Effect of sward attributes on legume selection by oesophageal-fistulated and non-fistulated steers grazing a tropical grass-legume pasture

H.D. HESS^{1,2}, M. KREUZER¹, J. NÖSBERGER³, C. WENK¹ AND C.E. LASCANO²

¹Institute of Animal Sciences, Swiss Federal Institute of Technology (ETH), Zurich, Switzerland

²*Centro Internacional de Agricultura Tropical* (*CIAT*), *Cali, Colombia*

³Institute of Plant Sciences, Swiss Federal Institute of Technology (ETH), Zurich, Switzerland

Abstract

A grazing trial was carried out in the Eastern Plains of Colombia to compare legume selection by transiently grazed oesophageal-fistulated steers and non-fistulated steers permanently grazing pastures. The 6 pasture types investigated were Arachis pintoi-Brachiaria humidicola mixtures which differed in legume and grass mass per hectare and grass:legume ratios. The sward attributes explaining the greatest variation in legume selection by fistulated and non-fistulated steers were legume percentage in the forage on offer $(r^2 = 0.67)$ and available legume mass $(r^2 = 0.56)$, respectively. Legume selection by both groups of steers was correlated with legume bulk density (kg DM/ha/cm). However, the relationship was linear ($r^2 = 0.53$) for fistulated steers with maximum dietary legume proportion reaching 92% and exponential ($r^2 = 0.52$) for nonfistulated steers with a plateau at 25% dietary legume with individual values never exceeding 35%. This study confirms that legume selection under grazing differs between oesophageal-fistulated steers transiently grazing the pastures and resident intact steers, and indicates that this difference is associated with their contrasting response to changes in sward attributes.

Introduction

Associating grasses with legumes offers an economically advantageous option for improving pasture quality and productivity and hence animal and whole system efficiency (Paladines and Leal 1979; Lascano et al. 1989). Among pasture legumes with forage potential in neotropical savannas, the perennial groundnut Arachis pintoi is very promising (Grof 1985). Grazing studies demonstrated up to 2-fold higher liveweight gains by animals grazing pastures of A. pintoi in association with different grasses, compared with pure grass pastures (Lascano 1994). Animal performance is a function of digestible nutrient intake, which is influenced by selectivity of the animals. In turn, a varying selection pattern greatly influences botanical composition (i.e., grass:legume ratio) of the respective pastures. The extent of selection by grazing animals is affected by canopy structure, which depends on grazing management (Hodgson 1982; Moore et al. 1985; Lascano 1987; Sollenberger et al. 1987; Nakanishi et al. 1993; Lascano 2000). Establishing the relationship between these 2 parameters aids in determining management recommendations. Most studies of diet selection have relied on animals fitted with oesophageal fistulae. This technique was used to show that A. pintoi in association with several grasses was selected in high proportions and contributed significantly to diet quality (Lascano and Thomas 1988; Hernandez et al. 1995). Nevertheless, other studies (Coates et al. 1987; Carulla et al. 1991; Jones and Lascano 1992) showed that extrusa samples collected from fistulated animals grazed for short periods of time may not reflect the selectivity exhibited by permanently grazed non-fistulated animals. Little information is available explaining the relationship between legume selection and sward attributes since, in previous studies, variations in sward composition within a given grass-legume association were small.

Correspondence: Dr H.D. Hess, Institute of Animal Sciences, Animal Nutrition, ETH Centre LFW, CH-8092 Zurich, Switzerland. E-mail: dieter.hess@inw.agrl.ethz.ch

Thus, the objectives of this study were: (i) to investigate the relationship between legume selection by growing steers and legume proportion, legume and grass mass as well as legume and grass bulk density of 6 different *Arachis pintoi-Brachiaria humidicola* swards; and (ii) to compare legume selection estimated by the oesophageal fistula technique with that estimated by the δ^{13} C technique using faecal samples of non-fistulated steers.

Materials and methods

Establishment and attributes of the experimental pasture types

The study was carried out at the Carimagua Research Station (4°30' N, 71°19' W; elevation 150 m) in the Eastern Plains of Colombia. Rainfall is distributed mainly from April through November with a mean annual figure (20 years) of 2348 mm. A very marked dry season occurs from mid-December to late March. Annual mean temperature is 26.6°C (24.5–28.2°C). Soils are classified as Oxisols (Haplustox Isohyperthermic) with pH 4.5 and low base status, and are deficient in almost all macro- and micro-nutrients. In addition, the cation exchange capacity of the soil is 86% aluminium-saturated (Grof 1985). Due to the high iron concentration, P-fixing capacity is also high (Spain and Ayarza 1992).

The experimental pasture was established by planting vegetatively the tropical legume Arachis pintoi cv. Amarillo (CIAT 17434¹) and the tropical grass Brachiaria humidicola (CIAT 679¹) 5 years before the experiment started. At that time, fertiliser was applied at 12 kg P, 18 kg K, 14 kg Mg, 22 kg S and 148 kg Ca/ha. Maintenance fertiliser was applied at half these rates every second year until the experiment started. The total area was divided into 6 paddocks of 1 ha each. Grazing started 6 months after establishment. Each paddock was subdivided into 2 plots of 0.5 ha which were rotationally grazed by growing steers throughout the year in a 28-day cycle (14 days grazing, 14 days rest) during the rainy season and a 14-day cycle (7 days grazing, 7 days rest) during the dry season. In order to achieve the intended

differences in sward canopy structure and botanical composition, pastures were grazed at 3 stocking rates. Stocking rates varied in the preexperimental period but were 2, 3 and 4 steers/ha immediately before and during the experimental period. Eventually, this management resulted in 6 different pasture types which differed in mass and proportion of *Arachis pintoi* and *Brachiaria humidicola*. The 6 pastures (2×0.5 ha plots) were (a) low legume/low grass (LL), (b) low legume/ medium grass (LM), (c) low legume/high grass (LH), (d) medium legume/high grass (MH), (e) high legume/low grass (HL) and (f) high legume/high grass (HH).

Experimental animals

Crossbred steers (*Bos indicus* × *Bos taurus*) either non-fistulated or equipped with oesophageal cannulae were used. The 18 non-fistulated steers grazing the pastures at the start of the experiment averaged 236 (±35) kg liveweight and were replaced after 3 months by a younger group of steers (171±16 kg). During the following year, the average liveweight of this group increased to 297 (±41) kg. Four crossbred steers weighing 180 kg grazed an *Arachis pintoi-B. humidicola* pasture for 2 months before surgery to insert oesophageal cannulae (McManus 1981) to ensure adaptation to the legume.

Experimental protocol

Starting in September, 7 samplings were undertaken (5 in the rainy and 2 in the dry season). During rainy and dry seasons, measurement periods consisted of 14 and 7 days, respectively, equivalent to the occupation periods of the 0.5 ha plots.

Before the steers entered experimental plots, samples of the standing sward were collected by hand-clipping the available forage at 2 cm above ground level from twenty 0.5 m² quadrats randomly distributed within each 0.5 ha plot. Before cutting, average legume and grass heights were measured in order to calculate sward bulk density. Sward samples were manually separated into grass and legume. Yield and botanical composition were calculated from quadrat data. Two subsamples of 200 g of grass and legume were dried at 60°C to constant mass. Additionally, to determine quality of herbage on offer in the 6 pasture

¹ Accession number used in the germplasm collection held at CIAT (Centro Internacional de Agricultura Tropical), Cali, Colombia.

types, separate hand-plucked samples of grass and legume, harvested to simulate forage selected by the grazing animal, were taken and dried at 60°C. Samplings were carried out on Days 1, 7 and 14 of grazing during the rainy season and on Days 1 and 7 during the dry season.

Four fistulated steers grazed each of the 6 pastures for approximately 20 min after an overnight fast. Extrusa samples were collected on Days 1, 7 and 14 of grazing during the rainy season and on Days 1 and 7 during the dry season. In the time between sampling days, the fistulated steers grazed a separate Arachis pintoi-Brachiaria humidicola pasture. From each steer, approximately 1 kg of extrusa per pasture type was collected. This added up to 456 (4 steers \times 6 pasture types \times 19 measurement days) individual extrusa samples. Legume proportion was analysed by stereoscope reading of 200 points per sample using the technique described by Heady and Torell (1959). For all other analyses, the 4 extrusa samples collected were bulked, subsampled and lyophilised.

The dietary legume proportion of resident intact steers was determined by the δ^{13} C-technique (Jones et al. 1979). Faecal samples from 2 steers per pasture type were collected rectally or from the ground immediately following defaecation on Days 1, 4, 7, 10 and 14 of each measurement period during the rainy season and on Days 1, 4 and 7 during the dry season. This yielded a total of 372 (2 steers \times 6 pasture types \times 31 sampling days) individual faecal samples. This frequency of faecal sampling was considered sufficient to get samples homogeneous enough to reflect the complete grazing periods since Coates et al. (1991) demonstrated that even a single faecal sample of free-grazing steers reliably reflected the diet consumed over a period of at least 3 days. Approximately 100 g of fresh faecal samples were placed into plastic bags and frozen. Later they were dried at 60°C and ground in a Wiley Mill fitted with a 1 mm screen. Subsequently, faeces [4 g dry matter (DM) per individual sample] were mixed to form composite samples across sampling days and only one composite sample per animal was finally analysed in each measurement period. This yielded a total of 84 (2 steers \times 6 pasture types \times 7 periods) composite faecal samples. To measure $\delta^{13}C$ levels in the forage on offer, subsamples of B. humidicola and A. pintoi (handplucked samples) were mixed across sampling days separately for the grass and the legume to

obtain representative composite samples. Dietary legume percentage of resident intact steers was calculated according to Jones *et al.* (1979) from the δ^{13} C data, considering differences in component digestibility:

% legume =
$$100 \frac{G_i(F_c - G_c)}{L_i(L_c - F_c) + G_i(F_c - G_c)}$$

where $G_i = 100 - in vitro$ DM digestibility of the grass; $L_i = 100 - in vitro$ DM digestibility of the legume; $F_c = \delta^{13}C$ faces; $G_c = (\delta^{13}C \text{ grass}) - 1$; $L_c = (\delta^{13}C \text{ legume}) - 1$.

Selectivity indices for *A. pintoi* were calculated by dividing dietary legume percentages by the legume proportion of the pasture sward. Indices exceeding 1 show preference for the legume and those below 1 indicate a selection against the legume.

Laboratory analyses

Dried samples of A. pintoi, B. humidicola and oesophageal extrusae were analysed for DM (105°C, 3 h) and crude protein (Micro-Kjeldahl technique; Chapman and Pratt 1961) as well as neutral and acid detergent fibre (van Soest 1963). Concentrations of hemicellulose were calculated as the difference between neutral and acid detergent fibre concentrations. Furthermore, the in vitro dry matter digestibility was determined by the Tilley and Terry (1963) method as modified by Moore and Mott (1974). Prior to analysis, dried grass, legume, extrusae and faecal samples were ground in a Wiley mill fitted with a 1 mm screen. For $\delta^{13}C$ analysis, sub-samples were ground in a self-constructed piston-action ball mill to a fine powder as described by Rondon and Thomas (1994). Analysis of δ^{13} C was performed using a continuous-flow isotope ratio mass spectrometer (Tracermass Stable Isotope Analyser, Europa Scientific Ltd, Crewe, UK). For that purpose, duplicate samples of 2-4 mg were sealed in tin capsules, dropped into a vertical combustion tube and flash combusted. In different traps, water and other contaminants were removed and the purified CO₂ was analysed for its ¹³C:¹²C ratio.

Statistical analysis

Means for each pasture type and measurement period were combined separately for rainy and

dry seasons from individual data on feed, extrusae and faeces. The tables give the means together with the standard deviations of the means. Regression analysis was performed to determine the degree of association between different pasture attributes and dietary legume proportion. Relationships were calculated using the respective procedures of SAS (1990).

Results

Characteristics of the different pasture types

The attributes of the standing herbage as measured in the 6 pasture types are given in Table 1. Depending on pasture type, the mean legume percentage of the total sward varied between 10 and 48% during the rainy season and between 4 and 29% during the dry season. Legume mass ranged from 188 to 882 kg/ha DM during the rainy season and from 62 to 643 kg/ha DM during the dry season. Mean legume mass across all pasture types showed the usual variation with season being higher in the rainy season (452 kg/ha DM) than in the dry season (263 kg/ha DM). Legume mass in herbage on offer was highest in the highlegume pasture types and lowest in the lowlegume pasture types. The highest grass availability was found in the high-grass pastures and the lowest in the low-grass pastures. The average legume bulk density for each pasture type was similar in the rainy and the dry seasons and ranged from 20 to 106 kg DM/ha/cm. Regardless of season, legume bulk density was highest in the pasture with high legume and low grass mass followed by the pasture with high legume and high grass mass. Differences in grass mass were less clearly reflected in bulk density and the values estimated were similar for all pasture types. Grass bulk density tended to be higher in the dry than in the rainy season.

Throughout the experiment, there were pronounced differences in nutrient composition and in vitro dry matter digestibility (IVDMD) between A. pintoi and B. humidicola (Table 2). The legume was higher in crude protein (more than twice the concentration in the grass) and IVDMD, and lower in fibre concentration, particularly hemicellulose (one-third of the value found in grass). Pasture type effects were small and were generally smaller than the differences between the legume and the grass. Furthermore, these variations could not be systematically attributed to the different levels of legume or grass mass. There were also seasonal differences with lower crude protein concentrations in forage during the dry season (120 vs 156 g/kg DM for A. pintoi; 37 vs 73 g/kg DM for B. humidicola) and slightly lower hemicellulose concentrations. The effect of season on IVDMD was much more pronounced in the grass than in the legume. While IVDMD was similar for B. humidicola and A. pintoi in the rainy season (60 and 63%, respectively), during the dry season B. humidicola had a considerably lower digestibility than A. pintoi (45 and 63%, respectively).

Pasture type Legume mass Grass mass	LL Low Low	LM Low Medium	LH Low High	MH Medium High	HL High Low	HH High High
Legume proportion (%)						
Rainy season	13±5	15±6	10 ± 2	10 ± 2	48±16	20±7
Dry season	7±0	4±2	4±1	4±1	29±1	15±0
Mass (kg/ha DM)						
Legume, rainy season	188±126	271±36	332±62	409±135	882±141	630±179
Legume, dry season	62±19	81±42	136±46	169±46	643±196	486±38
Grass, rainy season	1186±267	1745±711	3069±842	3799±1231	1112±585	2625±483
Grass, dry season	863±247	1796±187	3248±354	4255±111	1541±417	2754±260
Bulk density (kg DM/ha/cm hei	ght)					
Legume, rainy season	30±17	32±6	30±3	27±5	102±27	52±11
Legume, dry season	22±3	20±9	21±7	25±8	106±15	70±3
Grass, rainy season	108 ± 28	103±27	116±30	116±38	68±30	103±38
Grass, dry season	182±32	150±6	186±19	213±23	133±16	160±11

Table 1. Attributes of the standing herbage in rainy (n = 5) and dry seasons (n = 2) measured in the 6 *Brachiaria humidicola-Arachis pintoi* pasture types (means \pm S.D.).

Table 2. Feed quality of hand-plucked samples of *Arachis pintoi* and *Brachiaria humidicola* in 6 pasture types depending on season (means \pm S.D.).

Pasture type ¹	LL	LM	LH	MH	HL	НН
Crude protein (g/kg DM)						
Legume, rainy season	170±9	154±6	140±14	143±16	170±9	161±11
Legume, dry season	136±10	132±9	112±9	111±1	116±1	114±2
Grass, rainy season	77±14	77±13	63±14	62±13	91±7	70±11
Grass, dry season	44±4	35±3	29±1	33±1	40±1	41±2
Neutral detergent fibre (g/kg DM)						
Legume, rainy season	509±25	508±19	490±23	495±10	511±23	510±18
Legume, dry season	465±29	457±13	446±16	451±12	460±19	443±4
Grass, rainy season	826±10	830±23	819±15	821±29	834±26	820±22
Grass, dry season	770±11	784±9	798±13	786±8	792±5	781±12
Acid detergent fibre (g/kg DM)						
Legume, rainy season	335±12	352±16	343±17	347±17	338±24	348±19
Legume, dry season	319±10	335±7	321±4	331±7	324±6	315±1
Grass, rainy season	403±9	414±9	412±11	418±16	408±14	415±14
Grass, dry season	388±2	420±7	404±9	409±1	406±4	403±0
Hemicellulose (g/kg DM)						
Legume, rainy season	174±18	157±21	147±20	149±13	173±19	162±8
Legume, dry season	146±19	122±20	125±12	120±6	136±25	128±3
Grass, rainy season	422±9	416±15	408±12	403±22	426±14	405±12
Grass, dry season	382±9	364±16	394±4	377±7	386±9	378±12
In vitro dry matter digestibility (9	6)					
Legume, rainy season	64±1	64±1	63±1	63±1	63±1	63±1
Legume, dry season	64±2	62±1	64±1	63±2	62±3	64±1
Grass, rainy season	62±3	60±3	60±3	59±4	60±3	57±3
Grass, dry season	48±1	42±3	46±1	47±1	44±2	45±2

 1 LL = low legume, low grass; LM = low legume, medium grass; LH = low legume, high grass; MH = medium legume, high grass; HL = high legume, low grass; HH = high legume, high grass.

Botanical composition and quality of the diet selected

Legume percentage in the diet of fistulated steers ranged from 1 to 92% in the rainy season, and from 2 to 67% in the dry season (Figure 1). The highest legume proportion was selected in the pasture type which offered high legume and low grass mass (HL). With simultaneously high grass and legume mass (HH), the dietary legume percentage was intermediate. The lowest dietary legume percentages were measured in pastures which had low or medium legume mass. Legume percentage in the diet selected by the permanently grazed non-fistulated steers ranged from 2 to 32% in the rainy season, and from 0 to 38% in the dry season. In these steers, pasture type had less effect on legume selection than in the fistulated steers. In the rainy season, the non-fistulated steers followed the selection pattern of the fistulated steers, but at a considerably lower level of legume percentage selected. In the dry season, no clear effect of pasture type on legume selection could be observed in non-fistulated steers.

Higher levels of legume in the diet increased dietary crude protein in steers grazing the

different pasture types, particularly HL, regardless of season (Table 3). The crude protein concentration of the diet averaged across pasture types was higher during the rainy season (99 g/kg DM) than during the dry season (78 g/kg DM). Similarly, the NDF and hemicellulose concentrations in extrusa samples reflected the legume proportion of the diet, being lowest in the HL pasture type. The effect of pasture type on IVDMD of extrusa was inconsistent although there was a tendency for IVDMD to be higher in the pastures with high grass mass. However, IVDMD showed a clear seasonal variation, averaging 61% in the rainy season and 49% in the dry season.

Relationships between legume proportion in selected feed and sward attributes

Using data from all pasture types, regressions of legume proportion selected by fistulated and non-fistulated steers on various sward attributes were calculated separately for the rainy (n = 30) and dry (n = 12) seasons (Table 4).

Legume percentage of the standing sward. Dietary legume selected by oesophageal-fistulated



Figure 1. Legume proportion in the diet selected by (a) oesophageal-fistulated and (b) non-fistulated steers throughout the experiment (dots represent the mean values across all pasture types and bars represent the range observed).

Sward attributes and legume selection 233

and non-fistulated steers was linearly related to legume percentage in standing herbage during the rainy season (Figure 2). In this season, herbage legume accounted for 67% and 45% of the variation in dietary legume of fistulated and nonfistulated steers, respectively. For the fistulated steers, the slope of the regression (b = 1.31 ± 0.17) indicates that increases in legume proportion in the herbage on offer resulted in similar changes in dietary legume percentage over a wide range of legume proportions observed. In contrast, the slope of the regression calculated for the non-fistulated steers in the rainy season ($b = 0.32\pm0.07$) indicates that this group of steers selected against

Table 3. Legume proportion selected by oesophageal-fistulated and non-fistulated steers and feed quality selected by the fistulated steers grazing 6 *Brachiaria humidicola-Arachis pintoi* pastures in rainy and dry seasons (means \pm S.D.).

Pasture type ¹	LL	LM	LH	MH	HL	HH
Legume proportion selected (%)						
Fistulated, rainy season	17±9	28±13	22±12	7±3	70±22	28±19
Fistulated, dry season	8±5	18±10	21±7	26±19	51±17	46±17
Non-fistulated, rainy season	8±2	16±4	15±2	13±8	26±6	18±4
Non-fistulated, dry season	4±4	23±3	23±2	15±12	28±10	15±15
Legume selectivity index						
Fistulated, rainy season	1.3±0.5	1.8±0.4	2.1±0.9	0.8 ± 0.4	1.5±0.4	1.9±1.9
Fistulated, dry season	1.1±0.7	3.9±0.8	5.0±0.7	5.9±3.3	1.7±0.5	3.0±1.2
Non-fistulated, rainy season	0.7 ± 0.1	1.2±0.3	1.5±0.3	1.3±0.9	0.6±0.2	1.1±0.5
Non-fistulated, dry season	0.6 ± 0.6	6.4±1.9	6.4±1.9	5.1±4.7	1.0 ± 0.4	1.0 ± 1.0
Characteristics of feed selected by fis	stulated steers					
Crude protein (g/kg DM)						
Rainy season	88±9	104±19	84±18	73±9	148±24	97±12
Dry season	60±4	74±7	67±2	67±14	101±2	99±5
Neutral detergent fibre (g/kg DM)						
Rainy season	718±33	688±24	718±26	751±18	586±54	696±62
Dry season	747±22	713±27	729±41	698±63	627±42	625±37
Acid detergent fibre (g/kg DM)						
Rainy season	372±9	388±17	376±10	373±17	346±17	375±17
Dry season	394±5	403±12	400±8	383±8	387±2	377±13
Hemicellulose (g/kg DM)						
Rainy season	345±38	300±30	341±19	378±17	240±40	321±63
Dry season	353±17	310±39	329±33	315±55	240±4.1	248±25
In vitro dry matter digestibility (%)						
Rainy season	61±5	57±3	62±1	65±3	60±3	62±4
Dry season	43±4	48±3	49±2	52±2	48±4	52±3

¹ LL = low legume, low grass; LM = low legume, medium grass; LH = low legume, high grass; MH = medium legume, high grass; HL = high legume, low grass; HH = high legume, high grass.

Table 4. Regression equations between different sward attributes in *Brachiaria humidicola-Arachis pintoi* pastures (x) and legume proportion (%) selected by oesophageal-fistulated and non-fistulated steers (y), and between crude protein concentration of the grass (x) and legume selectivity index (y).

Sward attributes (x)	Steers	Season	Equation	r ²	Р	n
Legume proportion in standing herbage (%)	Fistulated Fistulated Non-fistulated Non-fistulated	Rainy Dry Rainy Dry	y = 3.5 + 1.31x y = 12.49 + 1.46x y = 10.0 + 0.32x y = 14.5 + 0.310x	0.67 0.44 0.45 0.06	<0.001 <0.05 <0.001 NS	30 12 30 12
Legume mass (kg/ha DM)	Fistulated Fistulated Non-fistulated Non-fistulated	Rainy Dry Rainy Dry	y = 4.3 + 0.054x y = 8.2 + 0.075x y = 6.9 + 0.020x y = 16.7 + 0.04x	0.35 0.75 0.56 0.02	<0.001 <0.001 <0.001 NS	30 12 30 12
Legume bulk density (kg DM/ha/cm height)	Fistulated Fistulated Non-fistulated Non-fistulated	Rainy Dry Rainy Dry	y = 1.9 + 0.59x y = 6.5 + 0.48x $y = 24.4 - 39.9 e^{-0.046x}$ y = 15.4 + 0.052x	0.53 0.66 0.52 0.02	<0.001 <0.001 <0.01 NS	30 12 30 12
CP concentration in the grass (g/kg DM)	Fistulated Non-fistulated	Total Total	$y = 1.5 + 147.5 e^{-0.12x}$ y = 0.85 + 133.1 e^{-0.11x}	0.40 0.45	<0.05 <0.05	42 42

the legume and for grass when legume percentage in the herbage on offer increased. In the dry season, the selection pattern of the fistulated steers was similar to that in the rainy season (b = 1.46 ± 0.52) but the legume selection of non-fistulated steers was not significantly related to the legume percentage of the herbage on offer (Table 4).

The legume selectivity indices calculated for the fistulated steers generally exceeded 1 throughout the experiment (1.7 on average) indicating a clear preference for the legume. The highest selectivity index was observed in the middle of the dry season (3.6), and the lowest at the end of the rainy season (1.1). In the nonfistulated steers, selectivity indices averaged at 1.0 suggesting that the mean dietary legume percentage coincided with the legume proportion in the herbage on offer. However, selectivity indices varied widely between pasture types and with season (Table 3). In general, non-fistulated steers tended to select for the legume (index>1) in pasture types with low or medium legume mass, but showed no preference or selected against the legume (index≤1) in pasture types with high legume mass. Overall selectivity index was highest at the end of the dry season (2.5) when the quality of the grass (i.e. CP concentration) was lowest, and lowest in the middle of the rainy season (0.5) when grass quality was highest. To analyse the relationship between selectivity index and crude protein concentration of the grass on

offer, data (n = 42) were fitted to the exponential regression model: $y = a + be^{-kx}$, where 'y' is the legume selectivity index and 'x' the crude protein concentration of the grass (Table 4). Selectivity indices for fistulated and non-fistulated steers were significantly related to the crude protein concentration of the grass (P < 0.05) and the degree of association was similar for both groups of steers $(r^2 = 0.40 \text{ and } 0.45 \text{ for fistulated and})$ non-fistulated steers, respectively). However, a large difference was found in the values for the asymptotes of the 2 regression lines, which were 1.5 for fistulated steers and 0.85 for nonfistulated steers. Accordingly, both groups of steers selected for the legume, when crude protein concentration of the grass was low, but showed a different selection behaviour at higher crude protein concentration. While the fistulated steers constantly selected for the legume, nonfistulated steers selected against the legume when the crude protein level exceeded 70 g/kg DM.

Legume mass in the pasture. In the rainy season, the legume proportion in the diet selected by both groups of steers was linearly related to the legume mass on offer in the pasture (Table 4). However, the degree of association was different for fistulated and non-fistulated steers. This sward attribute explained 56% of the variation in legume proportion selected by non-fistulated steers, but only 35% in the fistulated steers. The legume percentage selected by fistulated steers increased



Figure 2. Relationship between legume proportion in the diet (y) selected by fistulated (\square) and non-fistulated (\blacktriangle) steers and legume proportion in herbage on offer (x) of *Brachiaria humidicola-Arachis pintoi* pastures during rainy and dry seasons. Dashed and solid lines represent lines of best fit for fistulated and non-fistulated steer data, respectively.

about twice as fast per unit of additional legume mass provided by the pasture (b = 0.054 ± 0.014) as did legume percentage selected by nonfistulated steers (b = 0.020 ± 0.003). During the dry season, the relationship between legume selected by fistulated steers and legume mass in the standing herbage was similar to that in the rainy season (b = 0.075 ± 0.014) whereas in the non-fistulated steers no significant relationship was found.

Legume bulk density. During the rainy season, legume percentage in the diet selected by fistulated and non-fistulated steers was related to legume bulk density in the standing herbage. This sward attribute explained around 50% of the variation in legume percentage in the diet selected by both groups of steers (Table 4). However, a linear relationship was found for the fistulated steers $(b = 0.59 \pm 0.10)$, whereas an exponential relationship was observed for the non-fistulated steers with a plateau reached at around 25% dietary legume with individual values never exceeding 35% (Figure 3). In general, as legume bulk density increased from 10 to about 60 kg DM/ha/cm, legume proportion in the diet selected by the nonfistulated steers increased from 2 to 24%, but remained unaffected by any further increase in legume bulk density (finally 130 kg DM/ha/cm). In contrast, legume proportion of the diet selected by fistulated steers increased with legume bulk density throughout the whole range observed. In the dry season, the relationship between legume selected by fistulated steers and legume bulk density was similar to that in the rainy season (b = 0.48 ± 0.11 , r² = 0.66), whereas there was no clear relationship in non-fistulated steers.

Discussion

Characteristics of the experimental pastures

While differences in legume and grass mass were achieved in the 6 pasture types which allowed the examination of a range of sward grass:legume combinations, it is acknowledged that the effects of the different sward attributes on legume selection were confounded. Percentage, mass and bulk density of the legume did not change independently of each other. Therefore, it was not possible to partition the effects of these sward attributes on legume selection. Despite the high dry matter yields, especially in the high-grass pastures, swards were relatively loosely packed compared with temperate pasture swards, and sward bulk densities were low but within the range reported for other tropical pastures (Stobbs 1973a; 1973b). The range of legume proportions measured in the present study covered the range most likely to be encountered in improved legume-based tropical pastures and variation in the different sward attributes was high enough to cause significant variation in dietary legume percentage.



Figure 3. Relationship between legume proportion in the diet (y) selected by fistulated (\square) and non-fistulated (\blacktriangle) steers and legume bulk density in herbage on offer (x) of *Brachiaria humidicola-Arachis pintoi* pastures during rainy and dry seasons. Dashed and solid lines represent lines of best fit for fistulated and non-fistulated steer data, respectively.

Legume selection pattern of grazing steers

Legume selection varied widely between oesophageal-fistulated and resident non-fistulated steers which supports the findings of Coates et al. (1987) and Jones and Lascano (1992). In our study, we used sward structural characteristics in an attempt to explain these differences and found a contrasting response by the 2 types of test steers to changes in sward attributes. Although dietary legume percentage of fistulated and resident non-fistulated steers was influenced by the legume-related attributes in the sward, the importance of individual sward attributes and relationships between legume selection and these attributes varied with type of steers. The sward attribute most related to legume percentage in the diet of the fistulated steers was legume percentage in the herbage on offer. In contrast, legume selected by non-fistulated steers was more related to legume mass. Legume selection by both groups of steers was related to legume bulk density but was different for fistulated and non-fistulated steers. The relationship was linear for fistulated steers, but was exponential with an asymptote for non-fistulated steers. Additionally, changes in sward canopy composition resulted in considerably smaller changes in legume selected by intact steers than in fistulated steers and variation in dietary legume of intact steers was lower.

Several reasons may be responsible for this phenomenon. First of all, selection by the fistulated steers could have been affected by fasting (Newman et al. 1994). Rate of intake of forage is enhanced by lengthening the fasting period (Moseley and Manendez 1989). On the other hand, it is generally accepted that the potential rate of intake of legumes such as white clover and subterranean clover is higher than the intake rate of grasses (Hodgson et al. 1994; Rutter et al. 2000). Therefore, it can be assumed that overnight fasting, as practised in this study with the fistulated steers, assisted their inclination for a high intake rate and therefore may have modified their selection behaviour towards relatively higher intake of the legume. Additionally, during the time between sampling days, fistulated steers grazed a separate Arachis pintoi-Brachiaria humidicola pasture and were not accustomed to the sward structures of the individual experimental plots. It is acknowledged that comparison between the 2 types of animals would have been improved when fistulated steers would have been part of the resident group grazing each pasture. However, the procedure as applied is still very common in grazing studies because it allows the investigation of many experimental pastures with few fistulated animals.

The legume proportion selected by nonfistulated steers in the rainy season was very similar (15-18%) in contrasting pasture types which offered a legume mass from 271 to 630 kg/ha DM and a legume percentage from 10 to 20% (LM, LH, HH). This suggests that, when grass is not limiting during the rainy season, nonfistulated steers grazing A. pintoi-B. humidicola pastures set an upper limit to the proportion of legume they select, and this limit seems to be relatively independent of the legume percentage of the sward. This is supported by the fact that non-fistulated steers showed no clear preference or aversion for the legume when the legume proportion in herbage on offer ranged from 7 to 30%, but they selected clearly against the legume when the proportion was higher. In the dry season, effects of pasture type on legume selection of non-fistulated steers were minor, and the plateau observed in the rainy season for the selection of A. pintoi was not evident. Under water stress conditions, and when the quality of the grass declined, legume selection by non-fistulated steers was high in most pasture types, regardless of legume availability. Seasonal variability of selection patterns has been also reported from other studies (Böhnert et al. 1985; Lascano et al. 1989; Gardener and Ash 1994; Bennett et al. 1999; Michiels et al. 2000). It is interesting that, in the present study, independent of pasture type, selectivity index of the legume was highest towards the end of the dry season when crude protein concentration in the grass was particularly low, probably as a compensatory effect (Stobbs 1977; Maeno 1985). In contrast, legume selectivity indices were low in the middle of the rainy season when grass had a high crude protein concentration. At this time, selection against legumes was particularly pronounced at very high legume percentages in the sward, possibly due to palatability reasons but also possibly to avoid a metabolic excess of protein.

The differences in ingestive behaviour observed in our work agree with those reported by Baumont *et al.* (2000) and suggest that, in simple experimental situations (very short-term, as was the case for transiently grazed fistulated steers), animals tend to maximise their rate of

feed intake. Long-term diet composition, as measured with permanently grazed non-fistulated steers, however, is more likely to be controlled by post-ingestive effects to avoid nutritional excesses or deficiencies.

Conclusions

This study indicated that selection of A. pintoi from an A. pintoi-B. humidicola pasture by fistulated and intact steers differed and that this difference resulted to some extent from a contrasting response of the 2 types of test animals to changes in sward attributes. Independent of the legume-related attributes and the nutritional quality of the herbage, fistulated steers selected higher legume proportions than those found in the sward. In contrast, resident non-fistulated steers selected for the legume only when the diet was too low in crude protein and/or digestibility. This may be the greatest advantage of associated pastures, and even a moderate legume proportion in the herbage on offer seemed sufficient to allow this type of choice feeding. Further studies in a range of environments are needed to assess how widely these findings can be extrapolated.

Acknowledgements

We are grateful to the Swiss Agency for Development Cooperation (SDC) for the fellowship provided to the first author. We express our thanks to Santos Pérez Farfán for assistance at the research site, to Marco Rondón in the laboratory and to Gerardo Ramírez for help with statistical analysis.

References

- BAUMONT, R., PRACHE, S., MEURET, M. and MORAND-FEHR, P. (2000) How forage characteristics influence behaviour and intake in small ruminants: a review. *Livestock Production Science*, 64, 15–28.
- BENNETT, L.L., HAMMOND, A.C., WILLIAMS, M.J., CHASE, C.C. and KUNKLE, W.E. (1999) Diet selection by steers using microhistological and stable carbon isotope ratio analyses. *Journal of Animal Science*, **77**, 2252–2258.
- BÖHNERT, E., LASCANO, C. and WENIGER, J.H. (1985) Botanical and chemical composition of the diet selected by fistulated steers under grazing on improved grass-legume pastures in the tropical savannas of Colombia. I. Botanical composition of forage available and selected. *Zeitschrift für Tierzüchtung und Züchtungsbiologie*, **102**, 385–394.
- CARULLA, J.E., LASCANO, C.E. and WARD, J.K. (1991) Selectivity of resident and oesophageal fistulated steers grazing *Arachis pintoi* and *Brachiaria dictyoneura* in the Llanos of Colombia. *Tropical Grasslands*, 25, 317–324.

- CHAPMAN, H.D. and PRATT, P.F. (1961) Methods of Analysis for Soils, Plants and Water. (University of California, Division of Agricultural Sciences: Davis, California, USA).
- COATES, D.B., SCHACHENMANN, P. and JONES, R.J. (1987) Reliability of extrusa samples collected from steers fistulated at the oesophagus to estimate the diet of resident animals in grazing experiments. Australian Journal of Experimental Agriculture, 27, 739–745.
- COATES, D.B., VAN DER WEIDE, A.P.A. and KERR, J.D. (1991) Change in faecal δ^{13} C in response to changing proportions of legume (C₃) and grass (C₄) in the diet of sheep and cattle. *Journal of Agricultural Science (Cambridge)*, **116**, 287–295.
- GARDENER, C.J. and ASH, A.J. (1994) Diet selection in six Stylosanthes-grass pastures and its implications for pasture stability. *Tropical Grasslands*, **28**, 109–119.
- GROF, B. (1985) Forage attributes of the perennial groundnut Arachis pintoi in a tropical savanna environment in Colombia. Proceedings of the XV International Grassland Congress, Kyoto, Japan, 1985. pp. 168–170.
- HEADY, H.F. and TORELL, D.T. (1959) Forage preferences exhibited by sheep with esophageal fistulas. *Journal of Range Management*, 12, 28–34.
- HERNANDEZ, M., ARGEL, P.J., IBRAHIM, M.A. and T'MAN-NETJE, L. (1995) Pasture production, diet selection and liveweight gains of cattle grazing *Brachiaria brizantha* with or without *Arachis pintoi* at two stocking rates in the Atlantic Zone of Costa Rica. *Tropical Grasslands*, 29, 134–141.
- HODGSON, J. (1982) Influence of sward characteristics on diet selection and herbage intake by the grazing animal. In: HACKER, J.B. (ed.) Nutritional Limits to Animal Production from Pastures. Proceedings of an International Symposium, St Lucia, Queensland, Australia, 1981. pp. 153–166.
- HODGSON, J., CLARK, D.A. and MITCHELL, R.J. (1994) Foraging behaviour in grazing animals and its impact on plant communities. In: Fahey, G.C. (ed.) *Forage Quality, Evaluation, and Utilization.* pp. 796–827. (American Society of Agronomy, Inc.; Crop Science Society of America, Inc.; Soil Science Society of America, Inc.: Madison, Wisconsin, USA).
- JONES, R.J., LUDLOW, M.M., TROUGHTON, J.H. and BLUNT, C.B. (1979) Estimation of the proportion of C₃ and C₄ plant species in the diet of animals from the ratio of natural ¹²C and ¹³C isotopes in the faeces. *Journal of Agricultural Science (Cambridge)*, **92**, 91–100.
- JONES, R.J. and LASCANO, C.E. (1992) Oesophageal fistulated cattle can give unreliable estimates of the proportion of legume in the diets of resident animals grazing tropical pastures. *Grass and Forage Science*, **47**, 128–132.
- LASCANO, C.E. (1987) Canopy structure and composition in legume selectivity. In: Moore, J.E., Quensenberry, K.H. and Michaud, M.W. (eds) Forage-Livestock Research Needs for the Caribbean Basin. Caribbean Basin Advisory Group and Institute of Food and Agricultural Sciences. pp. 81–87. (University of Florida: Gainsville, USA).
- LASCANO, C.E. (1994) Nutritive value and animal production of forage Arachis. In: Kerridge, P.C. and Hardy, B. (eds) Biology and Agronomy of Forage Arachis. pp. 109–121. (Centro Internacional de Agricultura Tropical: Cali, Colombia).
- LASCANO, C.E. (2000) Selective grazing on grass-legume mixtures in tropical pastures. In: Lemaire, G., Hodgson, J., de Moraes, A., de F. Carvalho, P.C. and Nabiger, C. (eds) Grassland Ecophysiology and Grazing Ecology. pp. 249–263. (CAB International: Oxon, UK).
- LASCANO, C.E. and THOMAS, D. (1988) Forage quality and animal selection of *Arachis pintoi* in association with tropical grasses in the Eastern plains of Colombia. *Grass* and Forage Science, 43, 433–439.
- LASCANO, C., ESTRADA, J. and AVILA, P. (1989) Animal production of pastures based on *Centrosema* spp. in the Eastern plains of Colombia. *Proceedings of the XVI International Grassland Congress, Nice, France, 1989.* pp. 1177–1178.

- MAENO, N. (1985) Productivity of grass-legume pastures and its contribution to animal production in the tropics. *Tropical Agriculture and Research Series*, 18, 159–172.
- MCMANUS, W.R. (1981) Oesophageal fistulation technique as an aid to diet evaluation of the grazing ruminant. In: Wheeler, J.L. and Mochrie, R.D. (eds) Forage Evaluation: Concepts and Techniques. pp. 249–260. (American Forage and Grassland Council; CSIRO).
- MICHIELS, B., BABATOUNDE, S., DAHOUDA, M., CHABI, S.L.W. and BULDGEN, A. (2000) Botanical composition and nutritive value of forage consumed by sheep during the rainy season in a Sudano-guinean savanna (central Benin). *Tropical Grasslands*, 34, 43–47.
- MOORE, J.E. and MOTT, G.O. (1974) Recovery of residual organic matter from *in vitro* digestion of forages. *Journal of Dairy Science*, 57, 1258–1259.
- MOORE, J.E., SOLLENBERGER, L.E., MORANTES, G.A. and BEEDE, P.T. (1985) Canopy structure of Aeschynomene americana-Hemarthria altissima pastures and ingestive behaviour of cattle. Proceedings of the XV International Grassland Congress, Kyoto, Japan, 1985. pp. 1126–1128.
- MOSELEY, G. and MANENDEZ, A.A. (1989) Factors affecting the eating rate of forage feeds. *Proceedings of the XVI International Grassland Congress, Nice, France.* pp. 789–790.
- NAKANISHI, Y., TSURU, K., BUNGO, T., SHIMOJO, M., MASUDA, Y. and GOTO, I. (1993) Effect of growth stage and sward structure of *Macroptilium lathyroides* and *M. atropurpureum* on selective grazing and bite size in goats. *Tropical Grasslands*, 27, 108–113.
- NEWMAN, J.A., PENNING, P.D., PARSON, A.J., HARVEY, A. and ORR, R.J. (1994) Fasting affects intake behaviour and diet preference of grazing sheep. *Animal Behaviour*, 47, 185–193.
- PALADINES, O. and LEAL, J.A. (1979) Pasture management and productivity in the Llanos Orientales of Colombia. In: Sanchez, P.A. and Tergas, L.E. (eds) Pasture Production in Acid Soils of the Tropics. Proceedings of a Seminar held at CIAT. pp. 311–325. (Centro Internacional de Agricultura Tropical: Cali, Colombia).
- RONDON, M.A. and THOMAS, R.J. (1994) A piston-action ball mill for the rapid preparation of plant and soil samples for

the automated analysis of nitrogen (¹⁵N) and carbon (¹³C). Communication in Soil Science and Plant Analysis, **25**, 435–445.

- RUTTER, S.M., ORR, R.J. and ROOK, A.J. (2000) Dietary preferences for grass and white clover in sheep and cattle: an overview. In: Rook, A.J. and Penning, P.D. (eds) *Grazing Management. Occasional Symposium No.* 34. pp. 73–78. (British Grassland Society: UK).
- SAS (1990) SAS/STAT User's Guide. Version 6, 4th Edn. (SAS Institute Inc.: Cary, North Carolina, USA).
- SOLLENBERGER, L.E., MOORE, J.E., QUESENBERRY, K.H. and BEEDE, P.T. (1987) Relationships between canopy botanical composition and diet selection in *Aeschynomene*-Limpograss pastures. *Agronomy Journal*, **79**, 1049–1054.
- SPAIN, J.M. and AYARZA, M.A. (1992) Tropical pastures target environments. In: Centro Internacional de Agricultura Tropical (ed.) *Pastures for the Tropical Lowlands, CIAT's contribution.* pp. 1–8. (Centro Internacional de Agricultura Tropical: Cali, Colombia).
- STOBBS, T.H. (1973a) 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. (1973b) The effect of plant structure on the intake of tropical pastures. II. Differences 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. (1977) Seasonal changes in the preference by cattle for *Macroptilium atropurpureum* cv. Siratro. *Tropical Grasslands*, **11**, 87–91.
- TILLEY, J.M.A. and TERRY, R.A. (1963) A two-stage technique for the *in vitro* digestion of forage crops. *Journal of the British Grassland Society*, **18**, 104–111.
- VAN SOEST, P.J. (1963) Use of detergent analysis of fibrous feeds. II. A rapid method for determination of fiber and lignin. Journal of the Association of Official Analytical Chemists, 46, 829–835.

(Received for publication November 21, 2001; accepted August 30, 2002)