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Improving the production and utilization of sorghum and pearl millet as livestock feed: methodological problems and possible solutions

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Abstract

The overall objective of this work was the identification of simple, yet accurate, assessments of fodder quality of sorghum and pearl millet stover in crop improvement programs. Stover from 12 genotypes of sorghum and six genotypes of pearl millet grown under high and low fertilizer application was investigated for nitrogen, cell wall constituents, sugar, plant height, stem diameter, leaf number per plant and extent and rate of in vitro gas production of whole stover and of stover cell walls. Organic matter digestibility, organic matter intake, digestible organic matter intake (DOMI) and cell wall digestibility were measured in bulls. Significant genotypic variation was found for chemical, morphological and in vitro fermentation characteristics of stover but their relationship with digestibility and intake measurements was generally poor. While no single chemical, morphological or in vitro measurement described stover quality adequately, some combinations of these measurements resulted in good overall relationships with stover quality measurements. Across sorghum and pearl millet, 71% ($P < 0.0001$) of the variation in stover cell wall digestibility in bulls was accounted by the lag phase of in vitro gas production from cell wall preparations and by acid detergent lignin and acid detergent fiber content of stover. In pearl millet, 98% ($P < 0.0001$) of the variation in DOMI in bulls was accounted for nitrogen, lag phase and maximum rate of gas production and neutral detergent fiber content. The paper further discusses relationships between indirect animal performance measurements such as digestibility and voluntary feed intake (VFI) and animal productivity, e.g. live weight gain. VFI is shown to be a more crucial quality assessment in crop residues than digestibility and the relationship between both measurements was shown to be poor. It is argued that crop improvement programs should validate laboratory techniques as well as indirect animal performance measurements with direct animal performance measurements such as milk or meat production before deciding on laboratory selection criteria.

Keywords: Crop residues; Digestibility; Intake; In vitro gas production; Sorghum; Pearl millet; Animal performance

1. Introduction

Fodder quality is ultimately only defined by animal productivity, however, measuring milk yield or live weight changes can be logistically demanding. These direct animal performance trials are therefore

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frequently substituted by more short-term, indirect animal performance measurements such as digestibility or voluntary feed intake (VFI) (McDonald et al., 1988). Yet, even these short-term measurements are often impractical as routine analytical tools, for example in the case of genetic enhancement of fodder quality in forages or crop residues (Ceccareli, 1993; Zerbini and Thomas, 1999; Casler, 2001). These improvement programs rely on simple laboratory techniques since they are faced with many entries that provide little plant material unless specifically multiplied for animal experimentation.

Some laboratory techniques target chemical constituents with known nutritional implications (Van Soest and Robertson, 1985). Others simulate digestion in the animal as for example the Tilley and Terry (1963) in vitro digestibility technique or the Menke et al. (1979) in vitro gas production test. Estimates of in vitro and in vivo digestibility were generally well related. On the other hand, several authors (Crampton et al., 1960; Fahey and Hussein, 1999) have shown that VFI is more closely related to animal productivity than digestibility. However, VFI cannot be simulated in the laboratory but can only be predicted by laboratory techniques using regression analysis with experimentally measured VFI. As shown in a recent review on genetic enhancement of forage quality, in vitro (and related digestibility estimates) and chemical measurements are the most commonly used tools in the ranking of genotypes (Casler, 2001). These laboratory techniques are often complemented by examinations of morphological plant characteristics such as leafiness, which are then used as explanatory variables for observed differences in fodder quality by laboratory quality assessments (Casler, 2001).

The present work was undertaken with three objectives in mind. The first was to investigate relationships between chemical and morphological characteristics of stover from 12 genotypes of sorghum and six genotypes of pearl millet grown under high and low fertilizer application and digestibility and intake measurements of stover when fed to bulls. The second was to investigate the relationships between in vitro gas production profiles of stover and their cell wall preparations and intake and digestibility measurements. The third was to discuss relationships between indirect and direct animal performance measurements.

2. Materials and methods

2.1. Location and field trials

The study was carried out under rain-fed conditions, that is without irrigation, at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India in the rainy season 1999. ICRISAT is situated in the Deccan plateau, 30 km north-west from Hyderabad at an altitude of 543 m. The 12 genotypes of sorghum and the six genotypes of pearl millet were planted on a Vertisol watershed area in plots of 0.25 ha at two levels of fertilizer application (9 and 90 kg of N/ha). The genotypes of sorghum and pearl millet will be described and characterized in detail in a companion paper in the same issue of this journal (Blümmel et al., 2003).

2.2. Animal experimental design

Twenty-four F_1 crossbred bulls (Holstein × Sahiwal) between 12 and 21 months old and with an average live weight of 262 kg (S.D. = 36) were used for the experiment. A switch-over design was employed and a total of three experiments were conducted, two with sorghum stovers and one with pearl millet stover. Each genotype × fertility treatment was fed to at least two bulls in each of two periods (i.e. four bulls in total). For 15 genotype × fertility treatments, sufficient amount of stover was available for feeding over three periods (i.e. six bulls in total). Bulls were individually fed chopped stover in a stanchion barn at 09.00, 13.00 and 16.00 h for a period of adaptation of 12 days and a period of measurements of 6 days. Feed intake was recorded daily. Each bull was supplemented with 25 g per day of a salt–vitamin–mineral mixture. Faeces were collected with the aid of faecal bags made from canvas with an internal lining of polyethylene held by belts around the bulls girth and back. Following a 24 h collection, total output of faeces was weighed, properly mixed and a weighed portion of 100 g was taken for analysis.

2.3. Feed and faecal analysis

Nitrogen (N) was determined (Technicon Auto Analyser) in air dry feed material and was corrected for dry matter (DM). Acid (ADFs) and neutral

deter gent fibers (NDFs) and acid detergent lignin (ADL) were determined by the method of Van Soest and Robertson (1985). DM and ash were determined according to AOAC (1980). Sugar content in feed was analyzed by the colorimetric method by Dubois et al. (1956). Nitrogen was determined in wet faeces and was corrected for DM, thereby accounting for volatile nitrogen in faeces. Faecal NDF and faecal dry and organic matter were analyzed as in feed samples.

2.4. Re-calculation of published direct and indirect animal performance data on crop residue-based diets

Data on straw evaluation in barley improvement published by Capper et al. (1989) and Blümmel et al. (1998) were re-examined to investigate relationships between the indirect animal performance and direct animal performance measurements. Statistical relationships between in vivo digestibility and VFI and the relationships of these two measurements with changes in live weight in sheep fed straw from eight different genotypes of barley were calculated.

2.5. Morphological measurements

Plant height (PH), stem diameter (SD) and leaf number per plant (LNP) were determined in four field replicates as described by Pietzsch (1999). Plot size was defined by number, length and distance of rows of sorghum or pearl millet. Four rows of 2 m length each constituted one plot of either sorghum or pearl millet but row distance was species-specific. Genotypes were harvested at full maturity and morphological measurements were taken at harvest. Whole plant samples from the four field replications were subjected to the same chemical analysis as described for the feed samples.

2.6. In vitro gas production measurements

Rumen inoculum for the in vitro incubations was obtained from two rumen cannulated steers (local Indian breed) kept on a diet based on sorghum and pearl millet stover. A mixture of rumen fluid and particulate matter (approximately 60:40) was collected into CO_2-filled thermos bottles, transferred to and homogenized in a household blender, strained and filtered through glass wool. All handling of rumen inoculum was carried out under continuous flushing of CO_2.

Portions of about 200 mg air dry sample were accurately weighed (in triplicates) into 100 ml calibrated glass syringes, fitted with plungers as described by Menke et al. (1979) but modified as described by Blümmel and Ørskov (1993). A total of 30 ml of medium consisting of 10 ml of rumen inoculum and 20 ml of an ammonium and sodium bicarbonate–mineral–distilled water mixture was injected into the syringes. Three blanks containing 30 ml of medium were only included at the beginning and at the end of the incubation syringes. Accumulating gas volumes were recorded after 3, 6, 9, 12, 18, 24, 30, 40, 72 and 96 h of incubation.

Stover cell walls (NDF) were prepared as described by Blümmel and Becker (1997) by refluxing about 1.5 g of stover with neutral detergent solution (without sodium sulfite) according to Van Soest and Robertson (1985). After refluxing, the NDF was recovered on filter crucible of porosity 2 (40–100 μm) and rinsed at least 10 times with hot water to remove completely any remaining detergent solution. Approximately 200 mg of dry NDF was accurately weighed from the crucibles (kept in desiccators) into the syringes. Medium, incubation procedures and incubation times were as described for whole stover incubations.

2.7. Fit of gas production profiles by exponential and sigmoidal model and statistical procedures

The computer program GraphPad Prism (1994) was used to fit gas volumes recorded between 3 and 96 h of incubation to an exponential and a sigmoidal model. The exponential model $y = B * (1 - \exp(-c^*(t - \text{lag})))$ assumed one pool of asymptotic gas production (B) with a constant fractional rate of gas production (c) with a lag phase (lag) in the onset of gas production. The sigmoidal model, $y = \text{AS} * \exp(-\exp[(2.718\,\text{MR}^*\text{AS})^*(\text{LAG} - t) + 1])$ was derived from Gompertz and assumed also one pool of asymptotic gas production (AS); MR denotes the maximum rate of gas production and LAG the delay phase in the onset of gas production. In both models y equals gas production at time t.

The statistical software package of SAS (1999) Version 8 with the GLM program was used for

analysis of variance, comparison of means and simple correlations. Paired *t*-test was used to compare variables from high and low fertilizer application. Stepwise multiple regression procedures were used for the prediction of indirect animal performance measurements by in vitro gas production and chemical and morphological variables setting the probability of entry into a model to 0.05.

3. Results

3.1. Chemical and morphological characteristics of sorghum and pearl millet stover

Chemical and morphological characteristics of sorghum stover are reported in Table 1. Highly significant ($P < 0.0001$) genotype differences were found for nitrogen and estimates of cell wall (NDF) and cellulose (ADF) contents across high (HF) and low (LF) fertilizer application (FA) and within FAs and for ADL in HF. Very high genotype differences were observed for sugar content which could vary sevenfold between genotypes. The morphological measurements PH, SD and LNP were significantly ($P < 0.0001$) affected by genotype across and within FAs. When compared by paired *t*-test, fertilizer application increased nitrogen and sugar content of stover and decreased total cell wall content and that of cell wall fractions (ADF, ADL).

Chemical and morphological measurements of pearl millet stover are reported in Table 2. Except for cell wall content in HF ($P = 0.1$), significant ($P = 0.003$ to $P < 0.0001$) genotype-dependent differences were found for chemical stover composition across and within FAs. Genotype affected also significantly PH, SD and LNP. Fertilizer application significantly ($P < 0.05$) increased N content and decreased ADF, ADL and PH.

3.2. In vitro fermentation characteristics of sorghum and millet stover and of stover cell wall preparations

In vitro gas production profiles of sorghum and pearl millet stover and their cell wall preparations were fit to an exponential and a sigmoidal model and the models are introduced below. The exponential model is presented in Fig. 1a using the gas production profiles of a fast (ICSV 93046 LF) and a slow (LY HF) fermenting sorghum stover with similar potential fermentability (asymptotic gas volume). The difference in the fermentation kinetics of both stovers is expressed by the faster (3.9%) rate (c) of gas production in ICSV 93046 LF compared to LY HF ($c = 2.5\%$). A comparison of the exponential with the sigmoidal model using the gas production profiles of one sorghum stover (CSH 16) is presented in Fig. 1b. The sigmoidal model described this profile more accurately (smaller absolute sums of squares) than the exponential one, which underestimated gas production at early times of incubation while overestimating asymptotic gas volume (Fig. 1b).

The equation parameters from exponential and sigmoidal models fit to time series measurements of accumulating gas volumes from sorghum stover incubated for 96 h are presented in Table 3. High ($P < 0.0001$) genotype-dependent variations in asymptotic gas volumes, rates of gas production and lag phases were found for exponential and sigmoidal model regardless of level of fertilizer application.

Similarly, highly significant genotype-dependent variations were found for gas production profiles from cell wall preparations of sorghum stover. These data are summarized in Table 4 which presents mean equation parameters across FA and within HF and LF. Paired *t*-test comparison showed that cell well preparations had significantly higher ($P < 0.0001$) positive lag phases than whole stover incubations in both exponential and sigmoidal models. In the exponential model, asymptotic gas production was higher ($P < 0.05$) in cell wall preparations than in whole stover, while no such differences were found for rates of gas production. The reverse was true for the sigmoidal model which showed no differences between asymptotic gas production from whole stover and stover cell walls while rates of gas production were higher ($P < 0.0001$) in stover cell walls than in whole stover.

Equation parameters for gas production profiles from pearl millet stover are presented in Table 5. Asymptotic gas volumes, rates of gas production and lag phases were highly genotype-dependent in both exponential and sigmoidal model.

Table 1
Nitrogen (N, g/kg), NDF (g/kg), ADF (g/kg), ADL (g/kg), sugar (SUG, g/kg) content and PH (cm), SD (mm) and LNP of 12 varieties of sorghum stover grown under high (HF) and low (LF) fertilizer application (FA) and their statistical summary

	FA	N	NDF	ADF	ADL	SUG	PH	SD	LNP
Genotype									
CSH 9	HF	4.2	876	650	77	24	170	14.6	6.6
	LF	3.6	873	660	75	23	204	13.9	8.8
CSV 15	HF	3.8	772	557	72	95	244	13.0	8.4
	LF	2.6	794	563	78	85	248	12.9	8.7
ICSV 112	HF	5.0	830	637	76	32	194	14.4	9.7
	LF	3.1	840	633	79	48	189	13.7	9.0
ICSV 89057	HF	2.9	784	572	70	110	227	15.1	8.6
	LF	2.5	800	580	80	87	219	12.2	8.0
ICSV 93046	HF	3.7	747	569	82	153	281	13.0	9.9
	LF	2.9	713	523	77	160	235	13.9	10.8
LY	HF	5.3	845	615	89	65	293	13.7	8.4
	LF	2.6	812	598	81	87	337	13.1	10.7
C 43	HF	5.6	825	589	70	27	147	18.4	11.7
	LF	3.4	900	689	82	21	144	18.3	11.3
CSH 16	HF	6.2	829	601	64	29	196	17.0	9.0
	LF	3.6	867	657	73	28	181	12.7	8.1
HC 260	HF	4.5	836	601	78	70	279	12.2	6.9
	LF	3.0	829	598	70	61	280	10.3	7.4
ICSV 745	HF	3.4	808	582	73	77	222	14.2	9.8
	LF	2.3	835	605	79	61	231	14.6	10.3
ICSV 95132	HF	3.7	845	630	76	55	ND[a]	ND	ND
	LF	2.9	853	641	82	48	242	15.6	8.2
IRAT 204	HF	4.3	864	673	78	23	133	11.9	5.8
	LF	3.6	874	664	80	21	136	11.1	7.0
Statistical summary									
Mean	HF + LF	3.7	827.1	612.0	767.0	62.1	218	13.8	8.9
P		≤0.0001	≤0.0001	≤0.0001	≤0.0002	≤0.0001	≤0.0001	≤0.0001	≤0.0001
LSD[b]		0.86	19.2	19.9	5.6	7.3	34.4	2.64	1.65
Mean	HF	4.4	821.8	606.3	75.4	63.3	217	14.3	8.6
P		≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001
LSD		0.44	18.6	18.0	5.2	4.7	46.1	3.27	2.11
Mean	LF	3.0	832.5	617.6	78.0	60.8	219	13.3	9.1
P		≤0.0001	≤0.0001	≤0.0001	≤0.10	≤0.0001	≤0.0001	≤0.0001	≤0.0001
LSD		0.28	17.3	19.3	NS	4.9	42.4	3.52	1.93

[a] Not determined.
[b] Least significant differences ($P < 0.05$) related to differences between variety means across and within FA levels.

Similar findings were observed for cell wall preparations from pearl millet, which are summarized in Table 6. As was the case in sorghum, paired *t*-test comparison showed that cell well preparations had significantly higher ($P < 0.0001$) positive lag phases than whole stover incubations in both, exponential and sigmoidal models. In the exponential model, asymptotic gas production was higher ($P < 0.005$) in cell wall preparations than in whole stover, while no such differences were found for rates of gas

Table 2
Nitrogen (N, g/kg), NDF (g/kg), ADF (g/kg), ADL (g/kg), sugar (SUG, g/kg) content and PH (cm), SD (mm) and LNP of six varieties of pearl millet stover grown under high (HF) and low (LF) fertilizer application (FA)

	FA	N	NDF	ADF	ADL	SUG	PH	SD	LNP
Genotype									
ICMH 356	HF	6.0	857	606	95	19	165	8.2	6.1
	LF	3.7	861	534	91	16	148	7.6	5.8
ICMH 451	HF	5.0	849	585	97	21	202	10.0	7.9
	LF	3.1	854	564	80	26	167	10.0	7.6
ICMV 155	HF	5.4	842	626	103	22	225	12.0	8.6
	LF	3.9	844	556	84	25	199	11.5	7.3
ICMV 155 BMR	HF	5.1	869	558	74	21	205	11.2	8.3
	LF	3.5	831	550	71	35	205	10.7	7.4
ICMV 221	HF	6.4	850	574	89	28	215	13.4	7.9
	LF	3.1	806	527	82	55	192	11.2	7.6
NCD 2	HF	7.1	836	569	92	16	157	12.1	7.1
	LF	4.3	827	543	78	16	157	12.1	7.6
Mean	HF + LF	4.7	844	570	86	25	180	10.8	7.4
P		≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001
LSD[a]		0.53	13.3	11.3	2.4	1.5	11.4	1.4	0.6
Mean	HF	5.8	851	586	92	21	195	22.4	7.7
P		≤0.0001	≤0.10	≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.009	≤0.003
LSD		0.8	NS	17.2	3.5	1.4	19	2.5	1.1
Mean	LF	3.6	837	553	81	29	165	10.5	7.2
P		≤0.003	≤0.0001	≤0.0003	≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0002
LSD		0.8	14.8	16.4	3.8	2.7	14	1.5	0.7

[a] Least significant difference ($P < 0.05$) related to differences between variety means across and within FA levels.

production. The sigmoidal model showed higher ($P < 0.02$) asymptotic gas volumes from pearl millet cell walls than from wholes stover and gas volumes from cell walls were also produced at higher rates ($P < 0.0001$).

3.3. Ranges and means of indirect animal performance measurements and the relationship between digestibility and intake

Ranges and means of organic matter digestibility (OMD), organic matter intake (OMI), digestible organic matter intake (DOMI) (product of intake and digestibility) and cell wall digestibility (NDFD) of sorghum and millet stover observed when fed to bulls are reported in Table 7. For these in vivo measurements, ranges relative to mean values were greater in sorghum than in pearl millet. However, twice as many genotypes of sorghum than of pearl millet were investigated, which might account for the greater ranges in in vivo measurements in sorghum. For both species, relative ranges were greater for OMI than for OMD.

The relationships between OMD and OMI were generally poor (Fig. 2a). When compared across sorghum and pearl millet stover, OMD accounted for a mere 12% ($P = 0.04$) of the variation in OMI. In sorghum stover alone, OMD accounted for 18% ($P = 0.04$) of the variation in OMI while this relationship was insignificantly ($P = 0.22$) inverse in pearl millet stover. Cell wall digestibility (NDFD) of stover was more closely related to OMI (Fig. 2b) accounting for 24% ($P = 0.002$) of the variation in intake. This relationship was stronger within sorghum stover where NDFD accounted for 49% ($P < 0.0001$) of the variation in OMI. The relationship between NDFD and OMI was insignificant in pearl millet ($P = 0.57$).

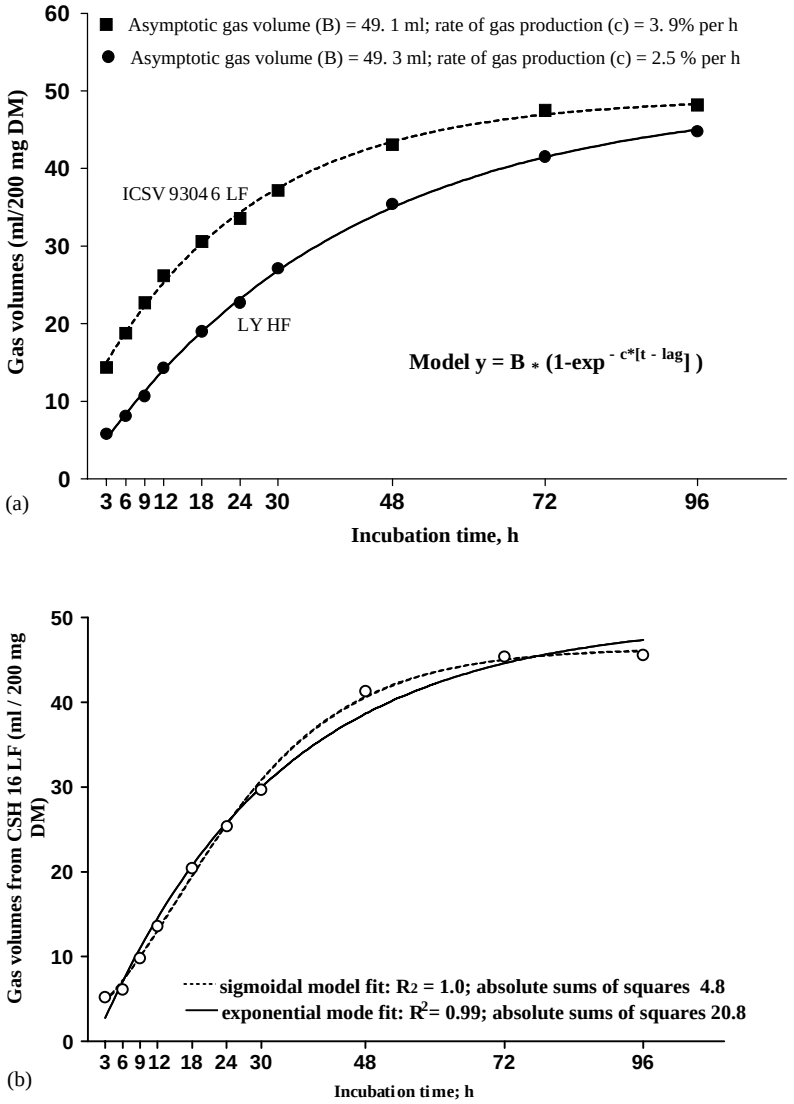


Fig. 1. (a) Comparison of in vitro gas production profiles of a fast and a slow fermenting sorghum stover and asymptotic and rate of gas production values as described by an exponential model. (b) Comparison of goodness-of-fit of an exponential and a sigmoidal model in describing in vitro gas production profiles of a sorghum stover.

3.4. Relationships between chemical and morphological stover characteristics and indirect animal performance measurements

Relationships between chemical and morphological stover characteristics and indirect animal performance measurements in sorghum are reported in Table 8. Generally, a limited number of significant associations were observed between chemical and morphological stover characteristics and in vivo measurements. Nitrogen content was poorly related to OMD and OMI, but a significant relationship was observed with cell wall digestibility in LF. Cell wall content was not related to OMD, OMI and DOMI but was significantly positively ($P = 0.002$ to $P < 0.0001$) related to cell wall digestibility. Similar relationships were observed for

Table 3
Equation variables calculated from the exponential model $y = B * (1 - \exp(-c^*(t - \text{lag})))$ and the sigmoidal model, $y = \text{AS} * \exp(-\exp[(2.718\,\text{MR}^*\text{AS})^*(\text{LAG} - t) + 1])$ applied to 96 h incubations of 200 mg of dry stover from 12 genotypes of sorghum grown under high (HF) and low (LF) fertilizer application (FA) and their statistical summary[a]

	FA	*B*	*c*	lag	AS	MUE	LAG
Genotype							
CSH 9	HF	58.2	0.0262	2.5	51.7	1.142	2.5
	LF	55.3	0.0261	2.9	48.7	1.116	3.4
CSV 15	HF	51.5	0.0303	−3.2	48.6	0.924	−7.7
	LF	51.0	0.0246	−4.8	47.2	0.756	−10.1
ICSV 112	HF	55.3	0.0209	0.8	47.3	0.859	0.0
	LF	54.0	0.0224	−0.3	47.6	0.843	−2.1
ICSV 57	HF	56.9	0.0310	−4.2	54.2	1.005	−9.6
	LF	56.6	0.0338	−3.3	54.4	1.049	−9.1
ICSV 46	HF	52.8	0.0353	−5.8	51.2	0.991	−12.3
	LF	49.1	0.0398	−6.1	48.1	0.996	−13.0
LY	HF	49.3	0.0250	−1.4	44.8	0.806	−4.4
	LF	48.9	0.0291	−3.2	45.9	0.851	−7.7
C 43	HF	48.2	0.0301	1.1	44.5	0.978	−0.4
	LF	55.9	0.0279	3.0	50.3	1.164	3.1
CSH 16	HF	54.8	0.0276	1.7	49.6	1.073	0.8
	LF	55.3	0.0311	1.8	50.9	1.193	0.8
HC 260	HF	54.3	0.0323	−1.0	51.4	1.067	−4.4
	LF	56.2	0.0249	−1.3	51.0	0.928	−4.0
ICSV 745	HF	50.2	0.0241	−3.7	46.0	0.756	−8.0
	LF	57.3	0.0207	−2.5	50.6	0.791	−5.8
ICSV 32	HF	50.5	0.0270	0.9	45.7	0.939	−0.6
	LF	46.1	0.0252	2.3	40.6	0.864	2.0
IRAT 204	HF	44.8	0.0224	5.1	37.1	0.873	7.1
	LF	46.1	0.0261	4.6	39.9	0.975	5.8
Statistical summary							
Mean	HF + L	52.4	0.0277	−0.6	47.8	0.956	−3.1
P		≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001
LSD[b]		1.2	0.001	0.5	0.9	0.03	0.8
Mean	HF	52.2	0.0277	−0.6	47.7	0.951	−3.1
P		≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001
LSD		1.5	0.002	0.9	1.1	0.04	1.4
Mean	LF	52.7	0.0277	−0.6	47.9	0.960	−3.1
P		≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001
LSD		1.9	0.002	0.6	1.4	0.04	1.0

[a] Equation variables of the model giving lower absolute sums of squares are given in italics.
[b] Least significant difference ($P < 0.05$) related to differences between variety means across and within FA levels.

ADF content. ADL content was inversely associated with all in vivo measurements but relationships tended ($P = 0.07$) to be significant with OMI across FAs. Sugar content was inversely associated with all in vivo measurements and these relationships were highly significant with cell wall digestibilities ($P = 0.002$ to $P < 0.0001$). PH was consistently inversely related to in vivo measurements and the relationship attained

Table 4
Statistical summary of mean equation variables calculated from the exponential model $y = B * (1 - \exp(-c^*(t - \text{lag})))$ and the sigmoidal model, $y = \text{AS} * \exp(-\exp[(2.718\,\text{MR}^*\text{AS})^*(\text{LAG} - t) + 1])$ applied to 96 h incubations of 200 mg of dry cell walls prepared from 12 genotypes of sorghum grown under high (HF) and low (LF) fertilizer application FA

	FA	*B*	*c*	lag	AS	MR	LAG
Mean	HF + LF	58.0	0.0273	4.9	50.4	1.325	6.6
P		≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001
LSD[a]		1.2	0.0008	0.4	1.0	0.031	0.6
Mean	HF	58.5	0.0270	4.9	50.7	1.327	6.6
P		≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001
LSD		1.9	0.001	0.6	1.5	0.052	1.0
Mean	LF	57.5	0.0275	4.8	50.18	1.323	6.5
P		≤0.0001	≤0.0001	≤0.0004	≤0.0001	≤0.0001	≤0.0001
LSD		1.7	0.001	0.5	1.4	0.038	0.8

[a] Least significant difference ($P < 0.05$) related to differences between variety means across and within FA levels.

Table 5
Equation variables calculated from the exponential model $y = B * (1 - \exp(-c^*(t - \text{lag})))$ and the sigmoidal model, $y = \text{AS} * \exp(-\exp[(2.718\,\text{MR}^*\text{AS})^*(\text{LAG} - t) + 1])$ applied to 96 h incubations of 200 mg of dry stover from six genotypes of pearl millet grown under high (HF) and low (LF) fertilizer application (FA)[a]

	FA	*B*	*c*	lag	AS	MUE	LAG
Genotype							
CMH 356	HF	45.3	0.0258	1.8	40.3	0.8337	0.8
	LF	47.4	0.0245	0.9	42.2	0.8229	−0.3
ICMH 451	HF	52.5	0.0166	1.5	41.8	0.6695	0.7
	LF	50.8	0.0228	1.5	44.3	0.8391	0.6
ICMV 155	HF	42.5	0.0229	0.8	37.3	0.6913	−0.7
	LF	42.6	0.0271	0.1	38.5	0.7912	−1.8
ICMV 155 BMR	HF	41.3	0.0361	2.5	38.6	1.0264	1.8
	LF	52.2	0.0300	1.9	47.7	1.1003	1.1
ICMV 221	HF	45.4	0.0305	0.4	42.2	0.8909	−2.1
	LF	50.3	0.0260	−2.0	46.4	0.8183	−5.8
NCD 2	HF	44.3	0.0281	2.3	40.0	0.8906	1.7
	LF	50.55	0.0304	4.1	45.3	1.1910	4.9
Mean	HF + LF	47.1	0.0268	1.3	42.15	0.880	0.1
P		<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
LSD[b]		1.3	0.0013	0.5	1.2	0.028	0.9
Mean	HF	45.2	0.0267	1.6	40.0	0.834	0.4
P		<0.0001	<0.0001	<0.0002	<0.0001	<0.0001	<0.0002
LSD		1.3	0.002	0.7	1.2	0.045	1.3
Mean	LF	49.0	0.0268	1.1	44.1	0.927	−0.2
P		<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
LSD		2.5	0.002	0.9	2.2	0.04	1.4

[a] Equation variables where sigmoidal model provided lower absolute sums of squares and the exponential model are given in italics.
[b] Least significant difference ($P < 0.05$) related to differences between variety means across and within FA levels.

Table 6
Equation variables calculated from the exponential model $y = B * (1 - \exp(-c^*(t - \text{lag})))$ and the sigmoidal model, $y = \text{AS} * \exp(-\exp[(2.718\,\text{MR}^*\text{AS})^*(\text{LAG} - t) + 1])$ applied to 96 h incubations of 200 mg of dry stover from six genotypes of pearl millet grown under high (HF) and low (LF) fertilizer application (FA)

	FA	*B*	*c*	lag	AS	MR	LAG
Mean	HF + LF	54.0	0.0258	5.0	46.3	1.173	6.6
P		<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
LSD[a]		1.2	0.001	0.3	0.9	0.04	0.6
Mean	HF	50.9	0.0254	5.2	43.3	1.105	7.1
P		<0.0001	<0.0001	<0.002	<0.0001	<0.0001	<0.0006
LSD		1.8	0.001	0.4	1.4	0.05	0.8
Mean	LF	57.1	0.0263	4.8	49.4	1.241	6.2
P		<0.0001	<0.0001	<0.006	<0.0001	<0.0001	<0.004
LSD		1.6	0.001	0.5	1.1	0.06	0.9

[a] Least significant difference ($P < 0.05$) related to differences between variety means across and within FA levels.

significance level ($P = 0.007$) for cell wall digestibility. Relationships between SD and in vivo measurements were inconsistent and did not attain or approach significance level. Except for OMI in HF, LNP was inversely related to in vivo measurements the relationship attained significance level for NDFD.

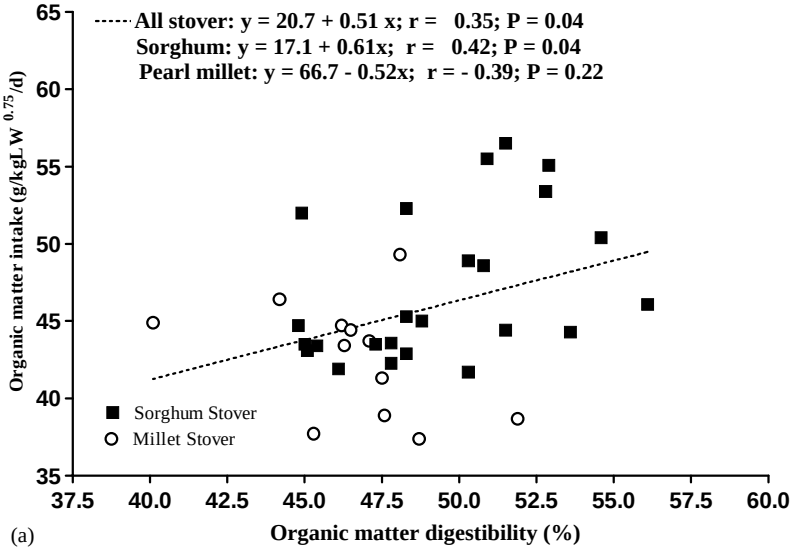
Table 7
Ranges and means of stover OMD, OMI, DOMI and cell wall digestibility (NDFD) of 12 genotypes of sorghum and six genotypes of pearl millet grown under high (HF) and low (LF) fertilizer application (FA)

Variable	Species	FA	Range	Mean
OMD (%)	Sorghum	HF	44.8–56.1	49.2
		LF	45.3–54.6	49.6
	Millet	HF	40.1–48.1	45.5
		LF	45.3–51.3	47.5
OMI (g/kg $LW^{0.75}$ per day)	Sorghum	HF	42.9–56.5	48.1
		LF	41.7–55.1	46.0
	Millet	HF	41.3–49.3	45.1
		LF	34.9–44.4	39.3
DOMI (g/kg $LW^{0.75}$ per day)	Sorghum	HF	19.5–29.2	23.7
		LF	19.5–29.2	22.9
	Millet	HF	17.9–23.8	20.6
		LF	16.6–20.8	18.7
NDFD (%)	Sorghum	HF	45.0–64.6	53.9
		LF	46.5–61.9	54.7
	Millet	HF	48.0–55.2	53.3
		LF	50.2–61.1	54.9

In pearl millet stover, no significant relationships were observed between cell wall content and composition and sugar content and any of the in vivo measurements (Table 9). Nitrogen was the only chemical measurement that exhibited some significant relationship with OMI and DOMI but significant relationships were limited to across FA comparison and no such relationship was observed either within HF or LF. From the morphological measurements, PH was positively related to OMI across FAs and to DOMI in LF. SD and LNP were not significantly related to any of the in vivo measurements.

3.5. Relationships between in vitro fermentation characteristics and indirect animal performance measurements

Using stepwise multiple regression procedures across sorghum and pearl millet comparisons, none of the gas production equation parameters presented in Tables 3 and 5 was significantly ($P > 0.05$) related to OMI, OMD and DOMI. The lag phases of the exponential and sigmoidal models accounted for 60 and 61% of the cell wall digestibility of sorghum and pearl millet but no other equation parameter attained significance ($P > 0.05$) with NDFD. In contrast, significant relationships were observed between the gas production equation parameter from cell wall preparations of sorghum and pearl millet and all in vivo measurements. However, less than 30% of the variation in any of the in vivo measurements were accounted for (results not tabulated).



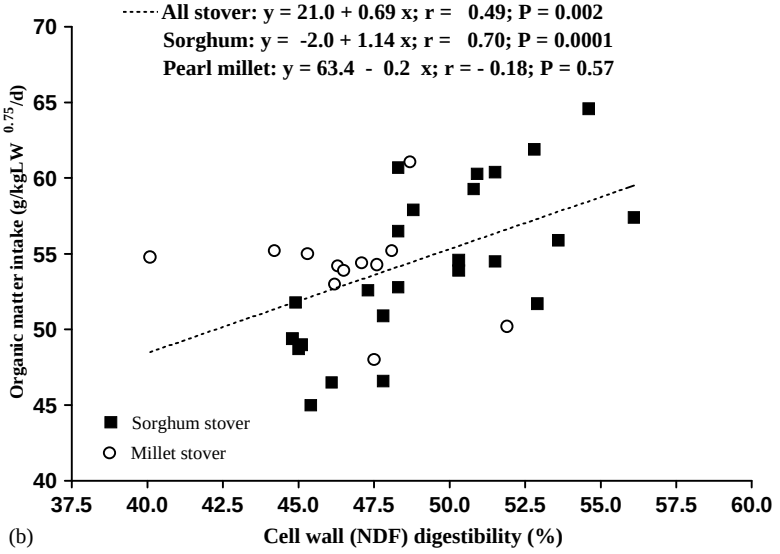


Fig. 2. (a) Relationship between OMD and OMI in bulls. (b) Relationship between cell wall digestibility and OMI in bulls.

When sorghum and pearl millet stover were considered separately, stronger significant relationships were observed between lag phase estimates and cell wall digestibility of sorghum stover with lag phases of the exponential (lag) and sigmoidal model (LAG) models accounting for and 78% ($P < 0.0001$) and 79% ($P < 0.0001$) of the variation in NDFD, respectively. No relationship was found between equation parameters from either exponential or sigmoidal model and OMI and DOMI. Relationships between in vitro gas production variables from cell walls of sorghum stover showed more significant relationships with in vivo measurements than gas production from whole stover but these relationships were not

Table 8
Correlation coefficients (r) for relationships between OMI, OMD, DOMI and NDFD and chemical and morphological characteristics in stover from 12 genotypes of sorghum (genotypes, fertilizer applications and abbreviations for variables follow those described in Tables 1 and 7)[a]

Variable	FA	N	NDF	ADF	ADL	SUG	PH	SD	LNP
OMI	HF + LF	0.29 (0.16)	0.23 (0.27)	0.12 (0.59)	−0.37 (0.07)	−0.33 (0.11)	−0.19 (0.39)	0.18 (0.40)	−0.03 (0.89)
	HF	0.22 (0.50)	0.12 (0.70)	−0.15 (0.65)	−0.47 (12)	−0.27 (0.40)	−0.11 (0.75)	0.25 (0.45)	0.17 (0.61)
	LF	0.18 (0.57)	0.40 (0.19)	0.39 (0.20)	−0.09 (0.78)	−0.44 (0.15)	−0.28 (0.39)	0.04 (0.89)	−0.23 (0.47)
OMD	HF + LF	0.06 (0.79)	0.28 (0.19)	0.32 (0.13)	−0.07 (0.75)	−0.25 (0.24)	−0.18 (0.42)	−0.15 (0.47)	−0.40 (0.06)
	HF	−0.05 (0.87)	0.32 (0.31)	0.34 (0.28)	−0.01 (0.98)	−0.29 (0.36)	−0.18 (0.59)	−0.40 (0.23)	−0.62 (0.04)
	LF	0.38 (0.22)	0.24 (0.45)	0.30 (0.33)	−0.25 (0.42)	−0.21 (0.51)	−0.18 (0.59)	0.10 (0.77)	−0.18 (0.57)
DOMI	HF + LF	0.23 (0.28)	0.30 (0.16)	0.23 (0.28)	−0.30 (0.16)	−0.36 (0.08)	−0.22 (0.32)	0.07 (0.74)	−0.20 (0.37)
	HF	0.17 (0.59)	0.23 (0.48)	0.04 (0.90)	−0.35 (0.27)	−0.32 (0.31)	−0.15 (0.66)	0.00 (0.99)	−0.13 (0.70)
	LF	0.30 (0.34)	0.39 (0.20)	0.41 (0.18)	−0.17 (0.60)	−0.41 (0.18)	−0.31 (0.36)	0.08 (0.79)	−0.24 (0.45)
NDFD	HF + LF	0.30 (0.15)	0.82 (0.0001)	0.82 (0.0001)	−0.05 (0.81)	−0.82 (0.0001)	−0.55 (0.007)	0.08 (0.70)	−0.41 (0.05)
	HF	0.40 (0.19)	0.78 (0.002)	0.75 (0.004)	−0.07 (0.83)	−0.80 (0.002)	−0.56 (0.07)	−0.05 (0.89)	−0.55 (0.08)
	LF	0.70 (0.01)	0.86 (0.0004)	0.89 (0.0001)	−0.07 (0.83)	−0.84 (0.0006)	−0.56 (0.07)	0.24 (0.46)	−0.29 (0.36)

[a] Values in parenthesis are probability values.

very strong. However, in all cases only one variable was entered into stepwise multiple regressions (Table 10).

In pearl millet stover, significant relationship between in vitro and in vivo variables was only observed for the lag phase of the exponential model (Table 5), which accounted for 34% ($P = 0.05$) of the variation in OMD and between the maximum rate of gas production (MR) of the sigmoidal model and cell wall digestibility were 35% ($P = 0.04$) of the variation were accounted for. As observed for sorghum, incubation of pearl millet cell walls resulted in generally stronger relationships between in vitro and in vivo variables than incubations of pearl millet stover although no relationship was found between in vitro variables and OMD. Asymptotic gas volumes (B) from exponential model accounted for 74% ($P = 0.0003$) and 39% ($P = 0.03$) of the variation in OMI and DOMI, respectively. Asymptotic gas volumes (AS) from the sigmoidal model accounted for 62% ($P = 0.002$) of the variation in OMI and MR of gas production of the same model accounted for 40% ($P = 0.03$)

Table 9
Correlation coefficients (r) for relationships between OMI, OMD, DOMI, NDFD and chemical and morphological characteristics in stover from six genotypes of pearl millet (genotypes, fertilizer applications and abbreviations for variables follow those described in Tables 2 and 7)[a]

Variable	FA	N	NDF	ADF	ADL	SUG	PH	SD	LNP
OMI	HF + LF	0.64 (0.02)	0.14 (0.67)	0.28 (0.38)	0.25 (0.43)	0.25 (0.44)	0.63 (0.03)	0.03 (0.93)	0.25 (0.43)
	HF	0.22 (0.67)	0.35 (0.49)	−0.41 (0.42)	−0.63 (0.18)	0.67 (0.15)	0.10 (0.85)	−0.14 (0.79)	0.05 (0.92)
	LF	0.03 (0.96)	−0.44 (0.38)	0.21 (0.70)	0.26 (0.62)	0.87 (0.03)	0.19 (0.71)	−0.32 (0.53)	0.13 (0.80)
OMD	HF + LF	−0.02 (0.53)	−0.15 (0.63)	0.08 (0.80)	0.31 (0.33)	0.09 (0.77)	−0.16 (0.63)	−0.22 (0.49)	−0.22 (0.49)
	HF	0.58 (0.22)	−0.20 (0.71)	0.59 (0.22)	0.15 (0.77)	0.19 (0.72)	−0.02 (0.97)	−0.10 (0.85)	−0.19 (0.72)
	LF	−0.43 (0.39)	0.17 (0.74)	0.03 (0.95)	−0.54 (0.27)	−0.16 (0.77)	0.12 (0.81)	−0.24 (0.65)	−0.24 (0.96)
DOMI	HF + LF	0.58 (0.05)	0.05 (0.89)	0.39 (0.21)	0.00 (0.98)	0.33 (0.30)	0.47 (0.12)	−0.10 (0.77)	0.07 (0.83)
	HF	0.57 (0.24)	0.09 (0.86)	0.25 (0.64)	−0.35 (0.50)	0.52 (0.29)	0.04 (0.94)	−0.09 (0.86)	−0.08 (0.89)
	LF	−0.16 (0.75)	−0.43 (0.39)	0.24 (0.64)	−0.05 (0.93)	0.77 (0.07)	0.85 (0.03)	−0.52 (0.29)	0.06 (0.92)
NDFD	HF + LF	−0.11 (0.75)	0.07 (0.83)	−0.01 (0.99)	−0.44 (0.15)	−0.11 (0.73)	−0.30 (0.34)	0.00 (0.99)	−0.12 (0.07)
	HF	0.41 (0.42)	0.05 (0.92)	0.15 (0.78)	−0.16 (0.78)	0.02 (0.97)	−0.03 (0.95)	0.27 (0.60)	−0.06 (0.91)
	LF	0.10 (0.85)	0.26 (0.62)	0.29 (0.57)	0.29 (0.57)	−0.30 (0.56)	−0.30 (0.56)	−0.33 (0.52)	−0.06 (0.91)

[a] Values in parenthesis are probability values.

Table 10
Significant relationships between equation variables fit from gas volumes recorded during 96 h incubations of 200 mg of cell wall preparations (NDF) from sorghum and pearl millet and OMI (g/kg $LW^{0.75}$), OMD (%), DOMI (g/kg $LW^{0.75}$) and cell wall digestibility (NDFD, %)[a]

$y = B * (1 - \exp(-c^*(t - \text{lag})))$			$y = \text{AS} * \exp(-\exp[(2.718\,\text{MR}^*\text{AS})^*(\text{LAG} - t) + 1])$		
Variable	*Y*-variate	R^2	Variable	*Y*-variate	R^2
Sorghum					
lag [5.7]	OMI	0.29 ($P = 0.007$)	LAG [2.8]	OMI	0.28 ($P = 0.008$)
lag [4.1]	DOMI	0.32 ($P = 0.004$)	LAG [1.5]	OMD	0.17 ($P = 0.04$)
B [0.66]	NDFD	0.35 ($P = 0.002$)	LAG [2.1]	DOMI	0.32 ($P = 0.004$)
			MR [21.9]	NDFD	0.38 ($P = 0.001$)
Pearl millet					
B [−0.8]	OMI	0.74 ($P = 0.0003$)	AS [−0.78]	OMI	0.62 ($P = 0.002$)
B [−0.27]	DOMI	0.39 ($P = 0.03$)	MR [9.8]	NDFD	0.40 ($P = 0.03$)

[a] Values in square brackets are regression coefficients.

of the variation in pearl millet cell wall digestibility (Table 10).

3.6. Multivariate analysis between chemical and morphological characteristics, in vitro gas production and indirect animal performance measurements

A summary of multivariate analysis between laboratory measurements and some digestibility and intake measurements is presented in Table 11. Across sorghum and pearl millet stover, NDFD predictions were significantly improved by combining lag phases (exponential model) of in vitro gas production of stover with ADL and acid detergent fiber (ADF) measurements. Multivariate analysis in sorghum stover did not result in more accurate prediction of indirect animal performance measurements than reported previously. In pearl millet stover, substantial improvements were observed by the combination of in vitro and chemical

Table 11
Stepwise multiple regressions between chemical, morphological and in vitro fermentation characteristics and intake (OMI, g/kg $LW^{0.75}$ per day), DOMI (g/kg $LW^{0.75}$ per day) and cell wall digestibility (NDFD, %)[a]

Substrate	Model	*Y*-variate	R^2
Across sorghum and pearl millet			
Whole stover	lag + ADL + ADF[b]	NDFD	0.71 ($P = 0.0001$)
	lag [1.04]		0.59 ($P = 0.0001$)
	ADL [−0.13]		0.06 ($P = 0.03$)
	ADF [0.03]		0.05 ($P = 0.04$)
Pearl millet			
Whole stover	Nitrogen + LAG	OMI	0.69 ($P = 0.005$)
	N [2.5]		0.41 ($P = 0.002$)
	lag [−0.9]		0.27 ($P = 0.02$)
Whole stover	Nitrogen + LAG + MR + NDF	DOMI	0.98 ($P = 0.0001$)
	N [1.22]		0.33 ($P = 0.05$)
	LAG [−0.9]		0.43 ($P = 0.003$)
	MR [8.12]		0.16 ($P = 0.002$)
	NDF [0.03]		0.06 ($P = 0.04$)
Cell walls	*B* + SD	OMI	0.85 ($P = 0.0002$)
	B [−0.8]		0.74 ($P = 0.0003$)
	SD [0.9]		0.10 ($P = 0.03$)

[a] Values in square brackets are regression coefficients.
[b] Abbreviations are same as given in Tables 1 and 3.

measurements, which accounted for 69 and 98% of the variation in OMI and DOMI, respectively.

4. Discussion

4.1. Relationships between digestibility and intake and their relationships with direct animal performance measurements

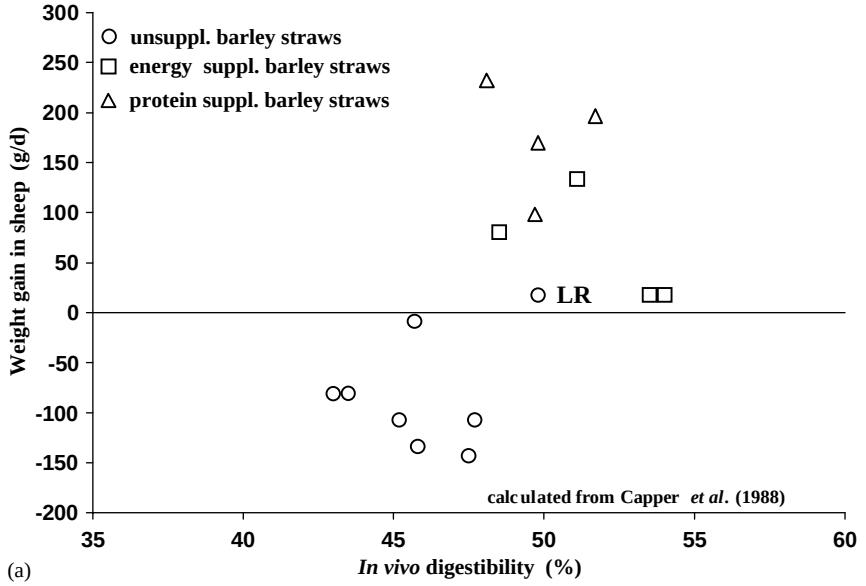
Indirect short-term animal experimentation measuring digestibility and VFI is often used to shortcut direct, longer-term experimentation measuring weight gains or milk production because it is more convenient to conduct than the latter. Of these two measurements, digestibility is the most common and universally used as a quality indicator in feedstuff tabulations (McDonald et al., 1988). Application of these shortcuts can be very helpful, for example, in crop improvement programs where many genotypes warrant examination and where fodder production for longer-term experimentations may meet logistical problems (Ceccareli, 1993; Zerbini and Thomas, 1999). Because of these constraints, only digestibility and intake were measured in this study. However, given the far-reaching implications of decisions in crop improvement programs, indirect performance measurements should be validated by direct performance evaluations with the target crops (Blümmel et al., 1998). We wish to demonstrate this need at the beginning of this discussion by the re-evaluation and re-calculation of data published on fodder quality of barley straw in plant breeding programs (Capper et al., 1989; Blümmel et al., 1998).

These experiments measured live weight losses/gains in sheep in addition to digestibility and intake. Fig. 3a shows the relationship between OMD of un-supplemented and supplemented barley straws and live weight changes in sheep. The overall relationship between digestibility and changes in live weight was weak ($r = 0.55, P = 0.03$). There was no statistical relationship ($r = 0.27, P = 0.52$) within un-supplemented barley straws, although the only straw promoting live weight gain—interestingly from a land race (LR)—also had the highest digestibility (Fig. 3a). However, the next best straw, which provided approximately for maintenance requirement, had only intermediate digestibility (Fig. 3a).

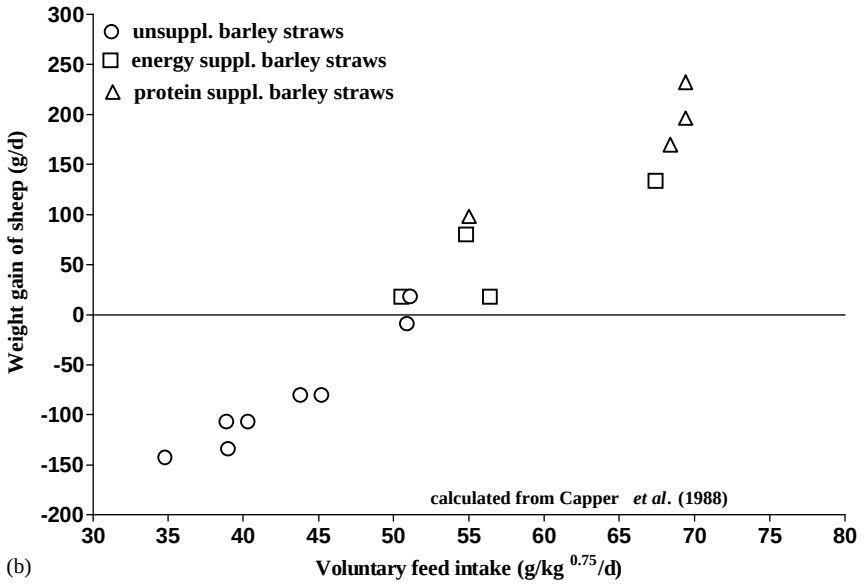
In comparison, relationships between VFI and changes in live weight were very good (Fig. 3b), across un-supplemented and supplemented barley straws ($r = 0.97, P < 0.0001$) as well as within un-supplemented straws ($r = 0.96, P < 0.0001$). These findings agree with data reported on the importance of VFI in forages by Crampton et al. (1960) who suggested that VFI accounted for approximately 70% of the total variation accounted for animal performance while digestibility contributed approximately 30% to the total variance accounted for. In the un-supplemented barley straws, multiple regressions with intake and digestibility accounted for 97% of the variation in live weight losses/gains with intake contributing 93.1% ($P < 0.0001$) and digestibility contributing 3.6% ($P = 0.07$). Based on this regression, changes in live weight can be predicted as: $y = -702.0 + \text{intake} \times 9.3 + \text{digestibility} \times 4.8$. It is also conceptually sound to assume that animal performance will largely depend on the amount of digestible feed consumed (Coleman and Moore, 2003).

There was no relationship ($P = 0.84$) between digestibility and intake in un-supplemented barley straw and this relationship across un-supplemented and supplemented straws was not strong ($r = 0.56, P = 0.03$) (Fig. 3b). These data are in line with the relationships observed between OMD and OMI of sorghum and pearl millet stover investigated in the current work, which were not strong and which were variable (Fig. 2a). One can argue, therefore, that digestibility measurements, while extensively used in plant breeding programs (Casler, 2001) are probably of more limited value in the evaluation of crop residues than sometimes thought.

However, digestibility is not a fixed feed trait but is modified, for example, by the level of feed intake: digestibility of a feed is usually higher under restricted than under ad libitum (voluntary) feed intake (Riewe and Lippke, 1970; Van Soest, 1994). In other words, higher intake can depress digestibility. The digestibilities presented in Figs. 2 and 3 have been measured under ad libitum intake. Digestibilities measured under restricted intakes might be differently related to ad libitum intake than reported in Figs. 2 and 3. Nevertheless, intake and digestibility are probably associated with different feed traits (Van Soest, 1994) with possibly different heritabilities and relationships to other crop traits. Quantification of the



(a)



(b)

Fig. 3. (a) In vivo digestibility of un-supplemented and supplemented barley straws from various genotypes and weight gain in sheep. (b) VFI of un-supplemented and supplemented barley straws from various genotypes and weight gain in sheep.

partial contribution of these two traits to animal productivity is, therefore, required in crop improvement programs where fodder quality is only one of several desirable traits. It is clear that direct animal performance trials with target crops are required at the onset of fodder crop improvement programs.

4.2. Relationships between chemical and morphological stover characteristics and indirect animal performance measurements

Indirect animal performance measurements cannot realistically be employed in crop improvement

programs on a routine basis but should serve, together with direct animal performance measurements, for the validation of laboratory analysis in the target crops. Chemical measurements such as nitrogen, cell wall fractions and sugars are convenient in that many entries can be analyzed within a short period of time (Van Soest and Robertson, 1985; McDonald et al., 1988). Many crop improvement programs invest in analysis of nitrogen and sugar content as nutritionally positive and cell wall fractions, particularly lignin, as nutritionally negative selection criteria (for review see Zerbini and Thomas, 1999, 2003). The present work shows that, while highly significant genotypic differences were found for nitrogen, cell wall fractions and sugar content in both sorghum and pearl millet stover, few of these measurements were related to indirect animal performance measurements (Tables 8 and 9). These data generally agree with findings published by Ørskov et al. (1988) who showed chemical measurements to be of only limited value for the prediction of animal performance on crop residue-based diets.

Nevertheless, the generally poor correlations between N and sugar content, and digestibility and intake measurements in the present work are surprising. The following explanations may apply. Rumen microbes require a minimum of about 12 g N/kg feed for utilizing the part of the ingested feed which is potentially responsive to microbial degradation (Milford and Minson, 1965; Ellis and Lippke, 1976). None of the genotypes of sorghum and millet investigated contained more than 7.1 g N/kg stover and the ranges in N content resulting from genetic variability and fertilizer application might have been biologically too narrow for eliciting significant effect in digestibility and intake. In fact, ongoing work shows highly positive response in digestibility, intake and nitrogen balance in sheep offered pearl millet stover when nitrogen content was increased by the choice of genotype and agronomic practice (date of harvest) to >90 g N/kg stover (Blümmel et al., unpublished). It therefore appears worthwhile to pursue breeding and selection for increased nitrogen content in stover despite the findings presented in this manuscript. Ongoing collaborative work between ILRI and ICRISAT on genotypic stover effects is measuring animal performance on restricted and ad libitum stover on offer as well as under N supplementation with legume hay to provide for 12 g N/kg of feed offered.

However, similar recommendation should not be given for sugar content at this point. The rationale for breeding and selection for high sugar content is apparently convincing. From a nutritional standpoint, sugars are highly and rapidly digestible thereby promoting DOMI (Van Soest, 1994). Selection for high sugar content in sorghum and pearl millet stover was also suggested by participatory rural appraisals studying farmers' perception of stover quality where ''sweetness'' emerged as an important quality characteristic (Underwood et al., 2000). However, selection for sugar content is not supported by the present work. Sugar content was negatively associated with in vivo measurements in sorghum (Table 8) and these relationships were variable in pearl millet (Table 9).

It is important to realize that sugars in sorghum and pearl millet stover are essentially concentrated in the stems. By extrapolation, differences in sugar content in stover can be caused by (a) differences in the sugar content of stems and (b) differences in stem:leaf proportions. In other words, genotypes with high sugar content in the stover may have a high proportion of stems. This would adversely affect VFI since ruminants prefer leaves to stems; the latter being rejected to a considerable extent (Minson, 1990). Sugar content in stover should therefore be compared with, and related to, stem:leaf proportions to prevent selection of genotypes with high stem content.

However, it should be noted that relationships between sugar content and digestibility and intake measurements varied between sorghum and pearl millet stover (compare Tables 8 and 9). Sugar content was inversely associated with all four in vivo measurements in sorghum stover and the association was significant ($P = 0.002–0.0006$) with cell wall digestibilities (Table 8). Given the positive association ($P < 0.0001$) between NDFD and OMI in sorghum stover (Fig. 2b), the present work suggests that dual-purpose sorghum genotypes should not be selected for high sugar content in the stover. In contrast, in pearl millet stover under low fertilizer application, a positive association was observed between sugar content and OMI ($P = 0.03$) and DOMI ($P = 0.07$). More work is required to investigate the obviously complex relationships between sugar content and stover quality in sorghum and pearl millet (see also below).

4.3. Relationships between in vitro production profiles and indirect animal performance measurements

Gas production profiles from sorghum stover were generally poorly correlated with indirect animal performance measurements. These relationships were variable for pearl millet stover, where asymptotic (*B*) gas volume was highly but negatively related to indirect animal performance (Table 10). The choice of the kinetic model, that is exponential vs sigmoidal, had little effect on these relationships. In ruminant nutrition, the exponential model is more widely applied than the sigmoidal because the constant fractional rate of gas production (*c*) can be directly linked with first order digestion kinetics in the digestive tract of ruminants. It would therefore appear advisable to prefer the exponential over the sigmoidal model in reports on nutritive quality in crop improvement programs. However, this question remains somewhat academic unless a closer relationship between the kinetic in vitro gas measurements and animal performance can be found than that presented in this study.

The overall poor relationships between in vitro gas production and animal performance measurements contrasts to comprehensive work reported by Menke et al. (1979) and Menke and Steingass (1988) who accurately predicted in vivo digestibility of more than 400 feedstuffs based on gas volumes produced during 24 h in vitro incubations. Blümmel et al. (1997) accounted for 75 and 82% of the variation in feed intake of 54 barley, wheat and the straws by in vitro gas profiles obtained during 96 h incubations of straws and their cell wall preparations, respectively. Some of the overall lack of correlation between in vitro gas production profiles and indirect animal performance measurements found in the present studies may be due to sugar content in the stems of sorghum and pearl millet. Fig. 4 presents the gas production profiles of stems, leaf blades and leaf sheaths of the pearl millet genotype ICMV 221 (however harvested in 2002 and therefore not of the same batch used in the animal experiment). High gas volume was produced from the stem almost instantaneously and more gas was produced from stems than from either leaf blades or sheaths. It is therefore possible that high and fast gas production from a genotype might ultimately be due to a high proportion of stems under some circumstances.

As already discussed, high stem proportion could adversely affect feed intake (Minson, 1990). In vitro gas production of whole stover appears, therefore, to be an inconclusive measurement for estimating nutritive quality of sorghum and pearl millet stover. While in vitro gas production profiles from cell wall

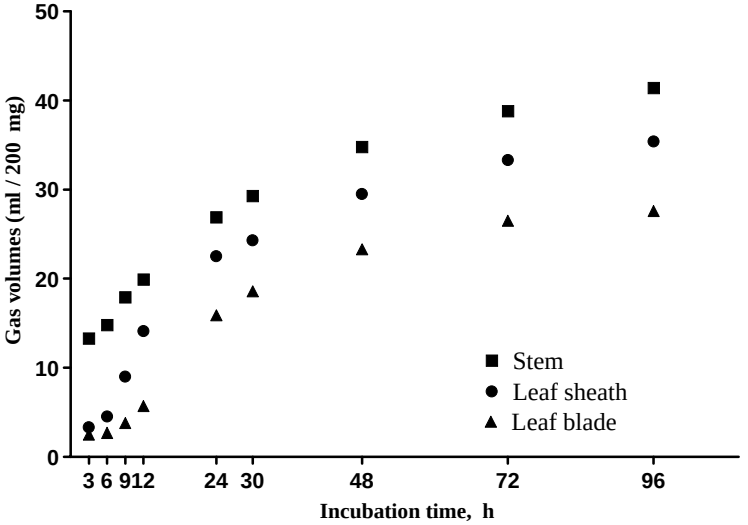


Fig. 4. Gas profiles from stem, leaf sheath and leaf blade of pearl millet stover ICMV 221.

preparations from sorghum and pearl millet stover showed some significant relationships with indirect animal performance measurements, relationships with OMD and OMI were poor and inconsistent (Table 10). Problems associated with interpretation of in vitro gas production measurements have recently been extensively discussed by Blümmel (2000) and Blümmel and Fernandez-Rivera (2002) who suggested that gas production measurements require complementary gravimetric analysis of how much substrate had been concomitantly digested to produce the gas. These authors suggested selecting fodder for high digestibility but proportional to the amount of substrate digested low gas production.

4.4. Prediction of indirect animal performance measurements by multivariate analysis including chemical, morphological and in vitro fermentation characteristics

While in vitro gas production measurements were not complemented by digestibility measurements in the present studies, the combination of gas production with chemical and morphological measurements using multivariate analysis resulted in some improved overall relationships with intake and digestibility measurements (Table 11). Across sorghum and pearl millet stover, 71% of the variation in cell wall digestibility was accounted by the combination of lag (exponential model) of in vitro gas production from stover cell wall preparations and ADL and ADF content of stover. However, to exploit these relationships in the future, NDFD measurements must be linked to animal productivity. Establishing such a linkage could be beneficial in crop improvement programs because NDFD is thought to be more genotype-dependent than total OMD (Van Soest, 1994; Blümmel et al., 2003).

Multivariate analysis did not result in improved relationships between laboratory analysis and intake and digestibility measurements in sorghum. However, substantial improvements were observed in pearl millet, where two chemical (N and NDF) and two gas production measurements (LAG and maximum rate of the sigmoidal model) accounted for 98% of the variation in DOMI. These findings clearly require further substantiation but in support of their validation, the fodder value of pearl millet could be predicted with great accuracy by laboratory techniques.

4.5. Possible effect of sample preparation on relationships between chemical, morphological and in vitro analysis and indirect animal performance measurements

Routine chemical and in vitro analysis uses samples ground to pass through a 1 mm mesh-sieve. Information on physical resistance of fodder to particle size reduction is lost in the grinding process. However, physical fodder structure can have tremendous impact on feed intake. The harder the structure and therefore the greater the difficulty the animal has to overcome by biting, chewing and ruminating, the lower the intake (Minson, 1990). It was shown in 40 barley straws that the grinding energy requirements (GERs) (electrical measurement of the physical resistance of hand-chopped straws (1.5–2.5 cm) to a particle size reduction of 1 mm) accounted for 83% of the variation in feed intake (Blümmel et al., 1996). Combinations of GER with measurements of in vitro gas production profiles increased the variation in intake explained to 87% (Blümmel et al., 1996). It is reasonable to assume that physical structure in sorghum and pearl millet stover might impact on feed intake at least as much as in barley straws. Application of GER measurements in the analysis of sorghum and pearl millet stover might improve prediction of indirect and, ultimately, direct animal performance considerably, particularly if combined with chemical and in vitro measurements. These measurements should be complemented by a more comprehensive and qualitative morphological examination of stover. The present study shows that measurements such as SD, PH and LNP showed very little relation to animal performance measurements. More recent studies measure, for example, the ratio of leaf blade:leaf sheath:stem and the green leaf area instead of just LNP. These measurements show considerable promise in the prediction of animal performance (Blümmel, unpublished).

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References

Association of Official Analytical Chemists (AOAC), 1980. Official Methods of Analysis, 13th ed. AOAC, Washington, DC.

Blümmel, M., 2000. Predicting the partitioning of fermentation products by combined in vitro gas volume and true substrate degradability measurements: opportunities and limitations. In: Gas Production: Fermentation Kinetics for Feed Evaluation and to Assess Microbial Activity. British Society of Animal Science, Penicuik, Midlothian, pp. 48–58.

Blümmel, M., Becker, K., 1997. The degradability characteristics of 54 roughages and roughage neutral detergent fiber as described by in vitro gas production and their relationship to voluntary feed intake. Brit. J. Nutrit. 77, 757–786.

Blümmel, M., Fernandez-Rivera, S., 2002. In vitro gas techniques and efficiency of microbial substrate degradation. Anim. Nutrit. Feed Technol. 2, 93–115.

Blümmel, M., Ørskov, E.R., 1993. Comparison of in vitro gas production and nylon bag degradability of roughages in prediction of feed intake of cattle. Anim. Feed Sci. Technol. 40, 109–119.

Blümmel, M., Paul, C., Goodchild, A., Becker, K., 1996. Grinding energy and in vitro gas technique for the assessment of Syrian barley straws: physical and microbial degradation and voluntary feed intake by sheep. J. Anim. Physiol. Anim. Nutrit. 76, 132–140.

Blümmel, M., Moser, M., Goodchild, A.V., Gland, A., Becker, K., 1998. Kooperation von Tierernährern und Pflanzenzüchtern: Bilanz einer 10-jährigen Zusammenarbeit mit ICARDA (Cooperation of animal nutritionists and plant breeders: review of 10 years of cooperation with ICARDA). In: Technischer Fortschritt im Spannungsfeld von Ernährungssicherheit und Resourcenchutz. Tagungsband, Hohenheim, pp. 199–204.

Blümmel, M., Zerbini, E., Reddy, B.S.V., Hash, C.T., Bidinger, F., Khan, A.A., 2003. Improving the utilisation of sorghum and pearl millet as livestock feed: progress towards dual-purpose genotypes. Field Crops Res. 84, 143–158.

Capper, B.S., Thomas, E.F., Riwali, S., 1989. Voluntary intake and digestibility of barley as influenced by variety and supplementation with either barley grain or cotton seed cake. Anim. Feed Sci. Technol. 26, 105–118.

Casler, M.D., 2001. Breeding forage crops for increased nutritional value. Adv. Agron. 71, 51–107.

Ceccareli, S., 1993. Plant breeding technologies relevant to developing countries. In: Gill, M., Owen, E., Pollot, G.E., Lawrence, T.L.J. (Eds.), Animal Production in Developing Countries, vol. 16. British Society of Animal Production Occasional Publications, pp. 37–55.

Coleman, S., Moore, T., 2003. Feed quality and animal performance. Field Crops Res. 84, 17–29.

Crampton, E.E., Donefer, E., Loyd, L.E., 1960. A nutritive value index of forages. J. Anim. Sci. 19, 538–544.

Dubois, M., Gilles, A.K., Hamilton, J.K., Rebers, P.A., Smith, F., 1956. Colorimetric method for determination of sugars and related substances. Anal. Chem. 28, 350–356.

Ellis, W.C., Lippke, H., 1976. Nutritional values of forages. In: Holt, E.C., Lewis, R.D. (Eds.), Grasses and Legumes in Texas—Development, Production, Utilization. Texas Agricultural Experimental Station Research Monograph, RM6C, pp. 26–66.

Fahey Jr., G.C., Hussein, H.S., 1999. Forty years of forage quality research: accomplishments and impact from an animal nutrition perspective. Crop Sci. 39, 4–12.

GraphPad Prism, 1994. GraphPad Software, San Diego, CA, USA.

McDonald, P., Edwards, R.A., Greenhalgh, J.F.D., 1988. Animal Nutrition, 4th ed. Longman Scientific and Technical, Essex, England.

Menke, K.H., Steingass, H., 1988. Estimation of the digestibility and metabolizable energy content of ruminant feedstuffs from the gas production when they are incubated with rumen liquor in vitro. Anim. Res. Develop. 28, 7–55.

Menke, K.H., Raab, L., Salewski, A., Steingass, H., Fritz, D., Schneider, W., 1979. The estimation of the digestibility and metabolizable energy content of ruminant feedingstuffs from the gas production when they are incubated with rumen liquor in vitro. J. Agric. Sci. Camb. 93, 217–222.

Milford, R., Minson, D.J., 1965. Intake of tropical pasture species. In: Proceedings of the Ninth International Grassland Congress, Sao Paulo, Brazil, pp. 815–822.

Minson, D.J., 1990. Forage in Ruminant Nutrition. Academic Press, New York.

Ørskov, E.R., Reid, G.W., Kay, M., 1988. Prediction of intake of cattle from degradation characteristics of roughages. Anim. Product. 46, 29–34.

Pietzsch, M.S., 1999. Agronomic parameters and morphological parameters and in vitro and in vivo digestibility of residues of different genotypes of sorghum and pearl millet. Training Report, ICRISAT, Patancheru, Andhra Pradesh, India.

Riewe, M.E., Lippke, H., 1970. Considerations in determining the digestibility in harvested forages. In: Proceedings of the National Conference on Forage Evaluation and Utilization, Lincoln, Nebraska, p. F-1.

Statistical Analysis System, 1999. SAS/STAT, Version 8. SAS Inc., Cary, NC.

Tilley, J.M.A., Terry, R.A., 1963. A two stage technique for in vitro digestion of forage crops. J. Brit. Grassl. Soc. 18, 104–111.

Underwood, M.P., Hall, A.J., Zerbini, E., 2000. Genetic enhancement of sorghum and millet residues fed to ruminants: farmers' perception of fodder quality in livelihood systems. Summary Report of PRA Case Studies in Andhra Pradesh, Gujarat, Maharashtra, Karnataka and Rajasthan States. International Livestock Research Institute (ILRI), Nairobi, Kenya and

International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India, 68 pp.

Van Soest, P.J., 1994. Nutritional Ecology of the Ruminant. Comstock University Press, Ythaca, NY, 476 pp.

Van Soest, P.J., Robertson, J.B., 1985. Analysis of forage and fibrous foods. In: Laboratory Manual for Animal Science, vol. 613. Cornell University, Ithaca.

Zerbini, E., Thomas, D., 1999. Plant breeding strategies for improving the feed resources for ruminants. In: Singhal, K.K., Rai, S.N. (Eds.), Emerging Trends for Livestock and Poultry Feeding Beyond 2000 AD. Animal Nutrition Society of India and Indian Council of Agricultural Research, pp. 189–202.

Zerbini, E., Thomas, D., 2003. Crops as livestock feeds in crop-livestock systems. Field Crops Res., in press.