Grazing Behavior of Ruminants and Daily Performance from Warm-Season Grasses

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ABSTRACT

An estimate of the animal-production potential of pastures can be assessed by knowing the daily dry matter (DM) intake of the grazing animal and the digestibility of the DM consumed. The objective of this paper is to examine the relationships between pasture canopy characteristics, ingestive behavior, and daily animal response from warm-season pastures. Of daily DM intake and digestibility of the DM consumed, the former is the most variable and the most difficult to determine. One approach to estimating daily DM intake has been to use the components of ingestive behavior to determine a short-term intake rate (g min^{-1}), which can be scaled using grazing time (min d^{-1}) to give a 24-h DM intake (kg d^{-1}). This approach has been used experimentally with some success, but has not found application in production settings. While aspects of ingestive behavior, including ingestive mastication, are common to all grazing ruminants, literature indicates that differences occur among ruminant species and that animals ingest different pasture species differently. This results in plant-animal interactions. Frequently these dynamics are not clearly addressed for cool-season and warm-season pastures in literature reviews, which adds undue confusion to the general area. Ingestive behavior is discussed relative to animal- and pasture-generated bounds which operate within paddocks and can greatly alter ingestive behavior estimates. Also presented are relationships between diet particle size, associated with ingestive mastication, and steer daily gains.

The utilization of pastures by the grazing animal remains a complex biological process that is not well understood. This general state exists in spite of ongoing grazing behavioral research since the initial studies on tropical grasses in the early 1970s (Allden and Whittaker, 1970; Stobbs, 1973a,b). Since this early work, much of the continuing research on grazing behavior has shifted to the utilization of temperate pastures (Hodgson, 1982b; Hodgson et al., 1994). In the development of grazing behavior research, the reductionist approach has emerged in which small segments of the soil–plant–animal complex (namely, the plant–animal interface) have been examined in intensive, short-term experiments (Cosgrove, 1997; Ungar, 1998).

These short-term studies have identified the important ingestive behavioral components of animal intake and the influential interacting components of the pasture canopy. This has led to considerable knowledge and understanding about how animals graze. Recent comprehensive reviews addressing animal grazing behavior are available and will be left to the reader (Coleman et al., 1989; Gordon and Lascano, 1993; Hodgson et al., 1994; Cosgrove, 1997; Ungar, 1998; Sollenberger and Burns, 2001).

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The various ingestive behavioral measurements have seldom been used to estimate long-term DM intake or to explain differences in intake on daily animal responses among grazing management strategies in a production setting. This is also true relative to predicting daily animal response. This need has been previously noted (Hodgson, 1982a; Hodgson et al., 1994) and attributed, in part, to a failure to see the role of ingestive behavior measurements in production systems (Cosgrove, 1997). Several examples of the usefulness of grazing behavioral data were provided by Cosgrove (1997). One is the importance of canopy height of ryegrass-based (*Lolium perenne* L.) pastures in maximizing daily forage intake of the grazing animal and an understanding of why it is important. Another is the importance of leaf area index, green leaf mass, and associated stem height of the canopy in understanding daily forage intake among grazing systems.

The general lack of application of grazing behavior measurements to production systems is neither a criticism of previous research nor of this general area of research. It does beg, however, for the incorporation of ingestive behavior measurements into long-term animal response studies to assess which of the numerous measurements have utility in aiding the producer in achieving greater efficiency in the animal enterprise. The focus of this study is to delineate important components of grazing behavior already identified for warm-season perennial grass pastures, to examine linkage between ingestive mastication and animal performance, and to discuss important boundaries that alter the grazing environment.

Complications

Grazing behavior research on both tropical and temperate pastures has resulted in valuable data, unique to a specific plant species-animal type within each experiment. Generally, each experiment is conducted to test a specific hypothesis. In the literature, however, ingestive behavior data from different experiments are frequently intermingled without regard for plant type (tropical or temperate) or animal type [cattle (*Bos* spp.), sheep (*Ovis* spp.), or goats (*Capra* spp.)] and occasionally the specific identity of the data are lost. This has probably resulted from the perceived need to explain relationships and has been accomplished by inserting related, but not necessarily the best, data to possibly fill a void in the understanding of the process and has thus complicated interpretation.

Clearly, while the elements of grazing behavior and

Abbreviations: ADG, average daily gain; BR, bite rate; BV, bite volume; DM, dry matter; HD, herbage bulk density; IB, intake bite; IR, intake rate; IVDMD, in vitro dry matter disappearance; NDF, neutral detergent fiber.

ingestive mastication operate in all grazing environments, the pasture canopy-animal dynamic will differ between temperate and tropical pastures and among animal species (Hodgson et al., 1994; Cosgrove, 1997; Ungar, 1998). Furthermore, pasture species and animal species interact. Therefore, this same concern is warranted, although to a lesser degree, among widely different experiments within the same pasture-animal types. Consequently, judicious application of grazing behavior literature should be practiced. For example, research on ingestive behavior is presently at a state that warrants a summary that delineates (i) animal ingestive behavior (including ingestive mastication) common to all grazing ruminants; (ii) ingestive behavior responses that are unique to each animal species; (iii) the relationship between ingestive behavior components and canopy characteristics separately by forage type (tropical vs. temperate) and morphologies within forage type (erect vs. more decumbent); and (iv) the interactions that are known. Although deficiencies will occur in quantitative data to estimate short-term intake rate for some situations, proper summarization and application of the data may simplify and clarify associated plant-animal relationships and will direct attention to areas of critical need. The recent review by Sollenberger and Burns (2001) begins to address this need as grazing behavior responses are focused mainly on perennial and annual warm-season grasses.

The Relationships

The relationship between DM intake and digestibility of forage for animal productive response is represented by the general expression:

$$\text{Animal response, kg d}^{-1}\ f\ \text{DM intake, kg d}^{-1} \times \text{Digestibility, \%.}$$

Daily Dry Matter Intake

The importance of knowing the nutritive value and quantity of forage DM consumed each day when feeding efficiency is of concern is well demonstrated by confined feeding systems where a total mixed ration is the norm. Because there is a limit to the quantity of DM animals can consume each day (Demment and Van Soest, 1985), feed efficiency is favored if each mouth full of feed consumed has the proper balance of nutrients. The ability to measure or predict daily DM intake and the nutritive value of the consumed forage is also important when animals graze, and has been the impetus for studies on the pasture–animal interface. Animals on pasture also seek to ingest a balanced diet through grazing behavior (selective grazing) and repeated bouts of grazing, but are ultimately constrained by either or both perimeter bounds and bounds that operate within the pasture setting. This general area also has important implications in an ecological setting, especially on managing wild herbivores for maintenance or production (Laca and Demment, 1998).

In grazing systems, DM intake (above expression) is generally the limiting factor for sustained high daily animal response (Hodgson, 1982a). Changes in daily animal response are frequently influenced far more by changes in daily DM intake than changes in forage digestibility (Noller, 1997), hence the interest in daily intake. Furthermore, under ad libitum grazing, the animal can exercise its full range of grazing behavior—including walking, ruminating, resting, and socializing—which can alter grazing time and subsequently daily DM intake.

Unfortunately, methodology to directly measure DM intake of the grazing animal does not exist as it does in confinement, but requires the use of some indirect form of measurement (Moore and Sollenberger, 1997). To this point, inert marker methods have been developed (Uden et al., 1980; Dove and Mayes, 1991; Ellis et al., 1994) and used in experimentation to estimate the individual intake of grazing animals (Burns et al., 1991). This can also be achieved through ingestive behavioral measurements by determining the short-term intake rate according to the following expression summarized by Hodgson (1982b) and recently reviewed by Moore and Sollenberger (1997):

$$\text{DM intake, kg d}^{-1} = (\text{BR min}^{-1} \times \text{BW, g} \times \text{Grazing time, min d}^{-1})/1000,$$

or

$$\text{DM intake, kg d}^{-1} = \text{IR, g min}^{-1} \times \text{Grazing time, min d}^{-1}/1000,$$

with BR = bite rate, BW = bite weight, and IR = intake rate.

Intake Rate

Intake rate is determined from the integration of a number of ingestive behavior components, as noted below along with their mathematical relationships (Cosgrove, 1997).

$$\text{IR} = \text{Intake bite}^{-1}\ (\text{IB}) \text{ or BW} \times \text{BR}$$

$$\text{IB} = \text{Bite volume (BV)} \times \text{herbage bulk density (HD)}$$

$$\text{BV} = \text{Bite area} \times \text{bite depth}$$

Additional detail incorporating aspects of jaw movements related to ingestive manipulation and mastication has been discussed by Ungar (1998) and integrated as noted in Fig. 1. The association between the above ingestive behavior components, plus several added from the literature, with canopy characteristics of warm-season forages can be summarized (Table 1). In general, canopy height, HD, and green tissue (leaf and herbage mass) have strong relationships with the various animal measurements. Whereas, only BW showed strong relationships among the animal measurements. Further, grass-canopy height was positively associated with amplitude of tongue sweep and BV but negatively associated with BR (Table 1). Herbage mass was negatively

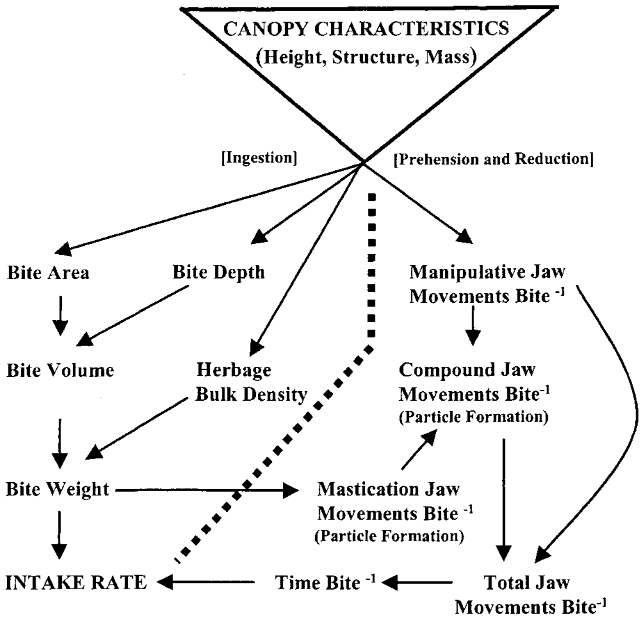

Fig. 1. Components of ingestive behavior, including prehension and mastication, that mediate canopy characteristics and short-term intake rate (after Ungar, 1998).

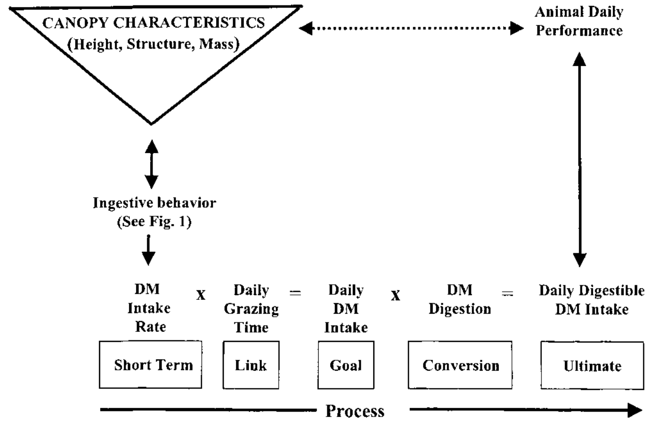

Fig. 2. The process to achieve the goal of estimating daily dry matter (DM) intake from short-term intake rate and ultimately animal daily performance.

associated with BW, BR, and intake rate. An exception is the positive association between herbage mass and BW when stocking rate was a variable (Table 1). In this case, high stocking rate would be associated with less herbage mass and smaller BW and, as stocking rate is reduced, herbage mass would greatly increase as would BW. This resulted in a positive association between BW and herbage mass. Proportion of green leaf or green leaf mass was positively associated with BW and the diet that was selected by the animal, while the proportion of dead leaf was negatively associated with the diet selected and the proportion of stem negatively associated with BV. Canopy bulk density was negatively associated with number of tongue sweeps, BV, and BW. Nutritive value of the pasture canopy and diet selected was positively associated.

In the case of legumes, canopy height, green leaf, leaf mass, and leaf:stem ratio were positively related with BW while legume percentage was negatively related with BR (Table 1). As noted for grass, nutritive value was positively associated with diet selection. The relationship among ingestive behavioral measurements showed BW to be of major importance, being negatively associated with BR for both grasses and legumes (Table 1). In the case of grasses, BW was also negatively associated with diet selection. These data indicated that BW tends to function as the mediator between canopy characteristics and short-term intake rate, which is consistent with the results of Brancio et al. (2000a). Grazing time, the link between short-term intake rate and daily DM intake (Fig. 2), was negatively related with green leaf, except in stocking rate studies and BW of warm-season grasses (Table 1), but positively associated with DM intake. In the case of legumes, grazing time and BR were negatively related (Table 1).

Table 1. General relationship between ingestive behavior measurements and pasture canopy characteristics.†

Animal measurements	Animal aspect‡					Canopy aspect§									
	BW	BR	GT	DS	SR	Ht	HM	GL	LM	DL	St	L:S	BD	NV	Le
Warm-season grasses:															
Tongue sweep:															
Amplitude						+			–						
Number													–		
Bite volume						+					–		–		
Bite weight							– (+SR)¶	+	+				–		
Bite rate	–					–	–						–		
Diet selection	–							+		–				+	
Intake rate	+						–								
Grazing time	–				+			– (+SR)	–						
Intake			+	–											
Legumes:															
Bite weight						+		+	+			+			
Bite rate	–														–
Diet selection														+	
Grazing time		–													

† Taken from Coleman et al. (1989), Cosgrove (1997), Ungar (1998), and Sollenberger and Burns (2001).
‡ BW = bite weight, BR = bite rate, GT = grazing time, DS = diet selection (species and plant part), and SR = stocking rate.
§ Ht = height, HM = herbage mass, GL = green leaf (%), LM = leaf mass, DL = dead leaf (%), St = stem (%), L:S = leaf to stem ratio, BD = bulk density, NV = nutritive value, and Le = legume (%).
¶ (+SR) = positive where stocking rate is a variable.

Ingestive Behavior and Animal Performance

The degree to which components of ingestive behavior relate to animal daily performance from warm-season grasses has not been well documented. While the principles of using ingestive behavior measurements to estimate daily DM intake are valid, the scale-up from a short-term intake rate to daily intake through daily grazing time may not give rational estimates (Moore and Sollenberger, 1997). A study by Brancio et al. (2000b) compared a marker method (Cr_2O_3) and ingestive behavior measurements for estimating intake of steers grazing guineagrass (*Panicum maximum* Jacq.) pastures. The two methods were positively correlated (r = 0.73) but mean daily DM intake estimates across 3 mo (September, November, and March), which represent different seasons, were 2.80 vs. 6.31 kg 100^{-1} kg body weight for the marker method and ingestive behavior method, respectively. Although there is no way to obtain a direct intake measurement of the grazing animal, the intake estimated by the marker method is within biological limits, while estimates using ingestive behavior components are not rational.

The complex issue of integrating the components of ingestive behavior in estimating a short-term intake rate and the process of achieving the goal of predicting daily forage intake and ultimately daily animal performance (Fig. 2) have also been approached through simulation models. A mechanistic-based model can integrate the multiple dimensions exhibited by the animal-induced and canopy-constraint dynamics of ingestive behavior (Cosgrove, 1997). A number of such models have been developed to address certain aspects of grazing behavior, such as ingestion and the canopy, mastication, or diet selection (Gordon and Lascano, 1993). Other models describing the interactions among the animal's diet, digestive processes, and metabolism (Elllis et al., 1999) have also been developed, but unfortunately none have been useful for predictive purposes.

Although data are limited for warm-season grasses, relationships between canopy characteristics and daily animal performance are evident. For example, leaf percentage, green herbage mass, and leaf mass were positively correlated with steer daily gain (Table 2). The positive relationships between green leaf and animal daily gain occurred even in a stocking rate study with bermudagrass where herbage mass declined with increasing stocking rate (Rouquette et al., 1984; Roth et al., 1990). In such studies, however, ingestive behavior also becomes a variable of stocking rate and can alter other normally expected relationships (as BW and herbage mass). Bite weight, reported by Chacon et al. (1978), was positively related to daily gain, but the relationship was modest when considering the proportion of the variation (31 to 34%) in daily gain that was accounted for by BW. This degree of association, however, may be biologically very important when considering the complexity of the total process.

Ingestive behavior relative to bite formation has also been used to estimate a short-term intake rate (Fig. 1). Assuming one prehending jaw movement per bite, and a constant chewing requirement per unit weight of forage ingested (chews g^{-1}), then

$$\text{intake rate, mass time}^{-1} = (\text{BW} \times j_t)/(1 + \text{BW} \times q),$$

where j_t = rate of total jaw movement (time^{-1}), and q = chewing jaw movements unit^{-1} mass ingested (Ungar, 1998). Another dimension of ingestive behavior then is ingestive mastication as included by Ungar (1998) and discussed by Cosgrove (1997). Ingestive mastication begins the breakdown process as forage is gathered for each bite and, consequently, has implications in animal performance (Dove, 1998).

Ingestive Mastication

Dry matter intake has been associated with particle size reduction and subsequent escape via the reticulo-omasal orifice to the lower tract (Poppi et al., 1980). Particles of ≈1.0 mm predominate in this passage process (Kennedy and Poppi, 1984). Particle reduction begins with ingestive behavior, continues through ingestive mastication with further reduction during rumination. Initial mastication can reduce as much as 25% of the particles to <1.2 mm, compared with 50% during the rumination process (McLeod and Minson, 1988). Further, Pond et al. (1984) showed ingestive mastication to be forage species dependent. Although ingestive mastication only begins the breakdown process of ingested forage, it operates at the functional level of particle dynamics. In essence, ruminants process forage a particle at a time (Dove, 1998).

The fractionation of particles in the ingestive mastication process, and their retention of that size ranking

Table 2. General relationships (r) between steer average daily gain, ingestive behavior measurements, and pasture canopy characteristics.

	Animal measurements†		Canopy characteristics‡								
Pasture species	**BW**	**GT**	**HM**	**GL**	**LM**	**GM**	**St**	**D**	**L:S**	**G:D**	**References**
Brachiaria						0.81					Euclides et al. (1993b)
Brachiaria spp.		−0.21	0.50	0.20	0.45	0.70		−0.10		0.64	Euclides et al. (2000)
Panicum maximum					0.60	0.64			0.44	0.52	Euclides et al. (1993a)
		−0.51	0.47	0.36	0.75	0.74		−0.80		0.55	Euclides et al. (1999)
Three species:				0.74			−0.89	0.12			Burns et al. (1991)
Panicum virgatum											
Cynodon dactylon											
Pennisetum flaccidum											
Setaria	0.58										Chacon et al. (1978)
Digitaria	0.56										

† BW = bite weight; GT = grazing time.
‡ HM = herbage mass; GL = green leaf proportion; LM = leaf mass; GM = green mass; St = stem proportion; D = dead tissue proportion; L:S = leaf to stem ratio; and G:D = green to dead ratio.

Table 3. Summary of canopy leaf, stem, and dead fractions and associated in vitro dry matter disappearance (IVDMD) of perennial warm-season grass pastures.†

	Leaf		Stem		Dead	
Pasture species	PDM‡	IVDMD	PDM	IVDMD	PDM	IVDMD
	%	g kg^{-1}	%	g kg^{-1}	%	g kg^{-1}
Experiment A:						
Tall fescue	78	721	7	748	15	415
Bermudagrass	37	638	47	590	16	358
Switchgrass	28	688	53	631	19	515
Flaccidgrass	33	713	32	661	35	552
Experiment B:						
Gamagrass	59	643	25	627	16	293

† Adapted from Burns et al. (1992) and Fisher et al. (1991).
‡ PDM = proportion of canopy dry matter.

during the digestion process, is of interest. In a confinement study comparing hays for a range of switchgrass (*Panicum virgatum* L.) maturities, the differential in particle sizes from ingestive mastication was retained, although reduced, in the feces after being processed through the digestive tract (Burns et al., 1997). Particles generated at initial mastication in this study appeared to already have biological importance.

Ingestive mastication (sample collected via esophageal cannula) has been evaluated in grazing experiments comparing perennial warm-season grasses where steer daily gains have ranged from a low of 0.22 kg for bermudagrass [*Cynodon dactylon* (L.) Pers.] up to 0.82 kg for gamagrass [*Tripsacum dactyloides* (L.) L.] and 0.92 kg for switchgrass (Burns et al., 1991, 1992; Fisher et al., 1991). Tall fescue (*Festuca arundinacea* Schreb.) was included in these studies as part of the grazing system evaluated to maximize season-long grazing. Grazing of tall fescue initiated in early April and continued into early June and resulted in highest daily gains of 1.2 kg. Herbage mass in these trials averaged >1800 kg ha^{-1}, and large differences were reported among species in leaf, stem, and dead portions of their canopies. Further, large differences occurred in the nutritive value among plant parts both within and among canopies, as estimated by in vitro DM disappearance (IVDMD) (Table 3). The canopy offered to the grazing animals by 'Coastal' bermudagrass was generally intermediate to the other grasses in the proportion of DM composed of leaf, stem, and dead tissue; but IVDMD concentrations of bermudagrass were generally inferior to the others, except for the dead fraction of gamagrass.

Separating the masticate into particle size classes of large, medium, and small showed bermudagrass to have a predominance of medium and small particles (Table 4). Further, the IVDMD of all particle classes of bermudagrass was lower than noted for the other grasses, while the IVDMD among the other grasses within particle class were similar. The lower daily gains noted from bermudagrass, compared with the other grasses, appeared to be associated with the nature of the canopy offered to the animal and to the inferior nutritive value of the forage that the animal removed and consumed through ingestive behavior. This condition has been further evaluated using intake and digestion measurements (Burns et al., 1985). Hays of similar cell wall concentrations [determined by neutral detergent fiber (NDF)] showed that bermudagrass was readily consumed, but digestion coefficients for DM, cell walls, and constituent fiber fractions were considerably inferior compared with the other grasses (Table 5). Neither the as-fed DM nor any of the DM fractions from bermudagrass had a digestion coefficient that exceeded 0.55, while those of the other grasses were 0.6 to 0.7.

The association between masticate (collected via esophageal cannula) particle size classes (large ≥1.7 mm; medium <1.7 ≥ 0.5 mm, and small <0.5 mm) from the abovementioned grazing trial (Burns et al., 1991; Fisher et al., 1991) and mean animal daily gain reveals several interesting relationships (J.C. Burns, D.S. Fisher, and K.R. Pond, 1993, unpublished data). First, particle classes, when expressed as a portion of masticate DM, were strongly ($r > 0.90$) correlated (Fig. 3A) with average daily gain (ADG). The large particle size class was positively related ($r = 0.95$) while the other two were negatively related ($r = -0.91$ to -0.93). Second,

Table 4. Summary of masticate particle size classes† and associated in vitro dry matter disappearance (IVDMD) of diet from perennial warm-season grass pastures.‡

	Large		Medium		Small	
Pasture species	PDM§	IVDMD	PDM	IVDMD	PDM	IVDMD
	%	g kg^{-1}	%	g kg^{-1}	%	g kg^{-1}
Experiment A:						
Tall fescue	30	769	61	759	9	700
Bermudagrass	8	539	72	664	20	640
Switchgrass	20	735	65	734	15	679
Flaccidgrass	21	716	69	722	10	676
Experiment B:						
Gamagrass	16	801	55	773	29	693

† Large ≥ 2.8 mm, medium < 2.8 and ≥ 0.5 mm, small < 0.5 mm.
‡ Adapted from Burns et al. (1992) and Fisher et al. (1991).
§ PDM = proportion of canopy DM.

Table 5. Dry matter (DM) intake and apparent digestion coefficients for DM and constituent fiber fractions of four perennial warm-season grass hays.†

Forage species	Hay NDF‡	Intake (100 kg body wt)	Digestion coefficients§				
			DM	NDF	ADF	HEMI	CELL
	g kg^{-1}	kg					
Steer trial:							
Bermudagrass	742	2.7	0.50	0.49	0.44	0.54	0.52
Switchgrass	758	2.1	0.61	0.65	0.59	0.72	0.68
Flaccidgrass	170	2.3	0.64	0.68	0.61	0.76	0.69
Sheep trial:							
Gamagrass	718	2.2	0.64	0.67	0.62	0.71	0.74

† Adapted from Burns et al. (1985, 1996).
‡ NDF = neutral detergent fiber.
§ ADF = acid detergent fiber, HEMI = hemicellulose, and CELL = cellulose.

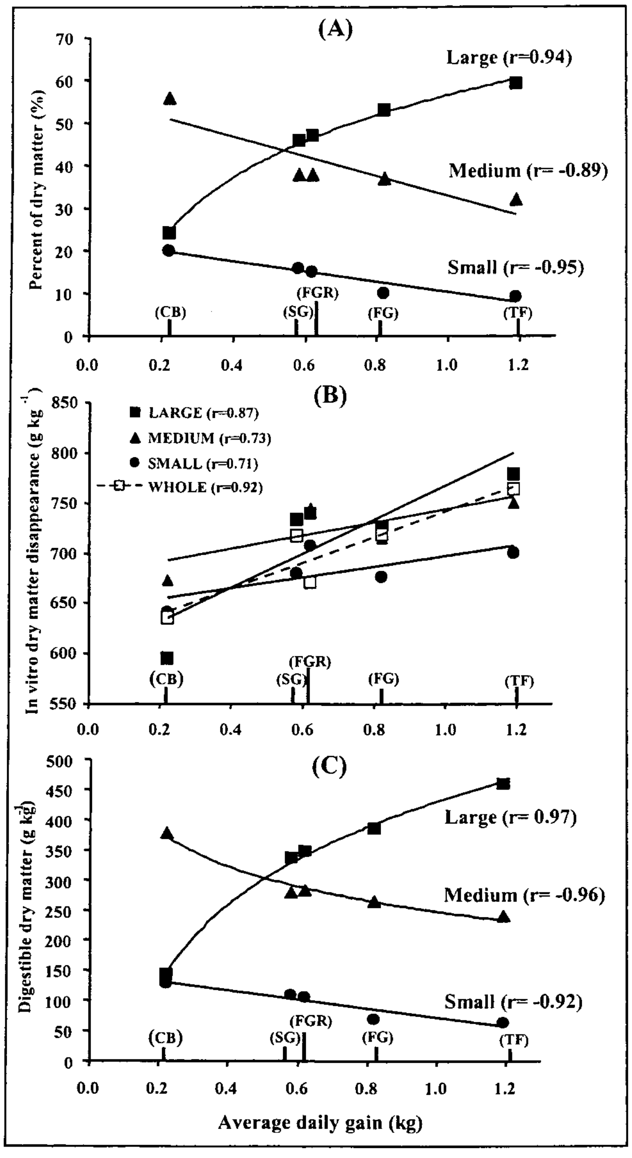

Fig. 3. Relationships between masticate dry matter (DM) and steer average daily gain for continuously stocked coastal bermudagrass (CB), switchgrass (SG), rotationally stocked flaccidgrass (FGR), flaccidgrass (FG), and tall fescue (TF) when expressed as (A) the proportion in large, medium, and small particle classes; (B) in vitro DM disappearance (IVDMD) of each particle size class, and (C) digestible DM concentration of each particle size class (proportion of masticate DM in each particle class × the IVDMD concentration of its DM).

the relationships between IVDMD concentration of each particle class and ADG were all positive (Fig. 3B). The large particle class IVDMD was more highly correlated with ADG (r = 0.87) than were the medium (r = 0.73) or small (r = 0.71) particle classes, but the whole masticate IVDMD showed the highest correlation (r = 0.92). Third, when the proportion of the DM in each particle class of the masticate was multiplied by its IVDMD concentration to generate the digestible DM concentration for that class, the relationship with ADG (Fig. 3C) was more strongly influenced by the proportion of the DM in each particle class (Fig. 3A) than by the IVDMD concentration of the DM (Fig. 3B). Fourth, a higher proportion of large particles and lower proportion of small particles are desirable and is consistent with the negative correlation between NDF concentration and particle size (Nelson, 1988; Bailey et al., 1990).

Although these data are extremely limited, the relationships indicate that perhaps particle size of the ingested forage may be the currency (medium of exchange) of ruminants that is being sought (Laca and Demment, 1998) that integrates characteristics of the pasture canopy with ingestive behavior, subsequent rumination, nutrient conversion, and ultimately with daily animal response.

Boundary Business and Ingestive Behavior

The grazing animal will select a diet from within the physical bounds allocated regardless of the total area allocated. In fact, if the opportunity exists, animals select the diet of their choice even in confinement (Burns et al., 2001). Exercising grazing management, defined as "the manipulation of animal grazing in pursuit of a defined objective" (Barnes and Beard, 1992), addresses one aspect of boundary business. This generally takes the form of a perimeter fence which restricts the animal to some area as part of a larger grazing system (e.g., continuous stocking, rotational stocking, strip grazing, or tethering). This boundary, although management controlled, can greatly alter animal grazing behavior depending on stocking density and length of stay, and influences ingestive behavior.

Two other types of bounds operate within the grazing paddock which can be subtle and with which the manager has no immediate control. These are animal-induced bounds and canopy-constraint bounds. Animal-induced bounds are rather volatile being highly animal-specific and, consequently, can vary widely among animals, even among animals of similar type, breed, and activity class. Further, these bounds can shift as the grazing season progresses. Canopy-constraint bounds, however, are far more stable and operate due to some characteristic of the pasture canopy, either inherent in the plant species (e.g., presence of heavy stems or some antiquality constituent) or induced by the grazing animal, which alters or prevents initial defoliation or defoliation of the subsequent regrowth. These bounds have been noted in general grazing management strategies (Mott, 1987) as well as in the conduct of intensive grazing experiments (Taylor, 1987). Because these bounds can alter ingestive behavior across short time periods, they may be of sufficient scope to nullify the use of ingestive behavior components to satisfactorily estimate daily forage intake (Forbes and Coleman, 1993). To this extent, they warrant discussion.

The generally perceived animal-induced bound is from fouling of the pasture and the avoidance of these areas by the animal in subsequent grazings. This bound is operative shortly after initial stocking and is usually referred to as patch or spot grazing. Personal observations indicate that this activity is far more complex than just the rejection of fouled areas as has been noted by others (Mott, 1987). Close examination of patch grazing, when moderately stocked, reveals a number of grazing styles which among them show subtle differences (Fig. 4). At the onset of grazing and at a reasonable herbage mass, the perimeter fence is the functional bound as animals uniformly graze with neither animal-induced nor plant-constraint bounds operating (Fig. 4A). Within 2 wk, uniform grazing slowly gives way to vertical or horizontal constraints of the pasture, which alters subsequent ingestive behavior. As grazing continues, the canopy surface takes on a wave form that we have designated as surf grazing, and plant constraints begin to emerge between waves (Fig. 4B). Some pasture species will show this form of grazing through much of the season, while it is seldom seen in other species. In some pastures (species specific), animals will graze in blocks, allowing portions of the canopy to mature and perhaps head-out, but the area between blocks is not sufficiently grazed to be an intake-limiting bound. This we designate as block grazing (Fig. 4C). After forage begins to mature in the block area, however, it in turn becomes a plant-constraint bound. Some animals exhibit random grazing behavior where they may graze both rather mature tissue as well as immature tissue by taking a series of bites from tall canopy areas as well as from short canopy areas. This we designated random grazing (Fig. 4D). Random grazing of the taller areas in a pasture can shift grazing behavior to block grazing, as the ungrazed portion of the canopy will continue to mature and will head out, becoming a plant-constraint bound. The grazed area, however, will regrow and will probably be regrazed, thereby keeping it vegetative but not so closely grazed that it becomes an intake-limiting bound. Finally, there is the typical spot grazing that is seen in pastures where animals graze mainly the immature regrowth (Fig. 4E). The consequence of spot grazing is an animal-induced increase in stocking rate because the land area being grazed is reduced to only the area between spots. This is in contrast to block grazing, where an intake-limiting bound does not occur. In spot grazing, the tall spots may or may not be fouled, but they form temporary bounds initially induced by the animal's decision and subsequently become plant constraints to ingestive behavior. These bounds can be of sufficient magnitude, such as short or tall canopy height or a high proportion of stem, to reduce animal daily intake and subsequently daily animal performance (Coleman and Forbes, 1998).

As the grazier sets new physical perimeter bounds, the constraints and bounds within pastures again form. In continuous stocking, or when animals regraze new pastures, carryover bounds can continue to operate at some level along with the emerging bounds associated with present grazing of new regrowth. The affect of bound dynamics within the pasture has not been evaluated in ingestive behavior studies. The variation that

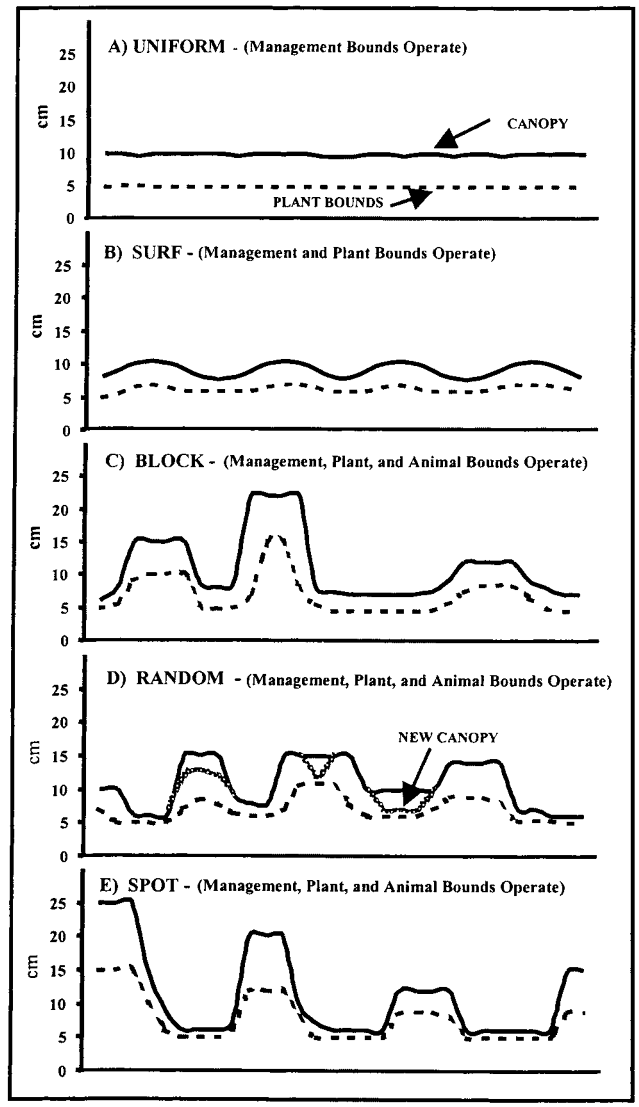

Fig. 4. Five grazing situations associated with management-imposed bounds and pasture canopy constraints interacting with animal grazing behavior.

within-pasture bounds can inject into short-term intake rate measurements within a day and from day to day can be appreciable and may not be adequately accounted for when expressing forage intake on a daily basis across an extended period of time. This variation will contribute and may be of sufficient size to prevent accurate prediction of daily DM intake based on ingestive behavior measurement (Forbes and Coleman, 1993). For example, this type of variation may be the major contributor to the large overestimation in daily DM intake of steers grazing guineagrass reported by Brancio et al. (2000b) when comparing marker technology and components of ingestive behavior. Marker technology consistently gave daily intake (kg DM 100^{-1} kg body weight) estimates that were biologically feasible (range = 2.3 to 3.3 kg) compared with estimates from components of ingestive mastication (range = 4.5 to 9.5 kg). The correlation noted between the two methods ($r = 0.73$), however, may have utility in assessing the relative intake potential among forages, but the value of such a measure is not clear.

Assessment and Summary of Grazing Behavior

The grazing ruminant is faced with the inordinate task of daily searching for, harvesting, and ingesting its DM intake demand one bite at a time. The identification of the components of ingestive behavior and the subsequent interrelationships that have been established between them have provided valuable information on how the ruminant selects, gathers in, and ingests its diet using discrete forage packets of ≈1 g or less.

Characteristics of warm-season grass canopies are such that height of canopy, the green leaf proportion, and green mass of the canopy are generally positively associated with certain components of ingestive behavior. Canopy bulk density, however, shows a negative relationship with some components of ingestive behavior. This results from the compensation of the components in ingestive behavior as canopy characteristics change. For example, as herbage mass declines, BW will also decline, but biting rate and grazing time will increase up to a point to offset the reduction in BW. The canopy attributes that appear important relative to animal daily forage intake and to daily gain are aspects of green leaf in the canopy (green leaf percentage, green leaf mass, or green mass). Although data are limited, the relationships are consistent and have practical implication in managing grazing systems.

As grazing proceeds, vertical and horizontal constraints develop within the pasture canopy. These bounds are both a characteristic of the pasture species and induced by the grazing animal. These constraints alter animal ingestive behavior and subsequently short-term intake rate. Further, daily grazing time, as the link between short-term intake rate and daily forage intake, can also be altered.

Ingestive mastication, as a part of ingestive behavior (Cosgrove, 1997; Ungar, 1998) disrupts plant tissue and incorporates saliva (a lubricant and a solvent), beginning the process of particle breakdown. Particle size classes of large, medium, and small showed strong association with ADG when expressed as proportion of DM or in terms of nutritive value. This aspect of ingestive behavior should have an important role in estimating long-term daily forage intake.

The elementary components of ingestive behavior operate in all grazing situations. The quantitative relationships, both among animal species and among plant species and their interactions, however, are not universal, and many external factors influence short-term intake rate (Ungar, 1998). The goal of ingestive behavior measurements is to predict daily DM intake through modeling. The approach used is reductionist science using mechanistic models to work backward from a component and place it into the context of a larger whole. Modeling communicates such complex interrelationships as found in the plant-animal interface. As Seligman (1993) notes, however, biological simulation models cannot predict the future, replace biological-process experiments, give site-specific responses, or replace objective assessment or value judgment. They can, however, examine system responses and identify system behavior patterns. The within-pasture vertical and horizontal variation that must be addressed, as discussed previously, may be sufficiently large to prevent the use of ingestive behavior components to reasonably estimate daily forage intake. Further, particle sizes of the ingested masticate may be the currency that relates characteristics of the pasture canopy ingested through chemical and physical properties of the particles to nutrient conversion, and subsequently to daily performance of the grazing animal.

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