61***	60.28***	20.11***
Year × har.date × maturity	20	3.70**	4.68***	1.76n.s.	5.55***	1.66n.s.
Year × har.date × var(mat)	50	0.91n.s.	1.30n.s.	0.93n.s.	1.50n.s.	1.31n.s.

* Significant at the 0.05 probability levels, respectively.
** Significant at the 0.01 probability levels, respectively.
*** Significant at the 0.001 probability levels, respectively.

large variation in crop development is reflected by the analysis of variance, where harvest date consistently represented the largest variance component (Tables 3 and 4). Apart from harvest date, environmental conditions had an impact on all measured cell wall fractions as indicated by significant main effects of year and 2-way interactions of year with harvest date and maturity (only for whole-crop). Genotype had a considerable influence as well, as substantiated by significant effects of maturity, variety within maturity, and their interactions with harvest date. The 3-way interaction year × harvest date × maturity was generally significant, but linear contrasts performed by the SAS slice option in PROC MIXED showed similar effects in each year. Few variety

Table 4
F-values and levels of significance for whole-crop contents of neutral detergent fibre (NDF), acid detergent fibre (ADF), hemicellulose, cellulose, and acid detergent lignin (ADL) of eight silage maize hybrids in three maturity groups harvested on six dates between 2001 and 2003

Effect	Num DF	*F*-value				
		NDF	ADF	Hemicellulose	Cellulose	Lignin
Year	2	84.51***	93.42***	48.17***	157.14***	65.74***
Maturity	2	108.11***	166.64***	14.79***	156.76***	3.25*
Var(mat)	5	7.86***	7.42***	6.36***	10.36***	2.21n.s.
Har.date	5	377.15***	367.10***	178.36***	432.77***	132.18***
Block	1	0.69n.s.	0.82n.s.	0.83n.s.	0.39n.s.	3.47n.s.
Maturity × har.date	10	18.92***	25.39***	3.96**	32.12***	3.46**
Var(mat) × har.date	25	1.90*	2.67**	1.36n.s.	1.96*	1.54n.s.
Year × maturity	4	6.74**	6.86**	2.78*	9.65***	1.55n.s.
Year × var(mat)	10	1.27n.s.	1.24n.s.	1.52n.s.	1.28n.s.	0.61n.s.
Year × har.date	10	30.69***	30.07***	16.28***	34.88***	16.74***
Year × har.date × maturity	20	3.04**	4.37***	1.60n.s.	4.12***	2.54**
Year × har.date × var(mat)	50	0.96n.s.	1.35n.s.	0.75n.s.	1.08n.s.	1.20n.s.

* Significant at the 0.05 probability levels, respectively.
** Significant at the 0.01 probability levels, respectively.
*** Significant at the 0.001 probability levels, respectively.

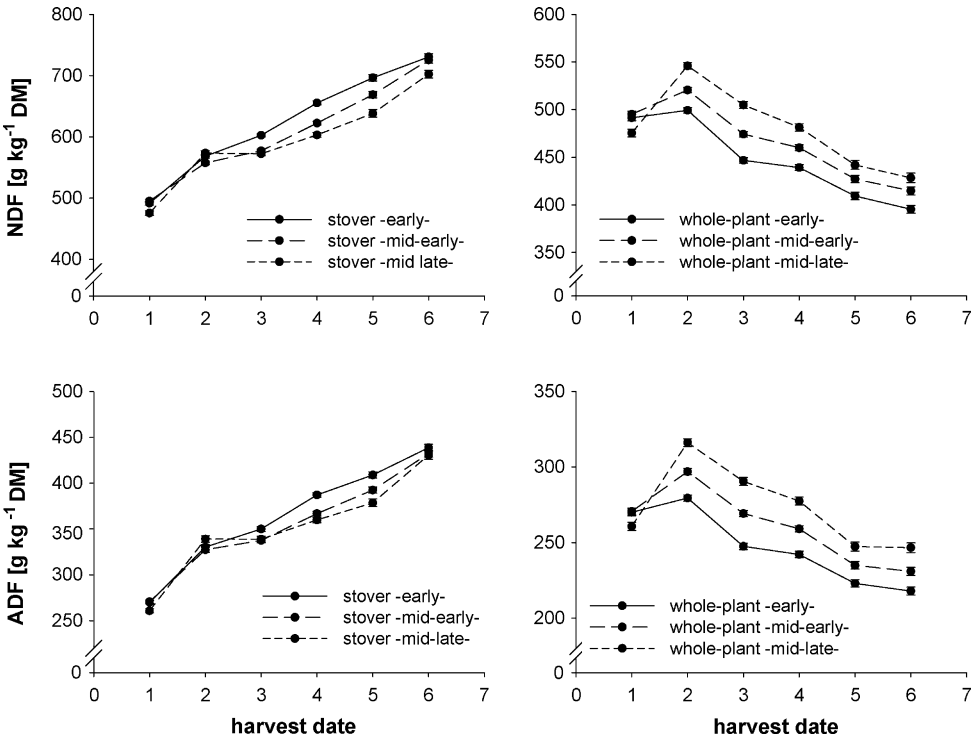

Fig. 1. Contents of neutral detergent fibre (NDF) and acid detergent fibre (ADF) of stover and whole-crop for the early, mid-early, and mid-late maturity groups, provided as means of three experimental years. Bars around points indicate standard error (S.E.); where bars are not shown, points were larger than the S.E.

within maturity × harvest date interactions were observed (data not presented); they generally appeared before silage maturity but showed no consistent trend. The following three sections will therefore focus on the impact of the maturity × harvest date interaction. The influence of environmental conditions will be addressed in the sections on modelling.

3.1. Cell wall fractions of the stover

In stover, advancing maturation resulted in substantial increases in NDF, ADF, hemicellulose, and cellulose (Figs. 1 and 2). There were fewer significances among maturity groups at harvest dates 1 and 2, i.e. before and shortly after silking. Differentiation among maturity groups became more evident at harvest dates 3–5, except for ADF, where the mid-early and mid-late group differed significantly only at date 5. The largest differences among maturity groups were recorded at harvest date 5 (amounting to 58.1 g NDF, 31.0 g ADF, 27.6 g hemicellulose, and 27.9 g cellulose kg^{-1} DM between the early and mid-late group), but decreased again afterwards. The lignin content increased from 44.3 to 75.5 g kg^{-1} DM (on average of the maturity groups) without any obvious trend concerning the ranking of the groups (Fig. 2).

3.2. Cell wall fractions of the whole-crop

The variation of whole-crop contents of fibre fractions reflects (i) the changes in the proportions of plant organs and (ii) in their respective ratios of cell wall and cell content. Stover fibre content usually continues to increase after silking, this is caused by an accumulation of cell wall material and by remobilisation of non-structural carbohydrates to the growing ear. Nevertheless the whole-crop fibre content decreases as a result of starch accumulation in the ear, which overcompensates for the rise in stover cell wall content (Phipps and Weller, 1979; Phipps et al., 1984). In the present study fibre contents increased for the mid-late group between harvest dates 1 and 2 (Figs. 1 and 2), i.e. around (near) silking, while for the early and mid-early group the increase was less pronounced (NDF, ADF) or non-existent (hemicellulose). After the onset of grain filling, assimilate remobilisation and starch accumulation resulted in a considerable decline, varying between 103.9–117.6 g NDF, 61.5–69.5 g ADF, 40.0–47.2 g hemicellulose, and 55.8–67.1 g cellulose kg^{-1} DM. Largest differences among groups were detected at harvest date 3, with 58.1 g NDF, 43.0 g ADF, 37.5 g cellulose, and 15.2 g hemicellulose kg^{-1} DM between the early and mid-late group. While for NDF, ADF, and cellulose the groups differed significantly at almost all harvest dates, hemicellulose had fewer significances at early growth stages and none at harvest date 6. Lignin content increased between harvest dates 1 and 2 and then remained relatively stable. There were few significances and no clear trend.

3.3. Modelling of fibre fractions

Fibre fraction content was strongly influenced by the year, as shown before. In applying the FOPROQ model, the less meaningful factor of year was replaced by the weather factors temperature, precipitation, and radiation in order to quantify separately their effect on fibre contents. Model calibration was

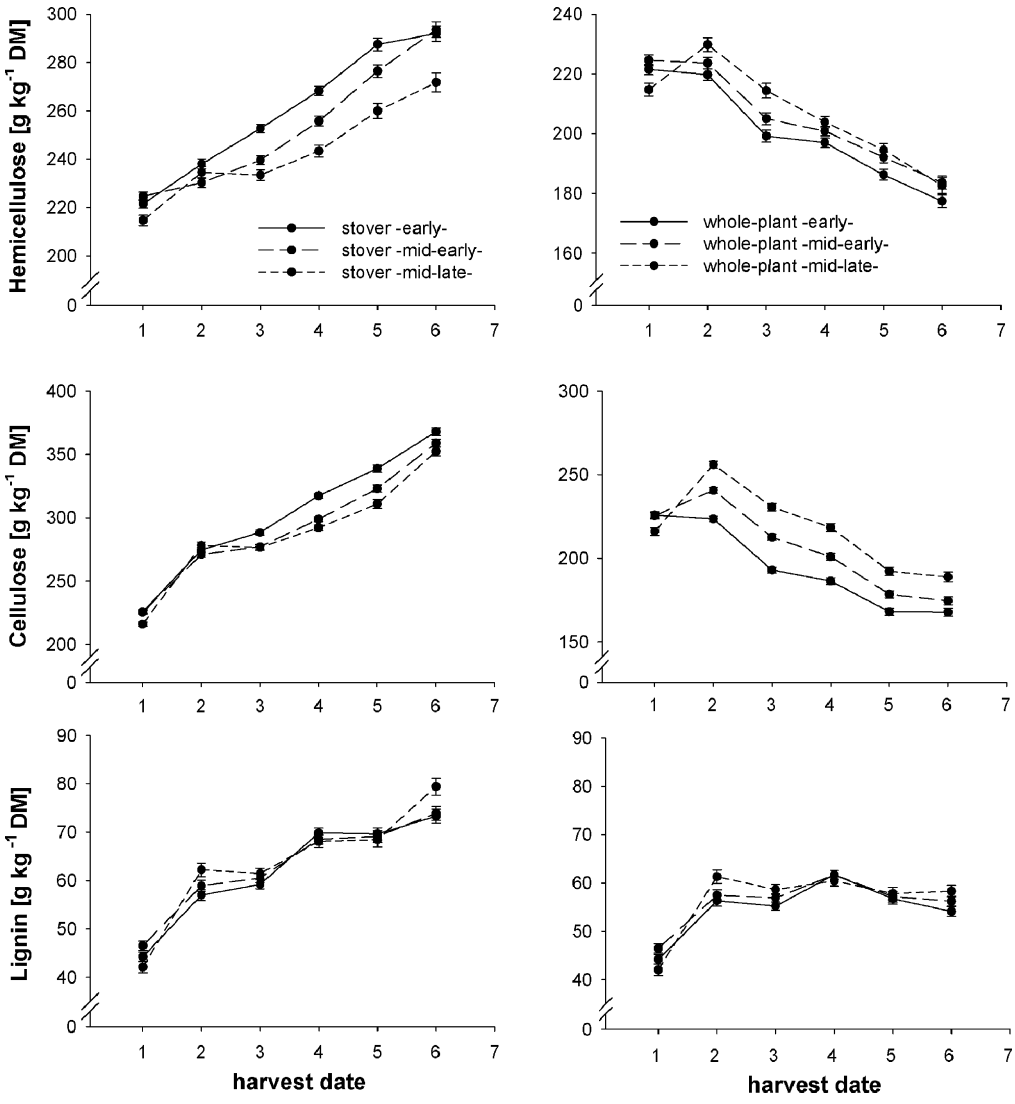

Fig. 2. Contents of cellulose, hemicellulose, and acid detergent lignin (ADL) of stover and whole-crop for the early, mid-early, and mid-late maturity groups, provided as means of three experimental years. Bars around points indicate standard error (S.E.); where bars are not shown, points were larger than the S.E.

performed separately for each hybrid. For the sake of clarity, however, we restrict the presentation of results to hybrid Oldham, representing the early maturity group, and to Fuego, representing the mid-early group. Other hybrids reacted in a similar manner and calibration resulted in comparable goodness of model fit. Since only increasing or decreasing cell wall fractions can be modelled (see model description), harvest date 1 was not included in the whole-crop simulation.

Figs. 3 and 4 display the modelled and observed whole-crop and stover contents of NDF, ADF, hemicellulose, and cellulose for the selected hybrids. In the growing period of 2003, environmental conditions led to an earlier and more intense change of cell wall constituents compared to 2001 and 2002 for both hybrids. That season was characterized by higher temperatures and a severe water deficit compared to 2001 and 2002, as the soil water index (Fig. 5) shows. However, model optimisation indicated that soil water availability did not contribute to changes in fibre content, but rather that temperature and radiation primarily determined the intensity of quality change (Fig. 6). Parameters t_c, T_{th}, r_c, and R_{th}, which describe the impact of temperature and radiation on quality change, turned out to be identical for all fibre fractions and both hybrids, except for hemicellulose (see Table 5). Values for Q_x, the maximum content of a given fibre component at maturity, have no physiological meaning, but instead were caused by environmental conditions, which did not allow harvest at physiological maturity. Dry matter contents suitable for ensiling (320 g DM kg^{-1}) were achieved 20 days earlier in 2002 and 35 days earlier in 2003 compared to 2001. Calculated fibre contents at silage maturity showed the largest variations between growing seasons 2002 and 2003, where whole-crop contents differed by 16.6 g NDF, 12.5 g ADF, 5.2 g hemicellulose, and 14.5 g cellulose kg^{-1} DM for Fuego. Corresponding values for stover were 44.7 g NDF, 23.1 g ADF, 21.1 g hemicellulose, and 20.7 g cellulose kg^{-1} DM. A similar range was detected for Oldham. Variation between hybrids was largest in 2003, where whole-crop contents of NDF, ADF, hemicellulose, and cellulose were 16.5, 10.6, 5.4, and 7.0 g kg^{-1} DM higher for Fuego, respectively. Corresponding stover fibre

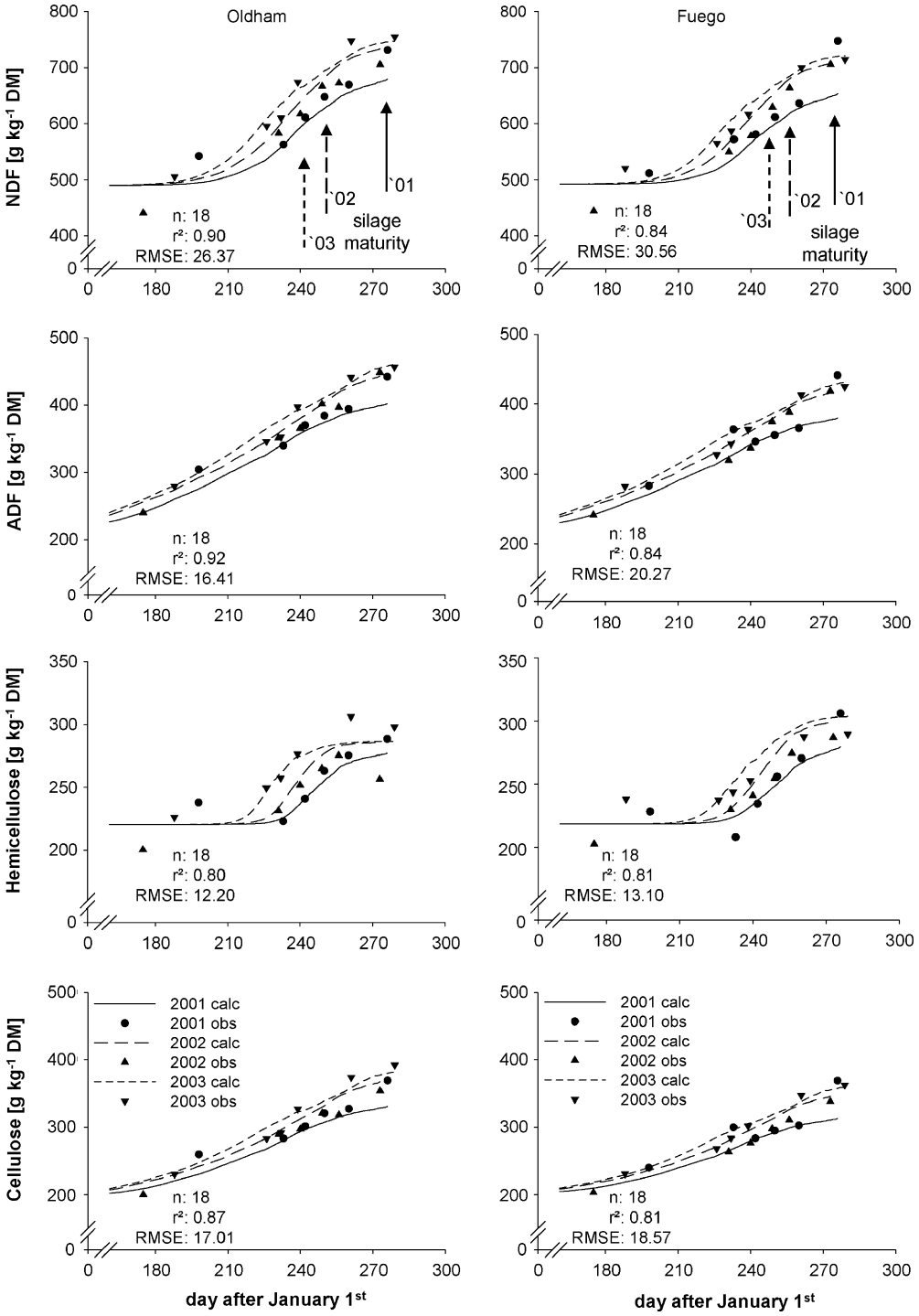

Fig. 3. Stover contents of neutral detergent fibre (NDF), acid detergent fibre (ADF), hemicellulose, and cellulose, provided as observed (symbols) and calculated (lines) values for hybrids Oldham (early) and Fuego (mid-early) and experimental years 2001–2003. Arrows indicate silage maturity in corresponding years (320 g kg^{-1} DM).

contents were 27.1, 20.7, 6.8, and 17.3 g kg^{-1} DM higher for Oldham.

The comparison of calculated and observed data in Figs. 3 and 4 demonstrates that fibre fractions were reasonably well estimated for both cultivars, explaining 73–93% of variation. Prediction errors (RMSE) ranged around 5% of the contents at silage maturity. Some discrepancies became apparent for the last harvest date of 2001, where the model systematically underestimated the simulated values. Additionally, hemicellulose calculations showed a somewhat higher variation (Figs. 3 and 4).

3.4. Simulation study

The results of the 30-year simulation study for hybrids Oldham and Fuego are displayed in Fig. 7. The fibre content

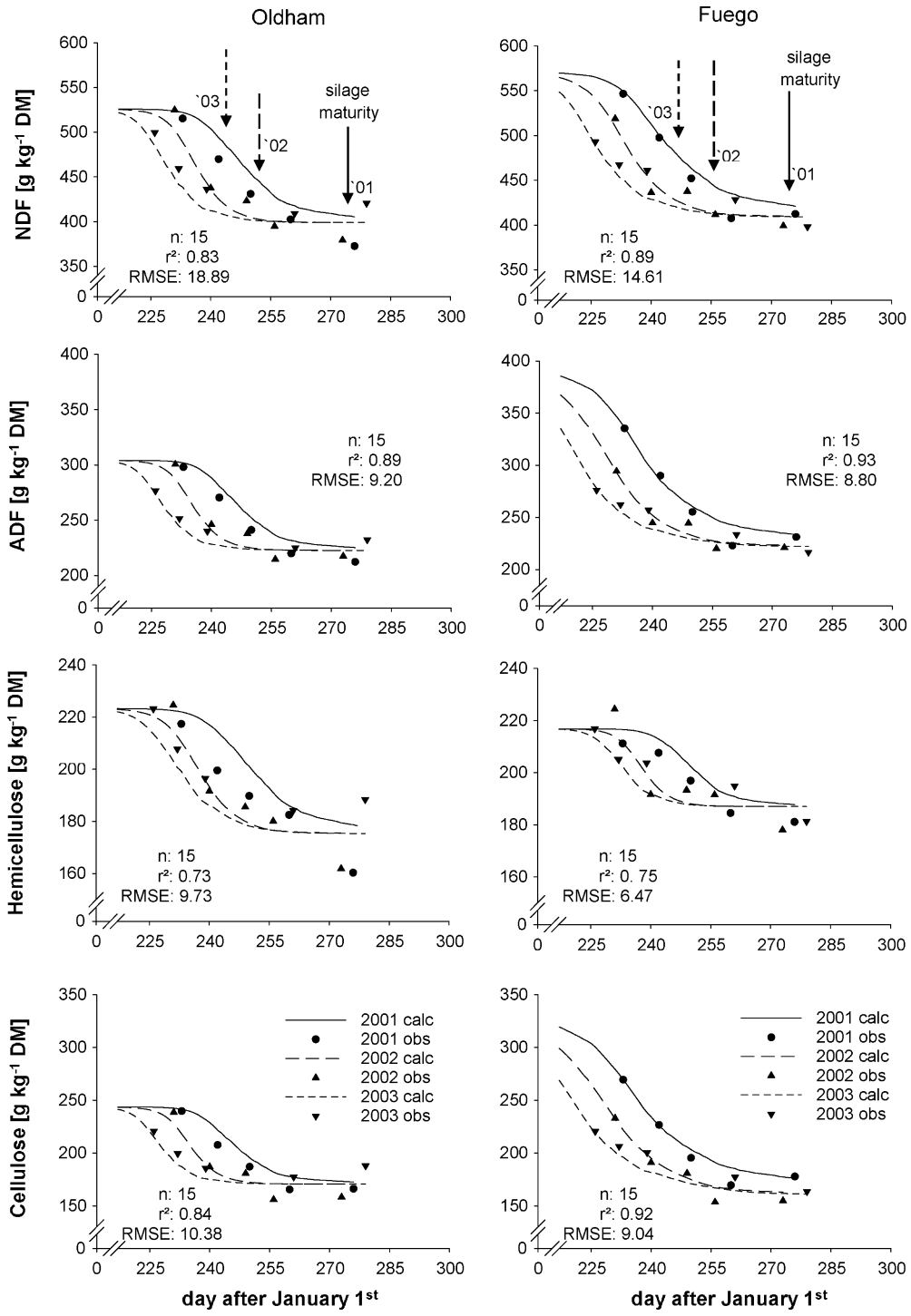

Fig. 4. Whole-crop contents of neutral detergent fibre (NDF), acid detergent fibre (ADF), hemicellulose, and cellulose, provided as observed (symbols) and calculated (lines) values for hybrids Oldham (early) and Fuego (mid-early) and experimental years 2001–2003. Arrows indicate silage maturity in corresponding years (320 g kg^{-1} DM).

distributions were characterised by their mean and median; apart from NDF, all were right skewed. The results of the simulation study document a strong weather-related variation for the DM content and a moderate influence on the content of cell wall constituents, as indicated by coefficients of variation between 2.6 and 17.3%. Hemicellulose contents seem to be somewhat less affected by environmental conditions, especially for Fuego. The striking outliers in the upper (fibre components) or lower (DM content) range of the distributions can be traced back to the year 1987, which was characterised by extremely low average temperature (12.9 °C vs. 14.8 °C long-term average) and radiation (13.0 MJ m^{-2} vs. 16.3 MJ m^{-2}) during the vegetation period. It seems likely that the observed variation is mainly due to the impact of weather conditions on the development of the crop,

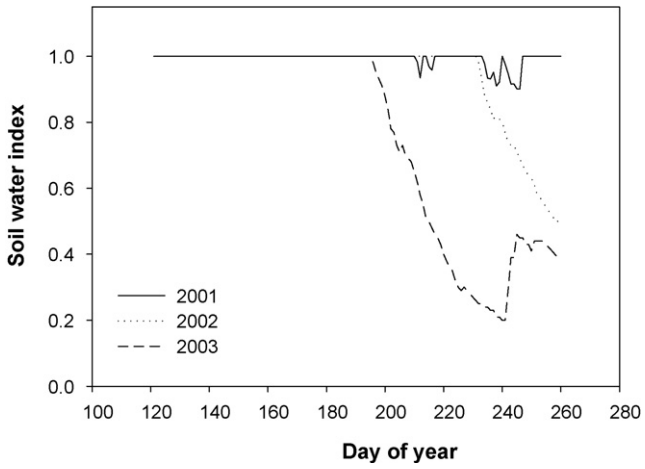

Fig. 5. Soil water index of the growing seasons 2001 to 2003, as calculated in the FOPROQ growth sub-module, exemplified for hybrid Oldham. The soil water index denotes the ratio of actual to potential evapotranspiration.

i.e. by indirect effects on fibre components, because the weather-related variability of DM content was considerably larger than the variability of fibre contents.

Differences in fibre content between hybrids, representing different maturity groups, were 16.5 g NDF, 12.8 g ADF, 9.7 g cellulose, and 10.8 g hemicellulose kg^{-1} DM, whereas variation among years amounted to 112.6 g NDF, 80.6 g ADF, 76.8 g cellulose, and 34.1 g hemicellulose kg^{-1} DM. Our experimental data as well as the simulation results suggest that environmental conditions exert a stronger impact on the plant's fibre content than the genotype does.

4. Discussion

4.1. Genotypic variation of fibre components

Hybrids showed a typical pattern of changes in stover and whole-crop fibre components over time (Figs. 1 and 2). Decreas-

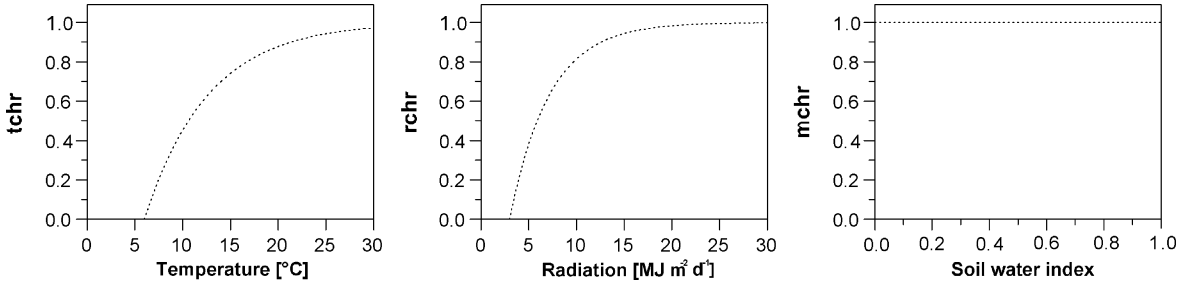

Fig. 6. Change rate functions for temperature (tchr), radiation (rchr), and plant available soil water (mchr) provided for neutral detergent fibre (NDF) of whole-crop. Parameters of the displayed functions were identical for both hybrids.

Table 5
Results of parameter optimisation of the FOPROQ quality sub-module for neutral detergent fibre (NDF), acid detergent fibre (ADF), hemicellulose, and cellulose in whole crop and stover of hybrids Oldham (early) and Fuego (mid-early)

	NDF		ADF		Hemicellulose		Cellulose	
	Whole crop	Stover	Whole crop	Stover	Whole crop	Stover	Whole crop	Stover
Oldham								
t_c	0.15	0.15	0.15	0.15	0.17	0.19	0.15	0.15
T_{th}	6.00	6.00	6.00	6.00	6.00	6.00	6.00	6.00
r_c	0.24	0.24	0.24	0.24	0.35	0.15	0.24	0.24
R_{th}	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
m_c	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Q_n	39.89	49.01	22.27	19.99	17.53	22.04	17.06	19.36
Q_x	52.60	79.34	30.41	2588.92	22.33	28.70	24.37	144.99
v	91.34	94.58	90.52	2266.45	101.73	90.68	90.30	261.20
c	28.16	7.34	30.69	1.56	24.70	20.30	31.18	2.22
Fuego								
t_c	0.15	0.15	0.15	0.15	0.17	0.23	0.15	0.15
T_{th}	6.00	6.00	6.00	6.00	6.00	6.00	6.00	6.00
r_c	0.24	0.24	0.24	0.24	0.35	0.165	0.24	0.24
R_{th}	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
m_c	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Q_n	40.87	49.25	22.09	20.91	18.7	21.84	15.88	19.89
Q_x	57.09	75.51	39.39	2557.69	21.68	30.70	33.18	141.76
v	89.04	96.26	84.74	2275.56	101.96	104.73	84.63	265.69
c	19.29	8.85	14.36	1.61	34.58	15.94	12.37	2.36

t_c: constant of temperature change function, T_{th}: temperature threshold in temperature change function, r_c: constant of radiation change function, R_{th}: radiation threshold in radiation change function, m_c: constant in soil moisture change function, Q_n: minimum content of fibre component at the onset of growth, Q_x: maximum content at maturity, c: the inclination of the threshold response curve, and v: the inflexion point of the threshold response curve.

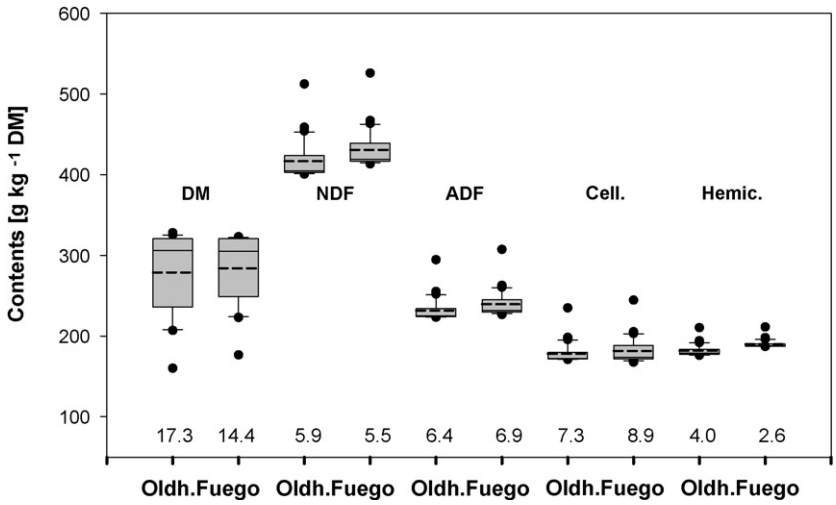

Fig. 7. Results of the 30-year simulation study of DM content (g DM kg^{-1} fresh weight), and of concentrations of neutral detergent fibre (NDF), acid detergent fibre (ADF), cellulose, and hemicellulose (g kg^{-1} DM) for hybrids Oldham (early) and Fuego (mid-early), provided as boxplots with 10, 25, 50, 75, and 90% percentiles, outliers (●), and mean (- - -). The figures below the boxes give the coefficients of variation (%).

ing whole-crop fibre contents (except for lignin) and increasing stover fibre contents observed with advancing maturation generally agree with previous investigations (Phipps and Weller, 1979; Cone and Engels, 1993; Irlbeck et al., 1993; Darby and Lauer, 2002). Likewise, the range of fibre contents recorded at silage maturity closely matches those obtained by other studies (Cox et al., 1994; Darby and Lauer, 2002). In contrast to Bal et al. (1997) and Wiersma et al. (1993), the present study did not find increasing whole-crop fibre contents after physical maturity.

Varietal differences within maturity groups were marginal, with only a few significances observed in early stages of development, which might be of interest for studies of anaerobic digestion in biogas plants. The optimum harvest time for maize grown for biogas production is presently a matter of intense discussion in Germany. No consensus has yet been reached, but recent research suggests that an earlier harvest time relative to silage maize production might be advantageous (Amon et al., 2004). At silage maturity we did not find any impact of variety on fibre components. Even the stay-green behaviour (mid-early cultivar Fuego and mid-late Benicia) did not show any effect, although results by Ettle and Schwarz (2003) suggest a slower increase in fibre components with later onset of senescence. It may be argued that the number of hybrids tested in our study was insufficient to draw general conclusions on the genotypic variability of fibre content. In fact the hybrids were specifically selected according to their maturation behaviour in order to represent the spectra of German silage maize varieties. In addition, our findings are consistent with those reported by Crasta et al. (1997) and Darby and Lauer (2002), who did not find any hybrid impact on cell wall constituents. Still, genotype × environment interactions reported in other studies (Kang and Gorman, 1989; Giauffret et al., 2000; Epinat-Le Signor et al., 2001), argue against the complete absence of genotypically driven variability, since hybrid performance may change with environmental conditions. Further support for some genotypic variability comes from Barrière et al. (1991), who documented a range of 407–496 g NDF, 195–249 g ADF, and 171–229 g cellulose kg^{-1} DM. However, since the dry matter content of samples varied between 295 and 388 g kg^{-1} fresh matter, the variation reported by Barrière et al. was likely caused in part by differences in developmental stage and not by genotypic variation alone. Similarly, differences in developmental stage account for most of the maturity × harvest time-interactions detected in our study, as indicated by the negative relationship between contents of dry matter and NDF, which was slightly closer for the ear compared to the whole-crop (Fig. 8). A similar relationship has been reported by Givens and Deaville (2001). Although the impact of genotype on variation of fibre content appears to be relatively low, its influence on cell wall digestibility may be more pronounced. Differences in NDF digestibility among non-brown-midrib hybrids reported by Barrière et al. (2003) range between 14.9% for late and 19% for early hybrids, respectively. Somewhat lower values were found by Deinum et al. (1984) and De Bover (2003). Interestingly, a shift towards lower digestibility has been observed in the last two or three decades (Givens and Deaville, 2001; Barrière et al., 2003).

4.2. Environmental variation of fibre components

Contents of cell wall constituents showed moderate variation due to environmental conditions, as indicated by significant effects of year and corresponding interactions (Tables 3 and 4). Model optimisation and simulation results revealed that the intensity of change in fibre components was strongly associated with temperature and radiation. These findings generally agree with the work of Cox et al. (1994), who found high temperature to reduce whole-crop fibre concentration. In contrast, Crasta et al. (1997) reported only a small, but significant contribution of temperature to NDF, ADF, and lignin variability at silage maturity. Soil water availability did not contribute significantly to variability of fibre components in our study, whereas Crasta et al. (1997) documented fibre contents to be more closely related to water availability than to temperature. Overall they were able to explain 48–55% of variability at silage maturity. These con-

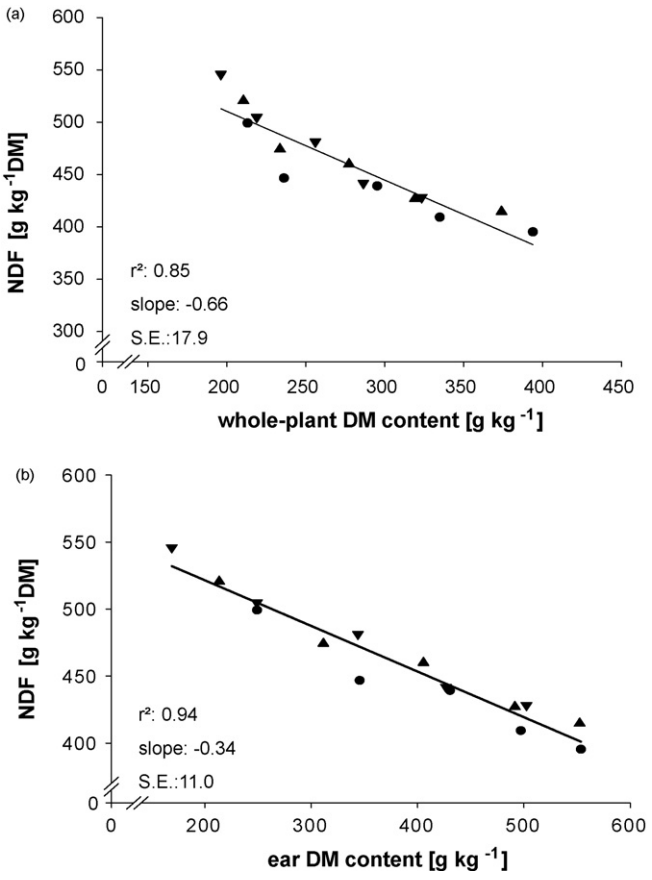

Fig. 8. (a) Relationship between whole plant neutral detergent fibre (NDF) and dry matter (DM) content calculated for all maturity groups. (b) Relationship between whole plant neutral detergent fibre (NDF) and ear dry matter (DM) content calculated for all maturity groups.

troversial results may be due to differences in the level of water deficiency. According to Grant et al. (1989), water use of maize remains unaffected by water availability unless the soil moisture index, i.e. the ratio of the actual to the maximum plant available soil water, falls below 0.2 to 0.3. In the growing season 2003 of our study, these conditions were not met until 14 days after silking (day 208, see Fig. 5), when the most sensitive period with respect to kernel set (Grant et al., 1989) had nearly passed. In summary, the model satisfactorily reflected the impact of environmental conditions on the changes of cell wall constituents during the vegetation period. For unknown reasons, the correspondence between measured and simulated values was less close for hemicellulose.

4.3. Model approach

The FOPROQ model, originally developed for forage grasses, could be applied to maize whole-crop and stover fibre components without any modifications of the model algorithms. Promising results of model calibration corroborate the model's general suitability. The underlying model concept, i.e. the dynamic simulation of daily weather-driven changes in forage quality traits, seems to have several advantages over less complex approaches. Thermal indices, for instance, are widely applied to predict harvest time or forage quality traits since temperature is often the major climatic factor to influence crop growth and development (Bloc et al., 1983; Dardenne et al., 1993; Van Soest and Hall, 1998; Dwyer et al., 1999; AGPM, 2000; Easson and Fearnehough, 2003). Other weather-related parameters, however, affect forage quality too, and their consideration can improve estimates of forage quality (Hill et al., 1995), as exemplified in the present study with respect to the significant influence of radiation intensity.

Despite these promising results, FOPROQ performance might be improved by introducing some model refinements. Struik et al. (1985), for instance, supposes that the influence of temperature on cell wall content is most significant during the period from the 8-leaf stage to grain set. Consequently, distinguishing the crop sensitivity to external factors at different developmental stages might enhance model power. This partitioning would permit the determination of separate response functions for each developmental period in order to quantify the impact of environmental conditions more accurately. Such an approach is supported by Stewart et al. (1998), who found substantial differences in the phenological temperature response between the vegetative and reproductive growth stages. It should be noted, however, that increasing model complexity does not necessarily improve prognostic accuracy and should thus be considered carefully, as overparameterisation may increase prognostic uncertainty (Jansen, 1998).

5. Conclusions

The results of the field experiment revealed substantial differences in the concentration of stover and of whole-crop cell wall constituents among maturity groups. Within maturity groups only little variability was observed among hybrids. The few genotype-related differences that did occur were restricted to early developmental stages, which are of no importance to ruminant nutrition, but may be of interest for methane production in biogas plants. While the impact of genotype on fibre content variation appears to be negligible, the influence on cell wall digestibility may be more prominent.

The application of the FOPROQ model allowed us to quantify the impact of weather factors on day-to-day changes in NDF, ADF, cellulose, and hemicellulose. Surprisingly, temperature and radiation turned out to be the major determinants of content of cell wall components, while soil water availability was of minor importance. It is possible that drought stress conditions in the underlying field study were not severe enough or occurred too late in the growing period. Measured data were predicted with acceptable accuracy, but model performance might be further enhanced by distinguishing crop response to environmental stress factors depending on developmental stage. A long-term simulation study, which permitted comprehensive quantification of the environmental variability in whole-crop fibre components, showed considerable variation, primarily from environmental influences on developmental stage. Overall, environmental conditions seem to exert greater influence on the contents of cell wall constituents than genotype does. Before the model can be introduced as a practical prognosis tool, its calibration database

should be extended to improve the reliability of model output for other regions with different weather conditions. Finally, the model requires validation with an independent data set.

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Appendix A. Model algorithms

This Appendix provides a brief description of the essential algorithms of FOPROQ, for further details see Kornher and Torssell (1983), Kornher et al. (1991), and Fagerberg and Nyman (1995).

A.1. Growth sub-model

FOPROQ model calculations were started at sowing, and daily change of biomass was estimated as follows:

$$\Delta W = WrAG_i, \tag{1}$$

and

$$A = \frac{1}{1 + (L/L_{50})^a}, \tag{2}$$

where W is the daily change of aboveground biomass per unit ground area ($g\,m^{-2}$), r the relative growth rate at onset of growth ($g\,g^{-1}\,d^{-1}$), and A the age function of leaf area index L to describe the decrease of relative growth rate with crop ageing, scaled between 0 and 1. Leaf area index L is calculated as a function of biomass (not presented). G_i the a growth index summarising the impact of weather conditions on growth rate, calculated as a product of the indices of temperature (°C), incident global radiation ($MJ\,m^{-2}\,d^{-1}$), and plant available soil water (mm), scaled between 0 and 1. L_{50} the half maximum LAI, and a the constant determining the curvature of the function.

The function relating mean daily temperature (°C) to temperature index is assumed bell-shaped. Optimum, base and maximum temperature were optimised 22, 6, and 42 °C, respectively, for all varieties uniformely. The relationship between incident global radiation R_s ($MJ\,m^{-2}\,d^{-1}$) and radiation index R_i is described as: $R_i = (1 - e^{(-kR_s/R_x)})/(1 - e^{-k})$, with R_x the radiation at light saturation of the canopy, and k a constant. Plant-available soil water S (mm) is simulated with a single layer budget in relation to precipitation P (mm), and depletion by actual evapotranspiration E_a:

$$\Delta S = \begin{cases} P_t - E_a, & \text{if } S < S_c \\ 0, & \text{else} \end{cases}, \quad \text{with } S_c, \text{ the available field capacity.} \tag{3}$$

At field capacity, E_a equals the potential evapotranspiration E_p. With decreasing soil water content E_a is reduced gradually according to the ratio of S to a soil water threshold S_{th}. Potential evapotranspiration, provided by the weather service, is reduced linearly as a function of leaf area index L, if L values fall below a threshold value. The ratio of E_a to E_p gives the soil water index W_i, which links the growth part of the model to the quality part.

A.2. Quality sub-model

The quality model assumes the existence of two levels of quality. Over the growing period, changes from one level to the other occur gradually. The levels and changes in quality depend on genetical, but also on management and environmental input. Environmental factors like temperature, radiation, and soil water are converted into corresponding change rates based on proper exponential or negative exponential functions.

Temperatures above a temperature threshold T_{th} are assumed to accelerate the change of fibre contents:

$$T_r = \begin{cases} 0, & T \le T_{th} \\ 1 - (\exp(-t_c(T - T_{th})), & T > T_{th} \end{cases} \tag{4}$$

with T denoting the daily mean temperature (°C), and t_c a temperature constant.

The corresponding function for the impact of irradiation is given as:

$$R_r = \begin{cases} 0, & R_s \le R_{th} \\ 1 - \exp(-r_c(R_s - R_{th})), & R_s > R_{th} \end{cases} \tag{5}$$

where r_c is a radiation constant and R_{th} a radiation threshold.

For plant available soil water, a linear function is more appropriate. Since soil moisture deficit is assumed to increase quality change, soil moisture change rate is defined as:

$$M_r = \begin{cases} 0, & W_i > m_c \\ 1 - (1/(m_c/W_i)), & \text{else} \end{cases} \tag{6}$$

with m_c a water availability constant, and W_i the water index, ranging between 0 and 1.

The daily change rates are combined multiplicatively to give the daily environmental change rate P_r, ranging from 0 to 1. The daily rates are summed to get the accumulated daily rate S_r, and forage quality traits are then modelled as functions of S_r. The relationship between S_r and contents of DM ($g\,(100\,g)^{-1}$ DM) and stover fibre components ($g\,(100\,g)^{-1}$ DM) is described by a threshold-response curve of switch-on type:

$$Q(S_r) = Q_n + \left(\frac{(S_r/v)^c}{(1 + (S_r/v)^c)} \right) (Q_x - Q_n), \tag{7}$$

where Q is the value of quality trait, Q_n the minimum content at the onset of growth (stover fibre components), Q_x the maximum content at maturity, c the determines the inclination of the curve, v the value of S_r at the inflexion point of the curve.

For whole-crop fibre components, which decrease with maturation, a threshold response curve of switch-off type is used:

$$Q(S_r) = Q_n + \left(1 + \left(\frac{S_r}{v}\right)^c\right)^{-1} (Q_x - Q_n)$$

where Q_n is the minimum content at maturity, Q_x the maximum content at start of calculations.

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