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Journal of Agricultural Science (2002), **138**, 73–84.
DOI: 10.1017/S0021859601001721 *Printed in the United Kingdom*

Effect of nitrogen on intake and digestibility of a tropical grass grazed by Creole heifers

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(*Revised MS received 20 June 2001*)

SUMMARY

So far, little has been done on the effect of nitrogen fertilizer on intake and digestibility in tropical grazing conditions. The effect of two nitrogen levels, 0 (NF) and 50 kg/ha (F) for three successive grazing cycles, on organic matter intake (OMi) and digestibility (OMd) for Creole heifers (208 kg live weight) was determined. Two groups of four tethered heifers, allowed 18 kg of dry matter daily, grazed individual NF or F circular areas at 28 re-growth days. The heifers were moved and watered daily. Sward characteristics (height, herbage mass, morphological and chemical composition and *in situ* tiller measurements), OMi, OMd and feeding behaviour (biting rate, bite size, intake rate, grazing and ruminating times) were evaluated simultaneously per circular area.

Under nitrogen fertilizer, the stems elongated rapidly (by 133%) as did the leaves, but to a lesser extent (by 40%). Consequently, canopy height, leaf and stem masses and crude protein content increased (respectively by 100%, 66%, 186% and 40%), while total bulk density decreased (by 10·5%). Throughout the successive grazing cycles, there was a particular effect on leaf number, both in the F and NF swards, whereas this parameter was not affected by the fertilizer level. Under fertilizer, OMi and OMd were both 9% greater than for the NF sward. The increase in herbage CP content partly explains the rise in OMi, and there is evidence that rumen load has a determining effect on OMi. Leaf mass is the major factor accounting for the 9% increase in OMd under fertilizer regime. On the other hand, whatever the fertilizer regime, OMd was positively influenced by the greater leaf number throughout the grazing cycles. Biting rate, bite size and intake rate were determined respectively by sward height, CP content and stem fraction, whereas grazing and ruminating times were partially influenced by sward characteristics.

INTRODUCTION

Nitrogen fertilizer is commonly used to increase animal production at pasture. In tropical pastures, the live weight (LW) gain reported varies between 1·3 and 4·7 kg LW/ha per year per additional kg of nitrogen added per hectare (Mears & Humphreys 1974; Jones 1990; Humphreys 1991). In most studies the greater herbage mass or crude protein content induced by the addition of nitrogen fertilizer are the main parameters put forward to explain the rise in animal production. However, few data in the tropics allow a precise explanation of the mechanism by which nitrogen fertilizer affects the intake of grazing animals. Nevertheless, such knowledge would be helpful for establishing a suitable fertilizer supply level, and also for developing alternative means to the addition of nitrogen fertilizer to generate greater intake at pasture.

Using equal herbage allowances, the effect of fertilizing an indigenous tropical sward based on *Dichanthium* spp., grazed by Creole heifers, on intake and on digestibility was investigated. The primary aim was to estimate the gain in intake and digestibility under fertilization, as these two parameters determine LW gain. A second objective was to determine any additional parameters involved in the improvement of gain.

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MATERIALS AND METHODS

The experiment was carried out at the experimental station of the National Institute for Agricultural

Research (INRA) in the French West Indies, Guadeloupe (16° 16′ N, 61° 30′ W). Average temperatures ranged from 21–25 °C to 27–31 °C. The mean rainfall on the experimental site is 1000 mm a year.

Experimental design

Two levels of nitrogen fertilizer (0 and 50 kg/ha) were applied to two plots of a sward based on *Dichanthium* spp. after 28 days re-growth. The plots were grazed by two groups of 4 tethered Creole heifers (12 months old and 208 kg LW), during three successive grazing cycles, according to a 2×2 Latin Square design. Each grazing cycle comprised two 4-day measurement periods, each following an 11-day adaptation period. The measurements were taken every 15 days. During the same grazing cycle, the heifers grazed alternately NF or F sward. They had a daily allowance of 18 kg of dry matter (DM).

Sward and animal management

Two plots were each divided into 28 subplots in early February. The subplots were all fertilized at the beginning of the experiment with 187 kg/ha of a 27–9–18 N–P–K fertilizer, in order to respect the annual management of this natural grassland. Every day from 24 February to 24 March, two subplots per plot were mown daily at ground level with a powered lawnmower equipped with a collection tray. After mowing, one of the mown subplots was fertilized (F) with 50 kg nitrogen per hectare as ammonium nitrate (NH_4 NO_3) whereas the second was not (NF). In order to avoid limiting water conditions, a positive water balance was maintained by irrigating all the plots, in accordance with the evapo-transpiration estimated from data collected by an adjacent automatic meteorological station (CIMEL). On 24 March, the last two subplots F and NF were mown which subsequently, together with those mown first, had their 28 day re-growth grazed for the first time by the heifers for 24 h. The first grazing cycle then began. Afterwards the subplots were grazed successively every 28 days. The other grazing cycles lasted 28 days each.

The two groups of 4 heifers grazed two subplots NF or F daily. Each of the eight heifers had a defined circular area of herbage to graze, determined by the chain length and the herbage mass, measured previously, and taking into account the heifer neck length. They were moved daily to fresh areas at 09.00 h and were watered individually at 13.00 h. Every 15 days, at the end of each period of measurement, the heifers were weighed at 09.00 h and were then treated against ticks by spraying. An anthelminthic treatment was applied once a month.

Sward characterization

The sward which the heifers were allowed to graze was characterized by physical and chemical parameters. Swards were measured for each of the eight circular areas of herbage intended for daily grazing by the heifers, for 2 days per measurement period. Sward height was measured with a rising-plate meter (Michell 1982) at 10 sites per circular area. Herbage mass was estimated at the same sites, by cutting the herbage under the plate over an area of 0·03 m², at ground level with hand-held electric clippers. Each of the 10 herbage samples cut was weighed fresh, and all of them were then pooled per circular area. Two subsamples of 300 g were kept, the first to determine dry matter (DM) and chemical composition, the second to determine morphological composition: stems, leaves and debris (including senescent and dead material) were sorted manually prior to drying.

The structure of *in situ* tillers was described before grazing. Ten random tillers per circular area (0·14 to 0·28 tillers/m²) were identified with a coloured ring, and for each one, extended length, stem length and leaf length were measured with a sliding ruler. The cumulated leaf length per tiller was calculated by adding all the leaf lengths from the same tiller. Total herbage bulk density (kg OM/m³) before grazing, was calculated by dividing the total herbage mass (kg OM/m²) by the mean extended tiller length (m). Stem and leaf bulk densities were also calculated by dividing the stem and leaf masses by the mean extended tiller length.

Determining OM intake and OM digestibility

Organic matter intake per day (OMi, kg OM/day) was determined from total faecal OM output and OM digestibility (Streeter 1969): OMi = faecal OM output /(1 − OM digestibility).

Faecal OM output per day (kg OM/day) was measured by manually collecting all faeces excreted by each heifer on the individual circular areas, over the 4-day measurement period. Faeces collection was facilitated by the high faecal DM content (184 g/kg faeces on average) and was carried out twice daily (07.00 h and 17.00 h) to reduce non-collection of faeces due to trampling. The amount of uncollected faeces was estimated to be 2% of the total amount excreted (Boval *et al.* 1996*b*). For each heifer, the entire amount of collected faeces over the 4-day measurement period was weighed and calculated per day. The faeces were then mixed and homogenized and a subsample of 500 g was taken to determine chemical composition.

OM digestibility (OMd) was estimated for each heifer from the crude protein content (CP, g/kg OM) of the faecal subsample taken, according to a local equation established by Boval *et al.* (1996*a*) with Creole steers fed on *Dichanthium* spp. herbage:

$$\text{OMd} = 0{\cdot}983 - 4{\cdot}002/\text{CP}$$
$$(R^2 = 0{\cdot}84;\ \text{S.E.} = 2{\cdot}53\ 10^{-2};\ \text{D.F.} = 37).$$

Digestible OMi (dOMi, g OM/kg $LW^{0.75}$ per day) was calculated by multiplying OMi, expressed by metabolic LW kg (g OM/kg $LW^{0.75}$ per day), by OMd. Non digestible OMi (ndOMi, g OM/kg $LW^{0.75}$ per day) is equal to faecal output expressed per kg of metabolic LW.

Determining ingestive behavioural parameters

The feeding behavioural parameters were determined by visually observing the heifers for 24 h twice per measurement period. The observers recorded the current activity of each heifer every 10 min: grazing (head down, searching for or gripping herbage), ruminating or idling. When the activity was grazing, the observer counted the number of bites (by listening to the noise of the herbage pulled out) taken for 1 min, to determine the biting rate (BR, bites/min). At night, heifers were observed with a flashlight. Grazing, ruminating and idling times (GT, RT and IT respectively) were calculated by multiplying the times of each activity recorded every 10 min, by 10. Bite size (BS, mg OM) was calculated by dividing OMi by the total number of bites (= BR × GT). Intake rate (IR, g OM/min) was calculated by multiplying biting rate by bite size.

Determining chemical composition

Dry matter (DM) contents of both herbage and faeces samples were determined by drying at constant weight at 60 °C in a forced-draught oven over 48 h. The samples were then ground (0·75 mm) prior to chemical analysis. The OM content was measured after a 10 h pyrolysis at 550 °C. Neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL) were estimated following the methods of Van Soest *et al.* (1991). Nitrogen concentration was determined by the Kjeldahl method. Crude protein content was calculated by multiplying the nitrogen content by 6·25.

Statistical analysis

Data were analysed according to a Latin Square design, with the GLM (General Linear Model) procedure of SAS (1989). Animal data and *in situ* tiller measurements were analysed according to the following model:

$$Y_{ijk} = m + F_i + G_j + H_k + (FG)_{ij} + P_l(G_j) + e_{ijkl}$$

where m is the mean, F_i is the fertilization effect (i = 1, 2), G_j is the grazing cycle effect (j = 1, 2, 3), H_k is the heifer effect (k = 1 to 8), $(FG)_{ij}$ is the fertilization × grazing cycle interaction effect, $P_l(G_j)$ is the period effect (l = 1, 2) within each grazing cycle and e_{ijkl} is the residual term. The other herbage data (sward height, herbage mass and morphological parameters) were analysed according to the same model, without the heifer effect.

The relationships between all the measured parameters were first shown by calculating correlation coefficients by the COR procedure of SAS (1989). Regressions were then calculated by the REG procedure using the MAXR (Maximum R^2 Improvement) method. This method tests each independent parameter with all the others, until the best *n*-parameter model (*n* fixed by user) is obtained, producing the highest R^2. The dependent variables were corrected for the heifer effect. The residual distribution was analysed.

RESULTS

Effect of nitrogen fertilizer and grazing cycles on sward characteristics

Under nitrogen fertilizer, the herbage mass increased by 1·6 t DM/ha, and the sward height was nearly twice that of the NF sward (Table 1). Both stem and leaf masses increased with nitrogen fertilizer, but not to the same extent (186 *v.* 66% respectively), and consequently the leaf/stem ratio decreased. Debris mass remained the same whatever the fertilizer level. The total and leaf bulk density values both decreased with fertilizer use (by 11% and 14% respectively), whereas the bulk density of the stems rose by 57%. The fertilized tillers grew much longer than the unfertilized ones, with the extended tiller length increasing by 67%. The stem and leaf lengths both increased but not to the same extent (by 133% and 39% respectively), whereas the leaf number per tiller remained the same for the F and the NF swards. The main chemical parameter modified by nitrogen fertilizer was the herbage CP content (40% higher in the F sward).

Throughout the successive grazing cycles on the NF sward, the leaf mass, leaf length and also the number of leaves, increased respectively, by 113%, 16% and 21% (Table 1). Leaf bulk density rose by 133% and consequently total bulk density increased by 52%. In the F sward, the grazing cycles had a significant effect on all the herbage characteristics, not only on the leaves as was the case for the NF sward. Canopy height as well as total, stem and leaf masses, increased sharply between the first and the third grazing cycle. All the morphological parameters were also significantly greater at the third grazing cycle than at the first.

Effect of nitrogen fertilizer and grazing cycles on intake, digestibility and ingestive behaviour

On the F sward, the heifers ingested 9% more OM and the herbage ingested was better digested by 6

Table 1. *Characteristics of unfertilized (NF) and fertilized (F) tropical* Dichanthium *spp. based swards, each grazed by tethered Creole heifers, during three grazing cycles (NF1, NF2, NF3 and F1, F2, F3)*

	Fertilizer effect			Grazing cycle effect							
	NF	F	S.E.	NF1	NF2	NF3	F1	F2	F3	S.E.	R.s.d.
Sward height (cm)	4·3^{b}	8·1^{a}	0·21	4·7^{d}	4·2^{d}	4·2^{d}	6·2^{c}	7·9^{b}	10·1^{a}	0·36	1·02
Total herbage mass (t DM/ha)	2·5^{b}	4·0^{a}	0·11	2·1^{c}	2·5^{c}	2·8^{c}	2·6^{c}	3·9^{b}	5·5^{a}	0·19	0·55
Stem mass (t DM/ha)	0·4^{b}	1·3^{a}	0·05	0·5^{c}	0·5^{c}	0·4^{ad}	0·7^{c}	1·4^{b}	1·7^{a}	0·08	0·24
Leaf mass (t DM/ha)	0·9^{b}	1·5^{a}	0·04	0·6^{d}	0·9^{c}	1·2^{b}	1·0^{c}	1·2^{b}	2·2^{a}	0·07	0·19
Debris mass (t DM/ha)	1·0^{a}	1·0^{a}	0·05	0·9^{b}	1·0^{b}	1·0^{b}	0·7^{b}	1·1^{ab}	1·3^{a}	0·09	0·25
Leaf/stem ratio	2·3^{a}	1·3^{b}	0·05	1·3^{c}	2·2^{b}	3·3^{a}	1·6^{c}	1·0^{d}	1·3^{c}	0·09	0·25
Extended tiller length (cm)	9·7^{b}	16·2^{a}	0·36	9·3^{d}	9·9^{d}	9·9^{d}	11·9^{c}	16·5^{b}	20·2^{a}	0·62	1·75
Stem length (cm)	3·3^{b}	7·7^{a}	0·33	3·2^{d}	3·4^{d}	3·3^{d}	4·3^{c}	8·1^{b}	10·8^{a}	0·58	1·63
Leaf length (cm)	4·6^{b}	6·4^{a}	0·08	4·3^{d}	4·4^{d}	5·0^{c}	5·9^{b}	5·7^{b}	7·4^{a}	0·14	0·38
Number of leaves per tiller	4·4^{a}	4·3^{a}	0·04	3·9^{d}	4·5^{c}	4·7^{b}	3·8^{d}	4·0^{d}	5·0^{a}	0·08	0·21
Total bulk density (kg DM/m^3)	5·7^{a}	5·1^{b}	0·11	4·6^{c}	6·3^{b}	7·0^{a}	4·3^{cd}	5·2^{c}	5·9^{b}	0·18	0·52
Leaf bulk density (kg DM/m^3)	2·1^{a}	1·8	0·05	1·2^{d}	2·1^{b}	2·8^{a}	1·6^{c}	1·5^{c}	2·1^{b}	0·08	0·21
Stem bulk density (kg DM/m^3)	1·0^{b}	1·6^{a}	0·04	0·9^{b}	1·1^{b}	0·9^{b}	1·1^{b}	1·7^{a}	1·7^{a}	0·07	0·22
DM	0·32^{a}	0·27^{b}	0·005	0·38^{a}	0·28^{b}	0·30^{b}	0·35^{a}	0·24^{b}	0·24^{b}	0·008	0·024
OM (g/kg DM)	887^{a}	865^{b}	2·4	881^{a}	869^{ab}	844^{c}	889^{a}	892^{a}	881^{ab}	4·2	12·2
CP (g/kg OM)	73^{b}	102^{a}	1·2	74^{ab}	69^{b}	78^{a}	99^{a}	104^{a}	103^{a}	2·1	5·8
NDF (g/kg OM)	708^{b}	722^{a}	2·9	716^{bc}	723^{b}	684^{d}	706^{c}	742^{a}	718^{bc}	5·0	14·2
ADF (g/kg OM)	351^{b}	357^{a}	2·1	368^{ab}	360^{b}	326^{d}	359^{b}	374^{a}	339^{c}	3·6	10·3
ADL (g/kg OM)	75^{a}	71^{a}	1·7	73^{ab}	80^{a}	72^{ab}	66^{bc}	81^{a}	66^{bc}	3·0	8·4

Values with different superscripts within fertilizer levels or grazing cycles are significantly different ($P < 0·05$).
R.s.d.: Root Mean Squared Error; S.E.: standard error.

Table 2. *Herbage allowances, OM intake, OM digestibility and ingestive behaviour parameters (Biting rate, Bite size, Intake rate, Grazing, Ruminating and Idling times) for tethered Creole heifers grazing unfertilized (NF) or fertilized (F) tropical* Dichanthium *spp. based swards, during three grazing cycles (NF, NF2, NF3 and F1, F2, F3)*

	Fertilizer effect			Grazing cycle effect							
	NF	F	S.E.	NF1	NF2	NF3	F1	F2	F3	S.E.	R.s.d.
Allowance (g OM/kg $LW^{0·75}$ per day)	342^{a}	351^{a}	10·4	297^{c}	343^{b}	386^{a}	287^{c}	389^{a}	377^{ab}	18·1	3·5
OM intake (g/kg $LW^{0·75}$ per day)	76·6^{b}	83·6^{a}	1·53	75·1^{b}	77·1^{b}	77·6^{b}	81·7^{ab}	89·1^{a}	80·1^{b}	2·65	7·50
OM digestibility	0·64^{b}	0·70^{a}	0·002	0·62^{f}	0·63^{e}	0·67^{d}	0·68^{c}	0·70^{b}	0·73^{a}	0·004	0·012
dOMi (g/kg $LW^{0·75}$ per day)	49·3^{b}	59·5^{a}	1·11	46·6^{bc}	48·8^{bc}	51·5^{b}	55·8^{ab}	62·0^{a}	58·3^{a}	1·93	5·46
ndOMi (g/kg $LW^{0·75}$ per day)	27·6^{a}	24·9^{b}	0·48	28·6^{a}	28·3^{a}	26·1^{ab}	25·9^{b}	27·1^{ab}	21·9^{c}	0·84	2·37
Biting rate (bites/min)	54^{a}	50^{b}	0·6	54^{b}	55^{b}	58^{a}	53^{bc}	51^{cd}	49^{d}	1·1	3·2
Bite size (mg OM)	186^{b}	267^{a}	6·2	205^{c}	172^{d}	181^{cd}	247^{b}	280^{a}	276^{ab}	10·7	30·4
Intake rate (g OM/min)	10^{b}	13^{a}	0·3	10·9^{b}	9·2^{c}	10·0^{bc}	12·8^{a}	13·8^{a}	12·8^{a}	0·5	1·5
Grazing time (min)	431^{a}	362^{b}	6·0	378^{b}	463^{a}	452^{a}	351^{b}	367^{b}	368^{b}	10·4	29·5
Ruminating time (min)	129^{a}	179^{a}	5·7	189^{b}	101^{d}	98^{d}	219^{a}	160^{c}	157^{c}	9·8	27·8
Idling time (min)	213^{b}	233^{a}	6·8	233^{a}	197^{b}	208^{ab}	232^{a}	233^{a}	233^{a}	11·8	33·4

Values with different superscripts within fertilizer levels or grazing cycles are significantly different ($P < 0·05$).
dOMi, digestible OM intake; ndOMi, non digestible OM intake; R.s.d., Root Mean Squared Error; S.E., standard error.

digestibility units than on the NF sward (Table 2). On the F sward the heifers grazed with a lower biting rate and for a shorter time than on the NF sward. Bite size and intake rate were both higher on the F sward.

From the first to the last grazing cycle, with both the NF and the F swards, digestibility increased by 5 digestibility units whereas intake did not vary (Table 2). On the F sward, the biting rate decreased whereas the grazing time did not vary between the grazing cycles. On the NF sward, both the biting rate and the grazing time increased (Table 2) from the first to the third grazing cycle.

Analysis of determining parameters for intake, digestibility and ingestive behaviour

Considering the entire sward data, OMi was mostly

Table 3*a*. *Correlation coefficients between OM intake* (*OMi*), *OM digestibility* (*OMd*), *Biting rate* (*BR*, *bites/min*), *Bite size* (*BS*, *mg OM*), *Intake rate* (*g OM/min*), *Grazing time* (*GT*, *min*) *and Ruminating time* (*RT*, *min*) *and sward characteristics*, *whatever the fertilization level*, *for tethered Creole heifers grazing tropical* Dichanthium *spp. based swards*

	OMi	OMd	BR	BS	IR	GT	RT
Sward height (cm)	$0{\cdot}24^{ns}$	0·70***	−0·71***	0·70***	0·39**	−0·30*	$0{\cdot}26^{ns}$
Total mass (t DM/ha)	0·29*	0·73***	−0·60***	0·61***	0·33**	$-0{\cdot}18^{ns}$	$0{\cdot}05^{ns}$
Stem mass (t DM/ha)	0·33*	0·74***	−0·61***	0·72***	0·46***	−0·31*	$0{\cdot}11^{ns}$
Leaf mass (t DM/ha)	$0{\cdot}21^{ns}$	0·77***	−0·51***	0·51***	$0{\cdot}27^{ns}$	$-0{\cdot}16^{ns}$	$-0{\cdot}03^{ns}$
Debris mass (t DM/ha)	$0{\cdot}23^{ns}$	$0{\cdot}24^{ns}$	−0·48***	0·27*	$0{\cdot}01^{ns}$	$0{\cdot}17^{ns}$	$0{\cdot}14^{ns}$
Leaf/stem ratio	$-0{\cdot}16^{ns}$	$-0{\cdot}25^{ns}$	0·40**	−0·58***	−0·48***	0·48***	−0·40**
Extended tiller length (cm)	$0{\cdot}26^{ns}$	0·70***	−0·66***	0·69***	0·40**	−0·28*	$0{\cdot}14^{ns}$
Stem length (cm)	$0{\cdot}24^{ns}$	0·65***	−0·65***	0·68***	0·39**	−0·28*	$0{\cdot}07^{ns}$
Mean leaf length (cm)	$0{\cdot}28^{ns}$	0·75***	−0·59***	0·63***	0·38**	$-0{\cdot}26^{ns}$	0·31*
Number of leaf per tiller	$0{\cdot}04^{ns}$	0·40**	$-0{\cdot}27^{ns}$	$0{\cdot}04^{ns}$	$-0{\cdot}15^{ns}$	$0{\cdot}24^{ns}$	−0·33*
Total bulk density (kg DM/m^3)	$0{\cdot}15^{ns}$	$-0{\cdot}04^{ns}$	0·41**	−0·35*	$-0{\cdot}22^{ns}$	0·44**	−0·53***
Leaf bulk density (kg DM/m^3)	$0{\cdot}08^{ns}$	$0{\cdot}15^{ns}$	0·33*	$-0{\cdot}27^{ns}$	$-0{\cdot}17^{ns}$	0·33*	−0·51***
Stem bulk density (kg DM/m^3)	0·37**	0·64***	$-0{\cdot}28^{ns}$	0·61***	0·54***	−0·30*	$-0{\cdot}04^{ns}$
CP (g/kg OM)	0·43**	0·75***	$-0{\cdot}25^{ns}$	0·79***	0·77***	−0·61***	$0{\cdot}03^{ns}$
NDF (g/kg OM)	$-0{\cdot}05^{ns}$	$0{\cdot}17^{ns}$	−0·60***	0·29*	$0{\cdot}02^{ns}$	$-0{\cdot}10^{ns}$	$0{\cdot}20^{ns}$
ADF (g/kg OM)	$-0{\cdot}01^{ns}$	$-0{\cdot}21^{ns}$	−0·32*	$0{\cdot}12^{ns}$	$-0{\cdot}01^{ns}$	$-0{\cdot}03^{ns}$	0·45**
ADL (g/kg OM)	$0{\cdot}18^{ns}$	−0·29*	$0{\cdot}05^{ns}$	$-0{\cdot}21^{ns}$	$-0{\cdot}23^{ns}$	0·43**	$0{\cdot}05^{ns}$

ns, non significant; *, **, ***: significantly correlated ($P < 0{\cdot}01$, 0·001, 0·0001 respectively).

Table 3*b*. *Correlation coefficients between OM intake* (*OMi*, *g/kg LW*$^{0{\cdot}75}$), *OM digestibility* (*OMd*), *digestible OM intake* (*dOMi*, *g/kg LW*$^{0{\cdot}75}$), *non digestible OM intake* (*ndOMi*, *g/kg LW*$^{0{\cdot}75}$), *Biting rate* (*BR*, *bites/min*), *Bite size* (*BS*, *mg OM*), *Intake rate* (*g OM/min*), *Grazing time* (*GT*, *min*) *and Ruminating time* (*RT*, *min*) *for tethered Creole heifers grazing tropical* Dichanthium *spp. based swards*, *whatever the fertilization level*

	OMi	OMd	dOMi	ndOMi	BR	BS	IR	GT	RT
OMd	$0{\cdot}21^{ns}$								
dOMi	0·92***	0·58***							
ndOMi	0·61**	−0·64***	$0{\cdot}24^{ns}$						
BR	$0{\cdot}19^{ns}$	−0·48***	$-0{\cdot}04^{ns}$	0·54***					
BS	0·52***	0·67***	0·71***	$-0{\cdot}14^{ns}$	−0·49***				
IR	0·70***	0·48***	0·79***	$0{\cdot}14^{ns}$	$-0{\cdot}03^{ns}$	0·88***			
GT	$-0{\cdot}15^{ns}$	−0·30*	$-0{\cdot}25^{ns}$	$0{\cdot}14^{ns}$	$0{\cdot}11^{ns}$	−0·67***	−0·73***		
RT	$0{\cdot}15^{ns}$	$0{\cdot}02^{ns}$	$0{\cdot}14^{ns}$	$0{\cdot}07^{ns}$	−0·32*	$0{\cdot}19^{ns}$	$0{\cdot}09^{ns}$	$-0{\cdot}12^{ns}$	

ns, non significant; *, **, ***: significantly correlated ($P < 0{\cdot}01$, 0·001, 0·0001 respectively).

correlated with the herbage CP content and stem bulk density (Table 3*a*). OMi was not correlated with OMd, even if these two variables are linked by calculation (Table 3*b*), but was correlated to dOMi and ndOMi. The dOMi increased with OMi on F or NF sward with a slope of 0·75, whereas ndOMi increased slowly, keeping close to an average value of 26·3 g OM/kg LW$^{0{\cdot}75}$, whatever the F or NF treatment (Fig. 1). Intake was also correlated with bite size and intake rate (Table 3*b*) but these correlations are also arguable, as the parameters concerned are linked by calculation. Considering the predictive regressions (Table 4), sward characteristics and even herbage CP content accounted for little of OMi (Table 4), explaining only 16% of OMi variance.

OMd was well correlated with several sward characteristics with correlation coefficients in the range 0·70–0·77: leaf mass and leaf length, CP content, stem mass and sward height or extended tiller length (Table 3*a*). With respect to ingestive behavioural parameters, OMd was negatively correlated with biting rate and grazing time (Table 3*a*). It was positively correlated with bite size and intake rate but, as already pointed out for OMi, these parameters are

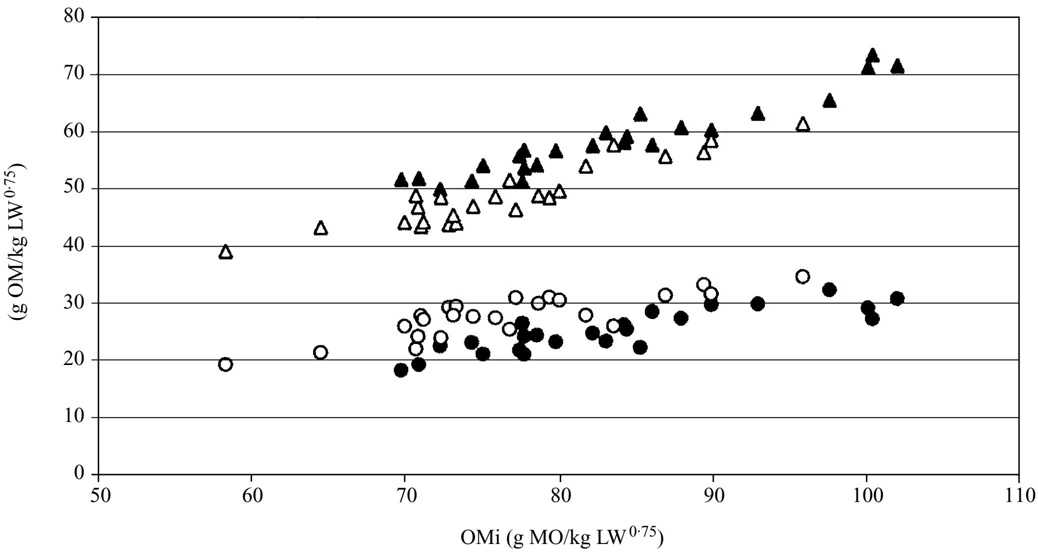
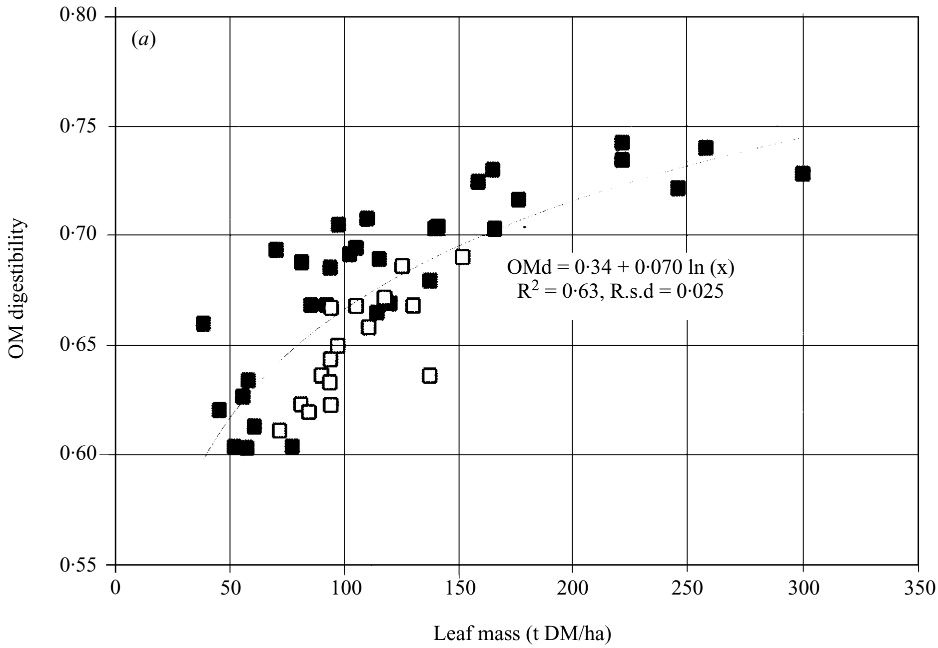


Fig. 1. Evolution of non digestible OM intake (ndOMi) and digestible OM intake (dOMi) with total OM ingested (OMi) in fertilized (F) or unfertilized (NF) *Dichanthium* spp. based sward. ▲, domi-F; △, domi-NF; ●, ndOMi-F; ○, ndOMi-NF.

Table 4. *Predictive regressions of OM intake (OMi, g/kg LW$^{0\cdot 75}$), OM digestibility (OMd), Biting rate (BR, bites/min), Bite size (BS, mg OM), Intake rate (g OM/min), Grazing time (GT, min) and Ruminating time (RT, min), from characteristics of tropical* Dichanthium *spp. based swards grazed by tethered Creole heifers*

Equations	Percentage variance explained (R^2)	Residual standard deviation (R.s.d)	Error degrees of freedom (D.F.)	Mean
OMi = 47·11 + 49·18 OMd	0·02	9·43	46	80·1
OMi = 58·3 + 2·48 Herbage CP	0·16	8·71	46	
OMi = 41·11 + 1·48 ndOMi	0·37	7·64	46	
OMi = −2·3 + 1·9 ndOMi + 3·69 CP	0·74	4·86	45	
OMd = 0·56 + 0·023 Sward height − 0·0008 Sward height^2	0·51	0·028	45	0·67
OMd = 0·59 + 0·018 Stem length − 0·0006 Stem length^2	0·51	0·028	45	
OMd = 0·51 + 0·017 Ext. tiller length − 0·0003 Ext. tiller length^2	0·57	0·026	45	
OMd = 0·34 + 0·070 Ln (Leaf mass)	0·63	0·025	46	
OMd = 0·52 + 0·00037 Leaf mass + 0·012 Herbage CP	0·76	0·019	45	
BR = 60·75 − 1·44 Sward height	0·51	3·92	46	52
BR = 112·6 − 1·108 Sward height − 0·754 Herbage NDF	0·57	3·62	45	
BS = 96·5 + 547·22 Stem fraction	0·58	35·1	46	226
BS = 96·51 + 386·75 Stem fraction + 6·15 Sward height	0·62	33·4	45	
BS = −2·35 + 26·07 Herbage CP	0·63	32·9	46	
BS = 11·65 + 19·30 Herbage CP + 7·34 Sward height	0·73	28·6	45	
IR = 6·8 + 20·19 Stem fraction	0·39	1·86	46	11·6
IR = 1·78 + 1·12 Herbage CP	0·59	1·54	46	
IR = 3·89 + 1·18 Herbage CP − 7·40 Leaf fraction	0·61	1·48	45	
GT = 283·4 + 63·9 Debris bulk density	0·38	51·4	46	396
GT = 485·9 + 7·9 Total bulk density − 21·3 Herbage CP	0·44	48·9	45	
RT = 355·9 − 37·34 Total bulk density	0·26	68·4	46	154
RT = 176·7 − 28·9 Total bulk density − 451 Herbage DM	0·38	62·6	45	

Ext. tiller length, Extended tiller length.



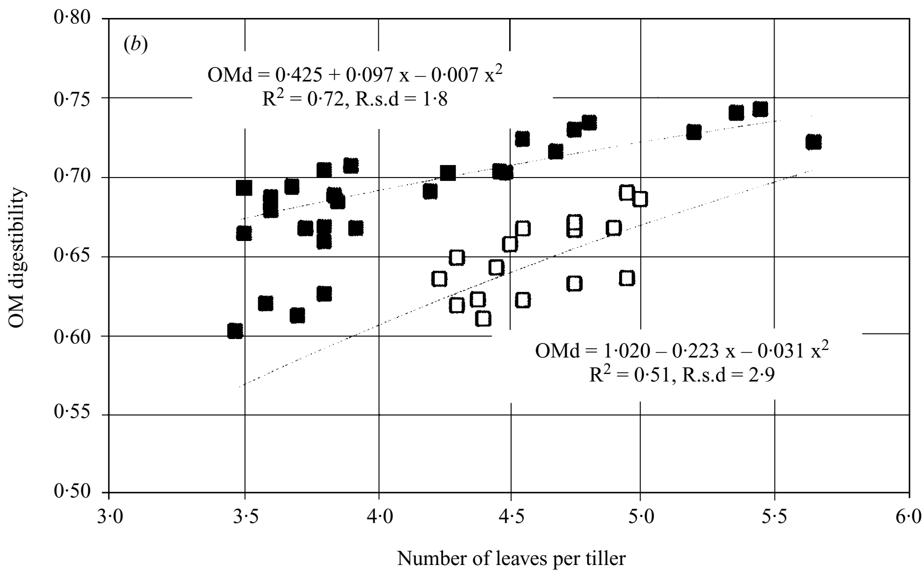
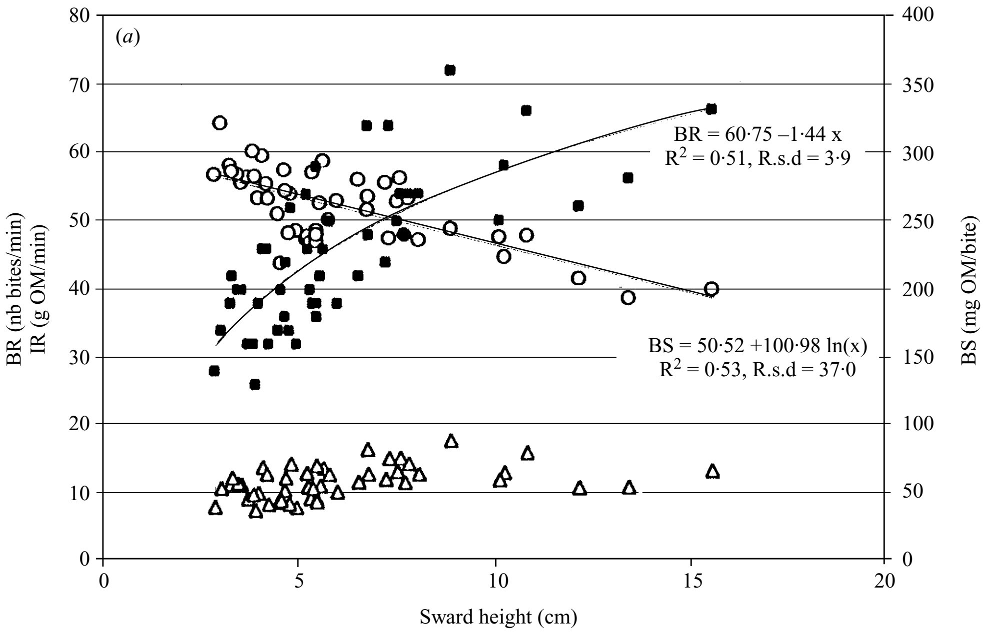


Fig. 2. (*a*). Effect of leaf mass on *in vivo* OM digestibility (OMd) measured on fertilized (F, ■) or unfertilized sward (NF, □) *Dichanthium* spp. based swards. (*b*) Effect of the number of leaves per tiller on *in vivo* OM digestibility (OMd) on fertilized (F, ■) and unfertilized (NF, □) *Dichanthium* spp. based swards.

linked to OMd by calculation. The predictive regression analysis shows that leaf mass was the main determining parameter for OMd. Indeed leaf mass alone explained 63% of OMd variance (Table 4, Fig. 2*a*) and, combined with the CP content, R^2 went up to 76% (Table 4). Stem length and sward height predicted OMd equally and the prediction was slightly better on the basis of extended tiller length. Considering F sward data separately, the number of leaves appeared to be the parameter which is best



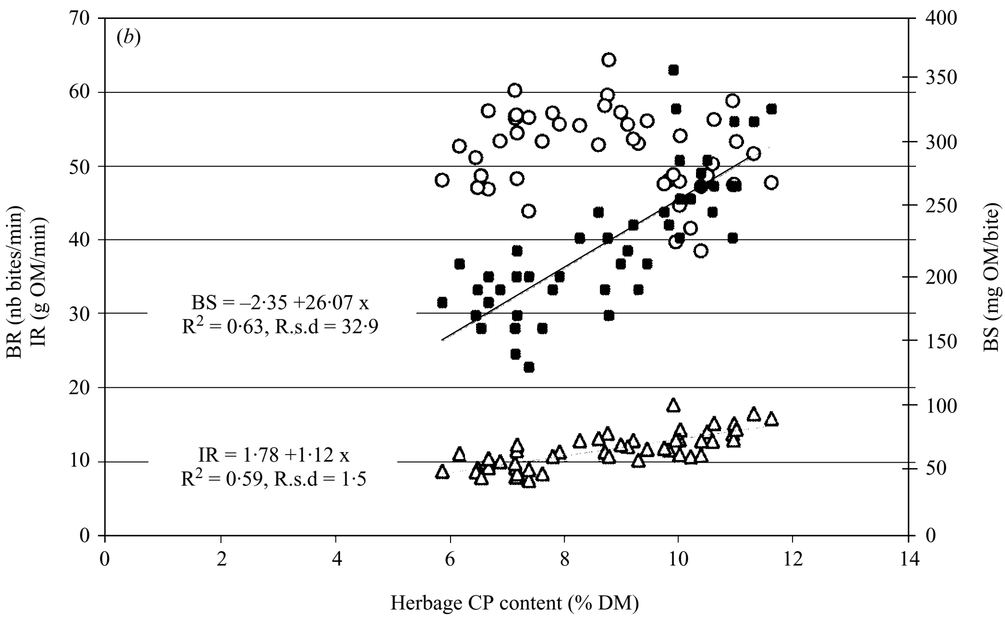


Fig. 3. (*a*). Evolution of biting rate (BR, ○), intake rate (IR, △) and bite size (BS, ■) with sward height of a *Dichanthium* spp. based sward, with or without fertilization, (*b*) with CP content of a *Dichanthium* spp. based sward, with or without fertilization.

correlated with OMd (Fig. 2*b*). This relationship was also significant in the NF sward.

The feeding behavioural parameters such as biting rate, bite size and intake rate were better correlated with sward characteristics than with grazing, ruminating or idling times. Biting rate was well correlated with, and predicted by sward height (Tables 3*a* and 4, Fig. 3*a*). Bite size and intake rate were first correlated with CP content (Fig. 3*b*), and to a lesser extent with stem fraction. Grazing and ruminating times were both predicted mainly by total bulk density.

DISCUSSION

Effect of nitrogen fertilizer and successive grazing cycles on Dichanthium *spp. characteristics*

The rise in herbage mass induced by the addition of nitrogen fertilizer was consistent with other reports, from 19 kg DM per additional kg N for *Digitaria decumbens* (Ethredge *et al.* 1973; Blunt & Haydock 1977) to 29·7 kg DM/kg N for *Cynodon dactylon* (Crespo 1984), two stoloniferous tropical grasses as are also *Dichanthium* spp. The higher CP content due to nitrogen fertilizer has also been reported in other tropical studies (Minson 1973; Monson & Burton 1982), whereas the rise we measured was greater, probably because of measurement conditions at pasture.

The rise in herbage mass and CP content under nitrogen fertilizer, is classically explained by leaf elongation and consequently a rise in leaf mass and leaf area index, for tillering grass species. These morphological modifications have been reported for temperate (Mazzanti *et al.* 1994) and tropical (Pinto *et al.* 1994) tillering grass species. In our experiment, the nitrogen effect on the *Dichanthium* spp. sward appeared mainly on the stems, which grew much longer than the leaves, with the leaf/stem ratio decreasing. This has previously been reported for *Dichanthium aristatum* (Schemoul 1988; Cruz & Boval 2000), *Digitaria decumbens* (Cruz *et al.* 1989) and *Cynodon dactylon* (Overman & Wilkinson 1989). Although to a lesser extent than the stems, the leaves also elongated and the greater leaf mass that followed helped to increase the CP content and the herbage quality. Moreover, it is possible that the addition of fertilizer doubled leaf density at the top of the sward compared to the lower layers, as shown by Stobbs (1973*b*, 1975) and Hendricksen & Minson (1985), easing thereby the accessibility of leaves for grazing animals.

It is generally considered that stem elongation causes a fall in the quality of the herbage offered, but this undoubtedly proves to be invalid under fertilization. The young elongated stems caused by fertilizer may be similar in digestibility to the leaves (Haggar & Ahmed 1970) and they do have less tensile strength than unfertilized stems (Flores *et al.* 1993). Furthermore, whereas the total herbage bulk density declined with the elongation of the stems under fertilizer, it remained higher than the threshold value of 100 kg DM/ha per cm, usually reported for tropical swards (Stobbs 1973*a*), which does not limit the bite size of grazing animals (Humphreys 1991). In such conditions the fertilized elongated stems may help grazing animals to get a good grip on high quality herbage.

Throughout the successive grazing cycles, a higher number of living leaves per plant, which were also much longer, was observed. This effect was measured on the NF sward as well on the F sward. Moreover, on the F sward all the other sward parameters varied, owing to the accumulation of nitrogen fertilizer from one application to another, combined with the effect of successive grazing cycles (Mears & Humphreys 1974). The higher leaf number may be explained by the successive frequent defoliation which can generate the production of shorter leaves and sheaths than with infrequent cutting, according to Davies (1977).

In the current study some typical effects of nitrogen fertilization, such as the rise in herbage mass, CP content and leaf elongation, were demonstrated for a grazed *Dichanthium* spp. based sward. However, the fertilizer effect on stem elongation is more specific to tropical stoloniferous grasses. In other tropical studies, the leaf expansion rate measured throughout the successive grazing cycles was not reported either. In fact there is a lack of characterization of various morphological tropical grasses at pasture (Hacker & Evans 1992; Cruz & Boval 2000).

Nitrogen fertilizer effect on intake and digestibility

At a fixed daily herbage allowance, intake and digestibility were higher for the fertilized sward, resulting in a rise in digestible OM intake (dOMi) by 20·6%. Minson (1973) with tropical *Chloris gayana* and Delagarde *et al.* (1997) with temperate perennial ryegrass, reported dOMi rises of 21 and 25·6%, from fertilizing respectively with 125 to 500 kg N/ha at 28 days of re-growth and from 0 to 60 kg N/ha at 32 days of re-growth. The 20·6% increase in dOMi is consistent with the LW gain during the experiment, for the NF and F swards (respectively 230 and 462 g/day), although it was measured over short periods. The energy input is sufficient to meet maintenance requirements (0·044UF/kg $LW^{0.75}$, Vérité *et al.* 1987), and the growth energy for a potential daily LW gain of 200 g and 425 g respectively for the NF and F swards. Taking into account the amount of fertilizer added, the LW gain from the NF to the F sward is equivalent to 1·47 kg LW/ha per additional kg of fertilizer. This value is close to values reported in other studies, from 1·3 to 4·7 kg LW/ha per year and per additional kg of nitrogen fertilizer (Mears & Humphreys 1974; Jones 1990). However, in those studies, the stocking rate was not adjusted with regard to the fertilizer level, and the LW gain recorded is generally explained by a rising herbage allowance.

The fertilizer effect measured seems in accordance with other studies, but the explanatory parameters may differ. Firstly, greater herbage allowance due to nitrogen fertilizer could not be invoked in the current experiment. On the other hand, the herbage CP rise from the NF to the F sward contributed to the increase in OMi. In the NF sward the herbage CP content is close to the limiting value reported for nitrogen deficiency in the rumen (Minson 1990).

According to Vérité *et al*. (1987) 126 to 135 g of CP is required to digest 1 kg of digestible OMi (dOMi), whereas for the NF sward, the amount of CP was 115 g. Consequently, under fertilization, the increase in herbage CP content may compensate for a CP deficiency, facilitating the cellulolytic activity in the rumen (Archimède *et al*. 1999) of the grazing heifers. However, the herbage CP rise accounts only for 16% of the OMi variance, and the rumen load could be the other main determining parameter for OMi in our experiment (Fig. 1). Ruminants are able to ingest a constant amount of nondigestible OM (ndOMi), irrespective of the total amount consumed and which is representative of the rumen load (Lehman 1941, quoted by Jarrige 1989). Whatever F or NF swards, ndOMi varied slightly with intake, keeping close to 26·3 g OM/kg $LW^{0.75}$. However on the F sward, ndOMi represented 29% of the total intake whereas it represented 36% on the NF sward (Fig. 1). So on the F sward, the amount of ndOMi was reached when a greater amount of digestible OM was ingested (dOMi) and consequently for a greater total intake, compared to the unfertilized sward. Such ndOMi values, have already been measured in previous experiments (Boval *et al*. 1996*b*; Boval *et al*. 2000) and in other tropical environments, as reviewed by Kennedy (1995) for cattle and buffaloes. This needs to be checked in further experiments, in which rumen load is measured.

Intake was influenced by neither of the physical sward characteristics, whereas the latter influenced the ingestive behaviour of the heifers. Indeed sward height determines biting rate and bite size as already reported for cattle (Laca *et al*. 1992) and sheep (Black & Kenney 1984; Burlinson *et al*. 1991). Stem fraction and herbage CP content also influenced bite size and intake rate. However, the other behavioural parameters, grazing and ruminating times for instance, were modified to a lesser extent by sward characteristics, except a little by herbage bulk density. It is possible that sward characteristics affect ingestive behaviour instantaneously, in the short-term, via parameters such as biting rate, bite size or intake rate. However on a daily basis there is compensation (Allden & Whittaker 1970; Jamieson & Hodgson 1979) between short-term parameters and this compensation may contribute to the maintenance of equal daily grazing and ruminating times. Indeed the non-limiting amount of fresh herbage allowed daily, may have helped the heifers to adapt their behaviour to satisfy their appetite and energy requirements. This probably also explains why OMi, resulting from many bites during the day, is not affected by sward characteristics such as short-term ingestive behavioural parameters. Thereafter, if the addition of nitrogen fertilizer influences both OMi and ingestive behavioural parameters, it does not occur in the same way and this implies the choice of the appropriate parameters to understand grazing animal nutrition on a daily basis.

Conversely, the increase in OM digestibility in the F sward is mainly explainable by physical sward structure. Leaf mass accounts for the best OMd gain which is better still when combined with CP content. Sward characteristics such as sward height and extended tiller length also explain the OMd rise under fertilizer quite well. Thus, even if nitrogen fertilizer elongated the stems more than the leaves, the stems produced did not constitute a limit for gripping high quality herbage, as is often reported for tropical herbage (Stobbs 1973*b*; Hendricksen & Minson 1980). There are a few references to the effect of sward characteristics on OMd, which was mostly estimated *in vitro*. However, Forbes & Coleman (1993) reported a significant effect of the leaf fraction of warm-season *Bothrichloa* spp. on OMd. Irrespective of leaf mass and CP content effects, the number of living leaves also determined OMd, inducing a 5 unit gain (Fig. 2*b*), whatever the fertilizer level on the sward. This 5 unit gain is close to the 6 unit gain measured as the fertilizer effect. This was unexpected and suggests that for the same leaf mass, shorter but more numerous leaves may be better than a few long leaves in improving the digestibility of the herbage consumed at pasture. Indeed Duru *et al*. (1999) reported that shorter leaves are more digestible than longer ones, because the time required for elongation is shorter and the leaves are less mature. It is worth noting that OMd as well as ingestive behavioural parameters are influenced by sward characteristics, whereas OMi is not. The relationship between sward characteristics, some ingestive behavioural parameters and OMd, can be explained by the fact that low quality individual bites have a higher influence on OMd than on OMi. OMi is indeed the resultant of many small amounts of herbage consumed per bite, throughout the day, and a given daily OMi can be reached by increasing either bite size, biting rate or grazing time (Allden & Whittaker 1970; Hodgson 1982). In return, if many low quality bites are achieved by grazing animals, this induces an irremediable drop in OMd, which is difficult to compensate.

CONCLUSIONS

Nitrogen fertilizer induced a rise in herbage mass, by way of a considerable stem and leaf elongation and a rise in herbage CP content. Having equal herbage allowances the heifers ingest 9% more OM, which is more digestible by 5 digestibility units, on the fertilized sward. The rise in OMi is just partly explainable by the rise in herbage CP content. In other respects, the stability of ndOMi regardless of nitrogen level, suggests a determining effect of rumen load on OMi, although the latter was not measured. In contrast to OMi, the gain in OMd is firstly explainable by physical sward characteristics such as leaf mass. The length of the fertilized stems and the subsequent sward height also help to increase OMd, probably by making the leaves easier to grip. Ingestive behaviour is closer to OMd than OMi. This suggests that studies at pasture which take into account just ingestive behaviour to indicate intake are not reliable.

Thus nitrogen fertilizer causes a significant improvement in digestible intake at pasture, by inducing a leafy sward with a greater young stem mass and a greater herbage CP content, irrespective of herbage allowance. This indicates that the structure of the sward has to be considered with the chemical components, to investigate ruminant nutrition at pasture. Knowledge of the effects of nitrogen fertilizer on animal nutrition via the morphological modifications of the herbage, allows better definition of suitable management for promoting nutrition at pasture. In that sense, knowledge provided by agronomists on morphological responses of tropical grass under various conditions, may be helpful.

We thank A. Nepaut and P. Mulciba for their great technical participation.

REFERENCES

Allden, W. G. & Whittaker, I. A. McD. (1970). The determinants of herbage intake by grazing sheep: the interrelationships of factors influencing herbage intake and availability. *Australian Journal of Agricultural Research* **21**, 755–766.

Archimede, H., Aumont, G., Saminadin, G., Depres, E., Despois, P. & Xande, A. (1999). Effects of urea and saccharose on intake and digestion of a *Digitaria decumbens* hay by black belly sheep. *Animal Science* **69**, 403–410.

Black, J. L. & Kenney, P. A. (1984). Factors affecting diet selection by sheep. *Grass and Forage Science* **35**, 565–578.

Blunt, C. G. & Haydock, K. P. (1978). Effect of irrigation, nitrogen and defoliation on Pangola grass in the dry season at the Ord Valley, north-western Australia. *Australian Journal of Experimental Agriculture and Animal Husbandry* **18**, 825–833.

Boval, M., Peyraud, J. L., Xande, A., Aumont, G., Copry, O. & Saminadin, G. (1996*a*). Evaluation of faecal indicators to predict digestibility and voluntary intake of *Dichanthium* spp. by cattle. *Annales de Zootechnie* **45**, 121–134.

Boval, M., Peyraud, J. L. & Xande, A. (1996*b*). Effect of nocturnal enclosing and splitting offered area on herbage intake of tethered creole heifers. *Annales de Zootechnie* **45**, 219–231.

Boval, M., Cruz, P., Peyraud, J. L. & Penning, P. (2000). Herbage allowance effect on intake of Creole heifers tethered at pasture. *Grass and Forage Science* **55**, 201–208.

Burlison, A. J., Hodgson, J. & Illius, A. W. (1991). Sward canopy structure and the bite dimensions and bite weight of grazing sheep. *Grass and Forage Science* **46**, 29–38.

Crespo, G. (1984). Variation in the response of tropical pastures to nitrogenous fertilizers througout the year. 1. Pangola grass (*Digitaria decumbens* Stent) without irrigation. *Cuban Journal of Agricultural Science* **18**, 63–73.

Cruz, P. & Boval, M. (2000). Effect of nitrogen on some morphogenetical traits of temperate and tropical perennial forage grasses. In *Grassland Ecophysiology and Grazing Ecology* (Eds G. Lemaire, J. Hodgson, A. de Moraes, C. Nabinger & P. C. de F. Carvalho), pp. 151–167. Wallingford: CAB.

Cruz, P., Alexandre, G. & Baudot, H. (1989). Cinétique de croissance foliaire et stolonifère d'un peuplement de *Digitaria decumbens* au cour de la repousse. In *Proceedings of the XVI International Grassland Congress, Volume I.* (Ed. Desroche), pp. 499–500. Nice: The French Grassland Society.

Davies, A. (1977) Structure of the grass sward. In *Proceedings of the International Meeting on Animal Production, from Temperate Grasslands* (Dublin, Ireland), pp 36–44.

Delagarde, R., Peyraud, J. L. & Delaby, L. (1997). The effect of nitrogen fertilization level and protein supplementation on herbage intake, feeding behaviour and digestion in grazing dairy cows. *Animal Feed Science and Technology* **66**, 165–180.

Duru, M., Ducrocq, H. & Feuillerac, E. (1999). *In vitro* digestibility response of cocksfoot (*Dactylis glomerata* L.) to growth and defoliation: a simple model. *Journal of Agricultural Science, Cambridge* **133**, 379–388.

Ethredge, J., Beaty, E. R. & Lawrence, R. M. (1973). Effects of clipping height, clipping frequency, and rates of nitrogen on yield and energy content of Coastal Bermudagrass. *Agronomy Journal* **65**, 717–719.

Flores, E. R., Laca, E. A., Griggs, T. C. & Demment, M. W. (1993). Sward height and vertical morphological differentiation determine cattle bite dimensions. *Agronomy Journal* **85**, 527–532.

Forbes, T. D. A. & Coleman, S. W. (1993). Forage intake and ingestive behaviour of cattle grazing Old World Bluestems. *Agronomy Journal* **85**, 808–816.

Hacker, J. B. & Evans, T. R. (1992). An evaluation of the production potential of six tropical grasses under grazing. 1. Yield and yield components, growth rates and phenology. *Australian Journal of Experimental Agriculture* **32**, 19–27.

Haggar, R. J. & Ahmed, M. B. (1970). Seasonal production of *Andropogon gayanus*. 2. Seasonal changes in digestibility and feed intake. *Journal of Agricultural Science, Cambridge* **75**, 369–373.

Hendricksen, R. E. & Minson, D. J. (1985). The voluntary intake, digestibility and retention time by cattle and sheep of stem and leaf fractions of a tropical legume (*Lablab purpureum*). *Australian Journal of Experimental Agriculture* **32**, 389–398.

Hendricksen, R. E. & Minson, D. J. (1980). The feed intake and grazing behaviour of cattle grazing a crop of *Lablab purpureus* cv. Rongai. *Journal of Agricultural Science, Cambridge* **95**, 547–554.

Hodgson, J. (1982). Influence of sward characteristics on diet selection and herbage intake by the grazing animal. In

Nutritional Limits to Animal Production from Pastures (Ed. J. B. Hacker), pp. 153–166. Farnham Royal: Commonwealth Agricultural Bureaux.

HUMPHREYS, L. R. (1991). *Tropical Pasture Utilisation*. Cambridge: Cambridge University Press.

JAMIESON, W. S. & HODGSON, J. (1979). The effect of daily herbage allowance and sward characteristics upon the ingestive behaviour and herbage intake of calves under strip-grazing management. *Grass and Forage Science* **34**, 261–271.

JARRIGE, R. (1989). *Recommended Allowances and Feed Tables* (Ed. R. Jarrige). Paris: INRA.

JONES, R. J. (1990). Nitrogen rate and stocking rate effects on steer gains from grazed irrigated pangola grass in the Ord Valley, Western Australia. *Australian Journal of Experimental Agriculture* **30**, 599–605.

KENNEDY, P. M. (1995) Comparative adaptability of herbivores to tropical environments. In *Proceedings of the IVth Symposium on the Nutrition of Herbivores* (Eds M. Journet, E. Grenet, M.-H. Farce, M. Theriez & C. Demarquilly), pp. 309–328. Paris: INRA.

LACA, E. A., UNGAR, E. D., SELIGMAN, N. G. & DEMMENT, M. W. (1992). Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. *Grass and Forage Science* **47**, 91–102.

MAZZANTI, A., LEMAIRE, G. & GASTAL, F. (1994). The effect of nitrogen fertilization upon the herbage production of tall fescue swards continuously grazed with sheep. 1. Herbage growth dynamics. *Grass and Forage Science* **49**, 111–120.

MEARS, P. T. & HUMPHREYS, L. R. (1974). Nitrogen response and stocking rate of *Pennisetum clandestinum* pastures. 2. Cattle growth. *Journal of Agricultural Science, Cambridge* **83**, 469–478.

MICHELL, P. (1982). Value of rising-plate meter for estimating herbage mass of grazed perennial ryegrass-white clover swards. *Grass and Forage Science* **37**, 81–87.

MINSON, D. J. (1973). Effect of fertiliser nitrogen on digestibility and voluntary intake of *Chloris gayana digitaria decumbens* and *Pennisetum clandestinum*. *Australian Journal of Experimental Agriculture and Animal Husbandry* **13**, 153–157.

MINSON, D. J. (1990) In *Forage in Ruminant Nutrition* (Ed. D. J. Minson). San Diego: Academic Press.

MONSON, W. G. & BURTON, G. W. (1982). Harvest frequency and fertilizer effects on yield, quality, and persistence of eight Bermudagrasses. *Agronomy Journal* **74**, 371–374.

OVERMAN, A. R. & WILKINSON, S. R. (1989). Partitioning of dry matter between leaf and stem in Coastal Bermudagrass. *Agricultural Systems* **30**, 35–47.

PINTO, J. C., GOMIDE, J. A., MAESTRI, M. & LOPES, N. F. (1994). Crescimento de folhas de gramineas forrageiras tropicales, cultivadas en vasos, com duas doses de nitrogenio. *Revista da Sociedade Brasileire de Zooteccnia* **23**, 327–332.

SAS (1989) *SAS/STAT User's guide, Version 6, Fourth Edition, volume 2*. Cary, NC: SAS Institute Inc.

SCHEMOUL, E. (1988). Productivité primaire et morphogénèse d'un peuplement de Petit Foin (*Dichanthium* spp. Will) en Guadeloupe. Mémoire DAA, ENSA Montpellier.

STOBBS, T. H. (1973*a*). The effect of plant structure on the intake of tropical pastures. I. Variation in the bite size of grazing cattle. *Australian Journal of Agricultural Research* **24**, 809–819.

STOBBS, T. H. (1973*b*). The effect of plant structure on the intake of tropical pastures. II. Difference in sward structure, nutritive value, and bite size of animals grazing *Setaria anceps* and *Chloris gayana* at various stages of growth. *Australian Journal of Agricultural Research* **24**, 821–829.

STOBBS, T. H. (1975). The effect of plant structure on the intake of tropical pastures. 3. Influence of fertiliser nitrogen on the bite size harvested by Jersey cows grazing *Setaria anceps* CV. Kazungula swards. *Australian Journal of Agricultural Research* **26**, 997–1007.

STREETER, C. L. (1969). A review of techniques used to estimate *in vivo* digestibility of grazed forage. *Journal of Animal Science* **29**, 757–768.

TILLEY, J. M. A. & TERRY, R. A. (1963). A two stages technique for *in vitro* digestion of forage crops. *Journal of the British Grassland Society* **18**, 104–111.

VAN SOEST, P. J., ROBERTSON, J. B. & LEWIS, B. A. (1991). Methods for dietary fibre, neutral detergent fibre and non starch polysaccharides in relation to animal nutrition. *Journal of Dairy Science* **74**, 3583–3597.

VÉRITÉ, R., MICHALET-DOREAU, B., CHAPOUTOT, P., PEYRAUD, J. L. & PONCET, C. (1987). Révision du système des protéines digestibles dans l'intestin (P.D.I). *Bulletin Technique du C.R.Z.V. de Theix, I.N.R.A* **70**, 19–34.