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CANOPY CHARACTERISTICS, INGESTIVE BEHAVIOUR AND HERBAGE INTAKE IN CULTIVATED TROPICAL GRASSLANDS

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Abstract

Compared to temperate systems, there have been few detailed assessments of canopy characteristics and associated grazing behavior in planted tropical grasslands. Reasons include the large number of forage species used in warm climates, the diversity of their morphology, research priorities emphasizing germplasm evaluation and management, and limited resources. This review describes canopy attributes of C₄ grass pastures, highlights the most important relationships between grazing behavior and these canopy characteristics, and discusses the implications of canopy characteristics and grazing behavior for long-term intake and animal performance. It is suggested that the largest differences in canopy characteristics between tropical and temperate swards are not total canopy measures but those of the upper canopy strata including leaf proportion and bulk density. This occurs because tropical swards, unlike many temperate ones, have large vertical heterogeneity in density, plant-part proportion and nutritive value. In temperate swards, bite weight is primarily a function of sward height, but leaf percentage, leaf mass, or green herbage mass of the upper strata of the canopy usually are more important with C₄ grasses. The manner in which leaf is presented to the animal and the degree to which it can be prehended separate from stem and dead material of low digestibility are also of great significance in pastures based on C₄ grasses.

Introduction

Intake is the most important determinant of animal performance (Poppi et al., 1997). If sward characteristics associated with high intake of grazing livestock can be identified, then it may be possible to devise practical management strategies to optimize production. This approach has been successful in temperate climate areas for continuously stocked ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) swards, where maximum animal performance has been achieved at canopy heights of approximately 6 cm for sheep (Parsons, 1984; Penning et al., 1991) and 8-10 cm for cattle (Wright and Whyte, 1989).

Development of management recommendations directly from detailed study of the plant-animal interface has not been widely achieved (Cosgrove, 1997). For any given set of conditions the complexity of pasture-herbivore interactions makes it difficult to predict intake and performance (Cosgrove, 1997; Ungar, 1996). The dynamic nature of sward canopy-herbivore interactions was shown in an early conceptual model (Moore, 1983) and data from field research (Chacon and Stobbs, 1976; Sollenberger et al., 1987) where canopy characteristics affected grazing behaviour, herbivory altered canopy characteristics, and subsequent grazing behaviour changed. In addition to the complexities associated with understanding the plant-animal interaction, there are many environmental and animal behaviour factors that are unrelated to the

sward but can influence ingestive behaviour (Cosgrove, 1997; Laca and Demment, 1996; Macoon, 1999; Ungar, 1996). Gordon and Lascano (1993) caution that the complexity of foraging behaviour and of the interactions between components of grasslands limit the ability of an empirically derived approach to provide an understanding of the dynamics of even relatively simple sown grassland systems.

There have been relatively few attempts at detailed assessment of sward canopies and grazing behaviour in planted tropical grasslands (Gordon and Lascano, 1993). One reason is that these systems rely upon more forage species than do temperate systems, and there is still considerable flux in species choice. Also, at many locations a primary research focus of forage programs has been the introduction of new germplasm subjected to evaluation for agronomic traits (persistence, yield, etc.), with no information or consideration given to detailed assessment of plant-animal interactions. In addition, there is great diversity of growth habits and morphology of tropical species and of management practices employed in their use. These factors make difficult the development of meaningful relationships that can be extrapolated beyond the context of a single experiment or environment. Finally, there have been few research programs with a critical mass of personnel and the significant long-term funding required to engage in this demanding, but important, research.

This review will summarize existing literature characterizing canopy attributes of pasture systems based on C_4 grasses, highlight the most important relationships between grazing behaviour and canopy characteristics, and discuss the relationships of canopy characteristics and grazing behaviour with intake. Non-canopy factors that affect grazing behaviour and intake will be identified. Lastly, the future merit and potential contribution of detailed plant-animal interface research to warm-climate grassland systems will be discussed.

Sward Canopy Attributes

Detailed characterization of tropical grassland canopies began with the work of Stobbs and his colleagues (Stobbs, 1973a and b; Chacon and Stobbs, 1976, Hendricksen and Minson, 1980; Ludlow et al., 1982). Relatively few scientists have followed in their footsteps. This section will describe canopies consisting primarily of C_4 grasses in terms of bulk density, tiller characteristics, and vertical heterogeneity.

Total and leaf bulk density of overall canopy

Stobbs (1973b) showed very low bulk density of total live herbage, ranging from 14 to 98 $\text{kg ha}^{-1} \text{cm}^{-1}$, for 2- to 8-wk regrowth of setaria (*Setaria sphacelata*) and rhodesgrass (*Chloris gayana*). Leaf bulk densities were low, ranging from 12 to 43 $\text{kg ha}^{-1} \text{cm}^{-1}$. Subsequent data for these species and digitgrass (*Digitaria eriantha*), however, showed greater total herbage and leaf densities (Stobbs, 1973a and 1975b, Chacon and Stobbs, 1976; Ludlow et al., 1982). More recent work across management practices and several genera show a range of total live herbage bulk densities from 70 to 600 $\text{kg ha}^{-1} \text{cm}^{-1}$ (Table 1). Most commonly these values are between 100 and 200 $\text{kg ha}^{-1} \text{cm}^{-1}$. Leaf bulk densities are often between 30 and 100 $\text{kg ha}^{-1} \text{cm}^{-1}$ (Table 1), but Forbes and Coleman (1993) reported values as low as 10 and 20 $\text{kg ha}^{-1} \text{cm}^{-1}$ for old world bluestem cv. Plains (*Botriochloa ischaemum*) and cv. Caucasian (*B. caucasica*).

These total bulk densities were similar to those of vegetative and reproductive growth of five temperate grasses (average of 120 and 97 $\text{kg ha}^{-1} \text{cm}^{-1}$, respectively) but generally less than

those of three legumes (average of 233 and 197 kg ha⁻¹ cm⁻¹ for vegetative and reproductive growth, respectively; Gong et al., 1996a). Further, they were generally less than pregraze measures of total live herbage bulk density of rotationally stocked perennial ryegrass pastures grazed every 4-5 weeks (160-220 kg ha⁻¹ cm⁻¹; Penning et al., 1994), and often much less than bulk densities reported for perennial ryegrass pastures continuously stocked and grazed at 2- to 12-cm heights (450-930 kg ha⁻¹ cm⁻¹ in spring and 600-1340 kg ha⁻¹ cm⁻¹ in autumn; Penning et al., 1991). Bermudagrass (*Cynodon* sp. cv. Tifton 85) was an exception with total herbage density ranging from 370-610 kg ha⁻¹ cm⁻¹ (Carnevali et al., 1999). Leaf bulk densities of continuously stocked perennial ryegrass were in the range of 160-330 kg ha⁻¹ cm⁻¹ in spring and 120-280 kg ha⁻¹ cm⁻¹ in autumn (Penning et al., 1991), but on rotationally stocked pastures they ranged from 80-130 kg ha⁻¹ cm⁻¹ (Penning et al., 1994). Leaf bulk densities of C₄ grass canopies are often lower than those of temperate species.

Longer regrowth intervals are associated with greater total herbage bulk density but generally lower leaf bulk density (Stobbs, 1973a and 1973b). Increasing N rate increased both total and leaf bulk densities (Stobbs, 1975b). Lower grazing height under continuous stocking was associated with greater total and leaf bulk density (Carnevali et al., 1999).

Tiller number and weight

Grasslands are composed of a population of tillers that respond to environmental stimuli and to defoliation (Mitchell and Moser, 2000). The nature and magnitude of this response will have an important impact on canopy structure.

Tiller density is extremely variable among swards of C₄ grasses. Mitchell and Moser (2000) reported 600 to 1600 tillers m⁻² for undefoliated switchgrass (*Panicum virgatum*) and 300 to 800 m⁻² for big bluestem (*Andropogon gerardii*) during plant development in Nebraska USA. Bermudagrass populations ranged from 6000 to 16 000 tillers m⁻² on continuously stocked pastures in Brazil that were grazed to heights ranging from 5-20 cm (Carvalho et al., 1999). Tiller populations of rotationally stocked (3-d stay and 32-d rest period) bahiagrass (*Paspalum notatum*) under different N rates and herbage allowances in Brazil ranged from approximately 2500 to 5400 m⁻² (Boggiano et al., 1999). Rotationally stocked (11-37 d rest periods) bahiagrass in southwestern Japan had tiller densities ranging from 3800 to 4800 m⁻² (Pakiding and Hirata, 1999).

As grazing height of continuously stocked bermudagrass increased from 5 to 20 cm, tiller density decreased from 14 300 to 6800 (Sbrissia et al., 1999). Tiller mass increased from 23 to 124 mg per tiller over this range of defoliation heights and leaf mass per tiller increased from 18 to 70 mg. There was greater total canopy bulk density for the 5-cm treatment than for taller heights. Similarly, tiller density was greatest on bahiagrass pastures with low herbage allowance and decreased at a decreasing rate as herbage allowance increased (Boggiano et al., 1999). At low grazing heights a greater density of smaller tillers (with less leaf area per tiller) optimises sward leaf area index (LAI), and conversely, at taller grazing heights a lower population density of larger tillers (with more leaf area per tiller) optimises sward LAI (Matthew et al., 1999).

Only the highest tiller densities observed for bermudagrass approach those reported for continuously (16 300 to 30 200 m⁻², Penning et al., 1994; 12 400 to 24 800 m⁻², Penning et al., 1991) or rotationally stocked ryegrass pastures (15 900 to 21 400 m⁻²). In contrast, tiller density from approximately 500 to 6 000 is reported for temperate species including *Phleum pratense*, *L. perenne*, *Festuca pratensis*, *L. multiflorum*, and *Bromus willdenowii* (Matthew et al., 1999). For

a steady state LAI of 3, Mazzanti et al. (1994) reported tiller density of 4000-6000 m⁻² for *F. arundinacea*, while a range of 10 000-15 000 was reported for *L. perenne* (Davies, 1988). In some cases, lower bulk density of C₄ than C₃ pastures may be attributable to lower tiller density in C₄ swards, but differences in tiller density among and within (depending on management) C₄ species can be quite large.

Vertical heterogeneity in total and component bulk density

Stobbs (1975a) noted that unlike temperate pastures, tropical pastures vary greatly in composition from top to bottom of the canopy. These changes result in marked differences in bulk density throughout the canopy. Data from Holderbaum et al. (1992) show that the top one-half of rotationally stocked limpograss (*Hemarthria altissima*) canopies had a total bulk density of 100 vs. 256 kg ha⁻¹ cm⁻¹ for the bottom half (Table 2). Moore et al. (1987) showed that the upper 10-20 cm of rotationally stocked limpograss-aeschynomene (*Aeschynomene americana*) pastures (5-wk regrowth interval) had an average bulk density of 60 kg ha⁻¹ cm⁻¹ compared with 130 kg ha⁻¹ cm⁻¹ for the overall canopy. Bulk density of setaria and rhodesgrass pastures increased moving from the top to bottom of the canopy (Stobbs, 1973b; Stobbs, 1975b), and bulk density of setaria pastures increased as they were progressively defoliated. For nine temperate forages (Gong et al., 1996a), the difference in bulk density between the grazed stratum of the canopy and the entire canopy generally was less pronounced than for these tropical species.

Changes in bulk density by vertical stratum are associated with changes in plant-part and species bulk density and proportion. Holderbaum et al. (1992) showed that leaf percentage in the top half of limpograss canopies was 33% compared to 10% in the bottom half. In the same experiment, leaf bulk density was greater in the top than bottom of the canopy, but stem bulk density was greater for the bottom half (Table 2). In contrast, Stobbs (1973b, 1975b) reported increasing setaria and rhodesgrass leaf bulk density from top to bottom of the canopy because leaf proportion was changing relatively little but total bulk density was increasing. In a mixed sward, Moore et al. (1987) reported that aeschynomene bulk density was nearly the same in the top 10-20 cm as in the entire canopy, but limpograss density was only one-third as great in the top layer as the whole canopy. Thus aeschynomene proportion in the mixture was much greater near the top of the canopy.

Vertical heterogeneity in nutritive value

If plant-part bulk density and proportion are changing across vertical strata, then nutritive value will change. Flaccidgrass (*Pennisetum flaccidum*), gamagrass (*Tripsacum dactyloides*), and bermudagrass were continuously stocked and canopies were characterized in 5-cm strata (Burns et al., 1991). Comparing the top and bottom strata, total herbage in vitro dry matter disappearance (IVDMD) was greater for the top strata for all species (Table 3). Differences in plant-part IVDMD were not great enough to account for the change in total herbage IVDMD (Table 3), suggesting that for these grasses differences in part-part and dead herbage proportion among canopy strata are key determinants of IVDMD.

Holderbaum et al. (1992) showed large decreases in crude protein (CP) concentration from top to bottom of a limpograss canopy, primarily due to changes in leaf and stem proportion (Table 2). In vitro organic matter disappearance (IVOMD) varied relatively little throughout the canopy and among plant parts, thus the ratio of herbage digestible organic matter (DOM) to CP

increased from the top to bottom of the canopy. Increasing herbage DOM:CP has been associated with greater response of cattle to protein supplement, suggesting that closer grazing of rotationally stocked limpgrass will increase the likelihood of an N deficiency (Sollenberger et al., 1997; Lima et al., 1999).

Fisher et al. (1991) compared IVDMD by 5-cm vertical strata for three C₄ (bermudagrass, flaccidgrass, and switchgrass) and one C₃ forage (tall fescue). All grasses were continuously stocked during the same time of year in North Carolina, USA, and canopies were of comparable height when sampled. They found that IVDMD increased from bottom to top layer by 21 g kg⁻¹ for tall fescue, 31 g kg⁻¹ for bermudagrass, 58 g kg⁻¹ for flaccidgrass, and 68 g kg⁻¹ for switchgrass. Leaf predominated in the tall fescue canopy, while stem and dead material were more prominent throughout the C₄ grass canopies. These data support the conclusion that C₄ grass canopies are more heterogeneous than C₃ in terms of plant-part proportion and nutritive value.

Ingestive Behaviour and Response to Sward Canopy Structure

Canopy height and density, plant-part and species proportion and spatial arrangement, herbage chemical composition and digestibility, and many other canopy and non-canopy factors influence grazing behaviour. The focus of this section will be grazing behaviour in response to canopy structure.

It has been difficult to determine the independent effects of canopy structure on the components of ingestive behaviour because canopy variables are often strongly correlated in natural swards (Demment and Laca, 1994). In addition, there are methodological impasses to overcome. Sampling sites chosen to represent the pasture as a whole may not represent grazed areas (Forbes and Coleman, 1993). Measures of bite weight or diet botanical or chemical composition using oesophageal-fistulated animals may not approximate those of resident animals (Carulla et al., 1991). Non-canopy factors (grazing environment, previous experience, etc.) may influence ingestive behaviour (Cosgrove, 1997).

To address these constraints, several kinds of researcher-created micro-canopies have been offered to animals (Black and Kenney, 1984; Laca et al., 1992b; WallisDeVries et al., 1998). Their use is designed to minimize canopy heterogeneity, to separate the effects of confounded canopy characteristics, and to ensure that the patch being grazed is represented accurately by sampling (Ungar, 1996). This technique has been widely used with temperate forages (Ungar, 1996), but to a limited extent with tropical and subtropical species (Black and Kenney, 1984; Ungar et al., 1991; Laca et al., 1992; Flores et al., 1993).

Components of ingestive behaviour

The inter-relationships of these components and measures of intake are shown in Figure 1 (adapted from Gordon and Lascano, 1993). Diet selection is not referred to explicitly in this description of grazing behaviour, but it has a major impact on bite mass and bite rate resulting from the canopy manipulation and gathering activities that are associated with selective grazing (Moore et al., 1987). The reader is referred to recent reviews for more detailed treatment of ingestive behaviour (Demment and Laca, 1994; Illius and Hodgson, 1996; Laca and Demment, 1996; Ungar, 1996; Cosgrove, 1997; Hodgson et al., 1997; Illius, 1997).

Bite volume. Bite volume is computed as the product of bite area and depth, although the true

shape of the volume swept or actually removed in a bite may be more complex (Ungar, 1996). The product of bite volume and bulk density of the grazed horizon is bite weight (Fig. 1). Bite volume is positively related to canopy height (Flores et al., 1993; Cosgrove, 1997) and will be discussed in terms of its components bite area and depth.

Bite area is that encompassed by the mouth gape and the sweep or sweeps of the tongue, and can be adjusted by the animal by varying the area and frequency of tongue sweeps as well as mouth gape (Flores et al., 1993). In general, the amplitude of tongue sweeps increases with canopy height and the number of tongue sweeps per bite decreases with canopy density (Ungar, 1996). Bite area is thought to be less sensitive to changes in the canopy than bite depth (Hodgson et al., 1997), but on hand-constructed dallisgrass (*Paspalum dilatatum*) presentations, bite area decreased linearly with increasing bulk density and increased quadratically with increasing canopy height (Laca et al., 1992a). Ungar et al. (1991) also reported that bite area increased with height of hand-constructed canopies of dallisgrass, and Cangiano et al. (1999) found similar responses for natural forage sorghum (*Sorghum sacharatum*) and *Panicum millaceum* canopies in Argentina. In contrast to these results, there were no differences in bite area, despite differences in height and bulk density, of perennial ryegrass, cocksfoot (*Dactylis glomerata*), and white clover canopies (Gong et al., 1996b).

Bite depth is positively related to height of vegetative canopies (Laca et al., 1992a), and a range of studies has shown the ratio of bite depth to canopy height to be from 0.35 to 0.50 (Burlison et al., 1991; Laca et al., 1992a). In reproductive micro-canopies of dallisgrass, however, bite depth appeared to be limited by the presence of stem (Flores et al., 1993). The authors concluded that when the canopy is short and dense, stems are a barrier that makes it difficult for the animal to insert its muzzle below stem height. For several temperate forages, bite depth showed a greater response to canopy height and density than did bite area, thus bite depth had the dominant influence on bite volume and bite weight (Gong et al., 1996b).

Bite weight. Bite weight or intake per bite is determined by bite volume and the herbage bulk density of the grazed horizon (Fig. 1; Gordon and Lascano, 1993). Short-term rate of intake tends to increase progressively as an asymptotic function of bite weight (Hodgson et al., 1997), and bite weight is usually the most influential factor determining short-term rate of intake (Cosgrove, 1997; Illius, 1997).

In early work with setaria and rhodesgrass, Stobbs (1973b) reported negative correlations between bite weight and herbage mass ($r=-0.61$) and canopy bulk density ($r=-0.70$), but positive correlations between bite weight and leaf percentage in the canopy ($r=0.63$) and in the upper strata ($r=0.73$). Animals grazing 6- and 8-wk regrowth had low bite weight despite high herbage mass and leaf bulk density. In subsequent work, N fertilization increased the proportion and quantity of leaf in the upper strata of the sward canopy, and bite weight was more highly correlated with leaf mass in the top strata than leaf mass in the entire canopy (Stobbs, 1975). When evaluating stocking rate of setaria and digitgrass swards, Chacon et al. (1978) found that bite weight was highly correlated with herbage mass and the green and leaf components of the sward canopy.

Chacon and Stobbs (1976) reported that bite weight was the major determinant of short-term intake and that it declined during the progressive defoliation of a setaria canopy. Bite weight was most closely related to leaf herbage mass, and to a lesser extent to leaf:stem ratio, and canopy bulk density. In another study involving progressive defoliation, Hendricksen and Minson (1980) found that bite weight of cattle grazing the legume *Lablab purpureus* was

significantly correlated with canopy height ($r=0.92$), green herbage mass ($r=0.74$), green leaf mass ($r=0.86$), green leaf proportion ($r=0.77$), and leaf/stem ratio ($r=0.81$). Correlation of bite weight with green leaf bulk density was not significant.

For a mixed canopy of limpgrass and aescynomene, the proportion of green herbage in the upper layer explained 56% of the variation in bite weight (Moore et al., 1987). For a wide range of old world bluestem swards, intake per bite increased with increasing herbage mass from 1 to between 4 and 7 Mg ha⁻¹ depending on cultivar (Forbes and Coleman, 1993). These authors found that short-term intake rate was most affected by green herbage mass. They suggested that green leaf appears to be the single most important component of the canopy whether measured as mass, proportion, density, or ratio.

When hand-constructed micro-canopies of dallisgrass were grazed, bite weight increased with increasing canopy height in the absence of stem (Flores et al., 1993). When stem was present in the bottom strata of the constructed canopy, bite weight was no longer related to canopy height but to lamina length.

Considering a range of C₄ grass pastures, it appears that canopy height, canopy density, and even canopy leaf density are often poorly correlated to bite weight. Green herbage mass or green leaf proportion in the canopy, and more specifically in the grazed horizon, show a much more consistent positive relationship with bite weight. High leaf mass or density alone do not guarantee high bite weight, however, because the leaf must be accessible to the grazing animal (Burns et al., 1991).

Bite rate. Jaw movements are partitioned into those used to gather herbage before prehending, those involved in the severing of bites, and those following bites to manipulate and masticate the forage (Coleman et al., 1989; Cosgrove, 1997). Bite rate refers to number of severing jaw movements per unit time. Changes in bite rate have been viewed as a compensatory mechanism attempting to maintain intake relatively constant when bite weight is changing (Chacon et al., 1978; Penning et al., 1991) and as a reflection of the degree of non-biting jaw movements or canopy manipulation associated with a bite (Cosgrove, 1997).

During progressive defoliation of a sward, Chacon and Stobbs (1976) and Hendricksen and Minson (1980) found that bite rate increased as bite weight decreased. Later in the same grazing period, as herbage mass and green leaf in the upper canopy strata continued to decline, this compensatory increase in bite rate ceased and bite rate began to decline.

At the beginning of grazing on rotationally stocked limpgrass-aescynomene pastures, rate of biting increased as legume percentage in the upper layer decreased and grass leaf bulk density increased, characteristics of shorter, more homogenous canopies (Moore et al., 1985). Considering relationships of bite rate with characteristics of the whole canopy, these authors found that bite rate on the first day of grazing decreased with increasing pasture height, bulk density, and herbage mass. Across a wide range of canopy structure and mass, Forbes and Coleman (1993) found little effect of the canopy on bite rate. Ungar et al. (1991) reported a greater bite rate for a 4- than a 10-cm dallisgrass micro-canopy. Hodgson et al. (1997) concluded that bite rate is generally negatively related to bite weight, reflecting the increasing importance of manipulative movements as bite weight increases.

Grazing time. The activity of the animal is divided into periods of grazing, ruminating, rest, and social interaction (Hodgson, 1982). The amount of time spent for each depends on sward characteristics, environmental conditions, and the nutritional requirements of the animal

(Coleman et al., 1989; Macoon, 1999). For a given short-term intake rate, the animal's daily intake depends on the length of time it spends grazing, thus grazing time is the link between short-term intake rate and daily forage intake (Hodgson et al., 1997; Illius, 1997).

Grazing time can compensate for changes in bite weight, being shorter when bite weight is high and increasing as bite weight decreases (Chacon et al., 1978). Studies conducted on temperate swards have generally shown a linear increase in grazing time as herbage mass or sward height decreased (Hodgson, 1982). While this has often been the case on tropical and subtropical pastures, the relationship has not been as consistent. Chacon et al. (1978) reported increasing grazing time with greater stocking rate and lesser herbage mass on setaria and digitgrass pastures. Grazing time was negatively related to herbage mass of a limpgrass-aeschynomene mixture (Moore et al., 1985). Chacon and Stobbs (1976) showed increasing grazing time as herbage mass of setaria decreased early in a grazing period, likely because animals were compensating for decreasing bite weight. Later in the grazing period, and in contrast to the expected response, further reductions in bite weight and canopy herbage mass caused grazing time to plateau and then decrease. Similar results were reported by Hendricksen and Minson (1980) for *Lablab purpureus*.

Forbes and Coleman (1993) reported that grazing time increased relatively rapidly as green leaf proportion increased from low to moderate levels, but thereafter began to level off or decline. The response of total bites to green leaf proportion was similar. This suggests that at high green leaf proportion bite weight may have increased sufficiently so that grazing time and total bites could be reduced. In grazing trials in southern Brazil with *Panicum maximum* and *Brachiaria* spp., grazing time decreased with increasing percentage of green leaves ($r = -0.63$ to -0.70), increasing leaf herbage mass ($r = -0.51$ to -0.86), and increasing green herbage mass ($r = -0.43$ to -0.85) (Euclides et al., 1991).

Macon (1999) found that grazing time was approximately 1 h per day shorter for lactating dairy cattle grazing rhizoma peanut (*Arachis glabrata*) than for bermudagrass pastures. This occurred despite greater intake for cattle grazing rhizoma peanut. Although bite weight and mass were not quantified, he speculated that bite rate was much greater on the shorter, more dense rhizoma peanut pastures allowing for a shorter grazing time.

Diet selection

Selective grazing by ruminants can nullify large differences in leaf, stem, and dead proportion in the canopy provided that the preferred plant fraction is easily prehended (Burns et al., 1991). Selection is often associated with more manipulative jaw movements per bite, which can increase bite weight and slow bite rate (Moore et al., 1987). In situations where leaf proportion is very low, as with canopies of mature C₄ grasses, selection for leaf may result in low bite weight and low intake (Stobbs, 1973b). The brief discussion that follows will consider effects of selection on nutritive value of the diet, factors affecting diet selection in grass-legume swards, and canopy sampling concerns when characterizing diet selection.

Effects of selection on diet nutritive value. Animals select for leaf and live herbage and discriminate against dead material, and as a result the nutritive value of the herbage consumed is greater than that of total herbage on offer. For three C₄ grasses, Fisher et al. (1991) reported that masticate IVDMD was 170 g kg⁻¹ greater than herbage mass samples; masticate neutral detergent fiber was 130 g kg⁻¹ less. Upper strata leaf IVDMD explained 67-74% of the variation in

masticate IVDMD and the slope of the linear function was 1.01. Burns et al. (1992) reported that masticate IVDMD of eastern gamagrass, flaccidgrass, and switchgrass was 92 to 173 g kg⁻¹ greater than IVDMD of herbage mass samples. The smallest difference between masticate and herbage mass IVDMD occurred for gamagrass which had the greatest percentage of leaf in the herbage mass.

Diet selection in grass-legume swards. Selection of legume in tropical grass-legume swards can be highly seasonal. Cattle grazing a mixture of *Andropogon gayanus*-*Pueraria phaseoloides*-*Stylosanthes capitata* in Colombia discriminated against legume in the rainy season and selected for legume in the dry season (Böhnert et al., 1985). Similar responses were noted for *Stylosanthes* spp.-grass pasture in Australia (Coates, 1996) and *Brachiaria dictyoneura*-*Arachis pintoii* pastures in Colombia (Carulla et al., 1991). Other studies have shown selection for *A. pintoii* throughout the year (Lascano, 1999). In Florida, cattle selected for bahiagrass in spring and early summer and for rhizoma peanut during late summer and autumn (Bennett et al., 1999). These seasonal trends are likely due to legumes staying green longer into the dry season than grasses and to the accumulation of grass stem and dead material late in a growing season. In Australia, Norton et al. (1990) observed that goats and cattle selected for legume during summer and autumn, cattle selected grass in winter, and sheep selected grass in all seasons. They attributed differences among species to grazing habit with goats browsing in the top of the canopy where legume was prevalent and sheep grazing in the bottom of the canopy where grasses were prevalent.

Chemical constituents in tropical legumes, especially tannins, affect their palatability and selection by cattle. In *B. dictyoneura* - *Desmodium ovalifolium* pastures, selection against the legume was attributed to its high tannin concentration (Lascano, 1999). Condensed tannin concentration is low for *Leucaena leucocephala* cv. Tarramba, high for *L. pallida*, and intermediate for the hybrid KX2 (*L. leucocephala* x *L. pallida*). In subtropical Australia, the *Leucaena* genotypes were planted in rows in pastures of *B. decumbens*. Time spent grazing *Leucaena* as a proportion of total grazing time decreased with increasing tannin concentration (Shelton, H.M., unpublished data).

Stratified sampling of the canopy is important in studies of diet selection. For rotationally stocked aeschynomene-limpograss pastures, legume percentage in oesophageal extrusa at the beginning of a grazing period was greater than in the upper canopy strata, showing selection for legume (Sollenberger et al., 1987). Proportion of aeschynomene in herbage consumed during a grazing period was greater than in the whole canopy, again suggesting selection for the legume. These authors found, however, that when average legume percentage in the diet across an entire grazing period was compared with legume percentage in the grazed horizon, there was no difference. Did selection occur? The authors concluded that low bulk density in the upper layer of the canopy allowed for selection of legume early in a grazing period, but as grazing continued legume leaf mass became limiting and herbage bulk density increased, effectively ending selection for the legume. Apart from quantifying the vertical distribution of species in a mixed canopy, inaccurate conclusions about diet selection can occur.

Relationships of Canopy Attributes and Grazing Behaviour with Intake

Relationships of canopy characteristics and grazing behaviour with short-term rate of intake have been established in many studies in temperate climates and in fewer, but a significant number of studies in warm climates. There are relatively few studies, however, that have

described canopy and behaviour relationships with long-term measures of intake or with animal performance.

Canopy attributes and intake/animal performance

The best model predicting milk yield per cow in subtropical Australia included positive coefficients for winter and summer leaf yield and autumn green herbage mass, but negative coefficients for summer stem mass (Davison et al., 1993). In year-round continuously stocked *Brachiaria* spp. pastures in southern Brazil, there was no relationship between total herbage mass and average daily gain, but green herbage mass was positively related to daily gain ($r=0.81$; Euclides et al., 1993b). In a more recent study (Euclides et al., 2000), dry matter intake of *B. decumbens* and *B. brizantha* were positively correlated with green herbage mass ($r=0.55$ to 0.61), leaf mass ($r=0.51$ to 0.59), and leaf percentage ($r=0.46$ to 0.65). For *Panicum maximum* pastures at the same location, average daily gain was positively correlated with green herbage mass ($r=0.64$), leaf mass ($r=0.60$), green:dead ratio ($r=0.52$), and leaf:stem ratio ($r=0.44$; Euclides et al., 1993a). Gain increased with increasing green herbage mass up to 900 kg ha^{-1} after which it leveled off.

For continuously stocked pastures of the C_3 grass tall fescue and the C_4 grasses switchgrass, flaccidgrass, and bermudagrass (Burns et al., 1991), steer daily gains were correlated with proportion of leaf ($r=0.74$) and stem ($r=-0.89$) in the canopy but were not correlated with canopy dead proportion ($r=0.12$) or dead IVDMD ($r=0.29$). These authors suggested that differences in animal access to leaf was helpful in explaining daily gain. Highest gains of 1.2 kg d^{-1} on tall fescue were associated with a high proportion of leaf (78%) in the canopy, the presence of leaf in all strata, and high leaf IVDMD in all strata. Lowest gains of 0.22 kg on bermudagrass were associated with a high proportion of stem (47%), the presence of stem throughout the canopy, and generally low IVDMD in all strata. Switchgrass had a lower percentage of leaf (29) and higher percentage of stem (54) than did bermudagrass, but IVDMD of these fractions was greater for switchgrass (Fisher et al., 1991). Additionally, switchgrass leaf grew higher than stem in the canopy, making possible selection for leaf and greater daily gain of cattle on switchgrass pastures (0.59 kg ; Burns et al., 1991). Flores et al. (1993) observed for dallisgrass micro-canopies that when the canopy is short and dense (as for bermudagrass in Burns et al., 1991), stems present a barrier that makes it difficult for the animal to insert its muzzle below the height at which stem occurs in the canopy and to select leaf. This effect disappears when stems are taller and sparse because cattle can push them aside andprehend leaf.

Over a wide range of canopy types for two old world bluestem cultivars, organic matter intake and digestible organic matter intake were best explained by green leaf mass (Forbes and Coleman, 1993). Both responses increased with increasing leaf mass up to approximately 1 Mg ha^{-1} after which they leveled off or decreased. This was attributed to increased difficulty in prehending leaf within a canopy in which live stem mass was increasing at a faster rate than live leaf, thereby decreasing the availability of the preferred component (Forbes and Coleman, 1993).

Grazing behaviour and intake/animal performance

There are only a few observations in the literature regarding the relationship between grazing behaviour and long-term intake or performance on tropical pastures. In terms of daily gain, Chacon et al. (1978) reported that bite weight was positively correlated with liveweight gain

for setaria ($r=0.58$) and for digitgrass ($r=0.56$). For continuously stocked pastures of switchgrass, flaccidgrass, and bermudagrass, steer daily gains were related to masticate IVDMD ($r=0.92$; Burns et al., 1991).

Several authors have reported relationships between grazing time and intake or performance. In grazing trials in southern Brazil with *Panicum maximum* and *Brachiaria* spp., average daily gain of cattle was greater with shorter daily grazing times ($r = -0.52$ to -0.73 ; Euclides et al., 1991 and 2000). Dry matter intake of *Brachiaria* spp. was negatively related to daily grazing time ($r=-0.58$ to -0.79), likely because grazing time was greatest during the dry season when green herbage mass and bite weight were least (Euclides et al. 2000). Macoon (1999) in Florida, observed greater forage intake and milk production but shorter daily grazing time for cattle grazing rhizoma peanut compared to bermudagrass. He also observed that predominantly white- compared to black-coat cows grazed longer per day and had greater forage intake and milk production.

Non-Canopy Factors Affecting Grazing Behavior

Cosgrove (1997) suggests that for a given set of canopy conditions it may not be possible to predict short-term intake rate because of non-canopy related behavioral factors. Newman et al. (1994) stated before further research is conducted on the physical and morphological determinants of bite weight and intake rate, a better understanding is needed of other factors affecting grazing behavior. The following is a brief overview of non-canopy factors that may affect grazing behavior. More detailed reviews were provided by Cosgrove (1997) and Laca and Demment (1996).

Grazing environment

Environmental conditions influence grazing time in warm climates and may be the most important non-canopy factor affecting grazing behavior (Hancock, 1950). Macoon (1999) evaluated the effect of temperature and solar radiation on grazing time of lactating Holstein dairy cows during summer and winter at 30E north latitude in Florida. There were no effects of temperature or solar radiation in winter on grazing time. In summer, grazing time during the day (between morning and evening milkings) decreased linearly with increasing average solar radiation (Fig. 2). Grazing time at night (between the evening and morning milkings) increased linearly with increasing solar radiation during the day, but not enough to compensate for the loss during the day, so overall grazing time decreased (Fig. 2). Similar responses were observed for average temperature. Average summer daytime temperature and solar radiation explained 60 and 98%, respectively, of the variation in time spent under shade during the day. Multiple regression equations including both summer temperature and solar radiation explained 83% of the variation in grazing time during the day, 95% of the variation at night, and 99% of the variation in time spent under shade during the day.

Across a range of temperature and solar radiation conditions in Florida, lactating Holstein cows that were predominantly white had slightly longer grazing time during the day (13 min d^{-1}) than did predominantly black cows (Macoon, 1999). White cows also spent less time per day under shade (20 min).

Animal management

Fasting. Fasted animals have a greater rate of intake than non-fasted. Patterson et al. (1998) reported greater DM intake, biting rate, and intake per bite during 1-h grazing periods following fasting. Greenwood and Demment (1988) found that fasted cattle had a 27% greater rate of intake than non-fasted cattle, primarily due to faster rate of biting.

Group size. Sheep in groups of 1-2 were found to have shorter grazing time than those in groups of 3 or more (Penning et al., 1993). There were no differences in intra-meal intervals, prehension bites, or number of meals, but animals in small groups tended to have shorter meals.

Age. Grazing behaviour and intake on cocksfoot swards were compared for mature non-lactating Charolais cows, 18-mo-old heifers, and 7-mo-old calves (Cazcarra and Petit, 1995b). As herbage mass declined, biting rate and grazing time increased for all ages. Bite weight of calves decreased more than older cattle as sward height decreased, which led calves to graze longer.

Previous treatment. Charolais heifers overwintered at a lower feeding level (daily gain of 0.31 compared to 0.70 kg d⁻¹ for the higher level) had a lower bite weight, equal bite rate, longer grazing time, and greater spring daily gains than those overwintered at a higher level (Cazcarra and Petit, 1995a). The authors suggested that longer grazing time may, in part, explain the compensatory gain observed for those overwintered at the lower feeding level.

Recent diet. Parsons et al. (1994) observed that ewes recently grazing monocultures of temperate forages showed short-term preference for another species. Over a period of 6 d they reverted back to a preference for their background diet. The results provide evidence of partial and changing preference by sheep, and the authors urge caution in inferring long-term grazing behaviour from short-term tests.

Distance to water. Water was positioned at one end of pastures that were 24 ha and rotationally stocked or 24 and 207 ha and continuously stocked (Hart et al., 1993). Forage utilization declined with increasing distance from water on the large but not the small pastures. Grazing time decreased linearly with increasing distance from water on the 207-ha pasture, resulting in over-utilization of areas close to water and lower animal performance than on small pastures.

Summary and Conclusions

Sward canopy attributes

The data indicate that total bulk density of C₄ grass canopies occurs within the range seen for temperate species, although in some cases near the low end of that range. Likewise, tiller density of C₄ grasses may or may not be lower than that of temperate species depending on genotype and defoliation management. In some cases, defoliation management has a greater impact on canopy bulk density and tiller density than genotype. Total and leaf bulk density of the grazed horizon of tropical pastures are often lower than in temperate pastures. This can be a function of the greater height attained by most tropical grasses and the fact that flowering response of many of these species is insensitive to daylength. As a result, flowering culms are a significant part of the canopy throughout much of the year.

Large vertical heterogeneity in bulk density, leaf percentage, and nutritive value are

characteristic of many C₄ grass canopies. Thus, sampling canopies in vertical strata may be more important in tropical than in temperate grass pastures because the latter are characterized by less variation from the top to bottom of the canopy. Measuring the density, plant-part composition, and nutritive value of upper canopy strata of C₄ grasses is often quite valuable in interpreting ingestive behaviour and animal performance responses.

Sward canopy effects on ingestive behaviour

The component of ingestive behaviour most closely related to short-term intake rate is bite weight. In temperate swards, bite weight is primarily a function of canopy height. There may be a positive relationship of canopy height and canopy leaf bulk density with bite weight for C₄ grass pastures, but these traits are not of primary importance. Most studies have identified leaf percentage, leaf mass, or green herbage mass, particularly of the upper strata of the canopy, as having the greatest influence on bite weight. Burns et al. (1991) showed that perhaps more important than leaf bulk density or leaf percentage are the manner in which the leaf is presented to the animal and the degree to which it can be prehended separate from stem and dead material of lower digestibility.

Plant-animal interface research in warm climates

It seems appropriate to consider whether detailed studies of pasture canopies and grazing behaviour merit greater priority in subtropical and tropical pasture research programs. For those primarily servicing the traditional agricultural community, there are few research programs in warm climates having the budget or facilities to engage in detailed canopy characterization and comprehensive measures of ingestive behaviour and diet selection. Considering the needs of the end users, it is appropriate to ask under what conditions should such research be undertaken if it can be funded. Because of the diversity of systems based on C₄ species and the cost of conducting studies, this research approach must be targeted carefully to those species and management practices that apply most widely and to situations where there is a specific production problem that can be addressed by understanding detailed canopy-animal interactions.

Yet it remains that within the basic components of pasture canopies resides the potential to improve their characteristics to favor efficient defoliation by the grazing animal. This helps to assure a potential maximum bite weight of highest nutritive value for each of a finite number of bites consumed each day. The pasture canopy that offers easy access to an abundance of the most preferred and nutritious component, the leaf, favors maximum daily digestible dry matter intake. The engineering of grazing-friendly canopy structures, which would include a high proportion of the desired canopy component, has never been more feasible. The recent development and acceptance of near-infrared spectroscopy used in combination with the emerging application of genomics procedures offer potential to appreciably alter the canopy of existing, well-adapted pasture species. To this extent, plant-animal interface research has a justifiable and strong purpose. The animal industries that have a high dependency on pasture lands need to recognize this potential and provide sustained funding to encourage research in this area.

Beyond their importance to graziers, grasslands are now being recognized as valuable sources of green space, wildlife habitat, wetlands, and ground water recharge, attributes which impact all of society. Within that sphere, there may be opportunities to address detailed plant-herbivore interactions, but for reasons other than increased intake and animal performance of

domestic livestock. Research may identify practices that allow the grassland resource to be better sustained, that provide conditions favoring desired wildlife species, and that minimize potential for negative impacts on water quality.

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Table 1 - Species or mixture effects on canopy height, total herbage mass, total bulk density (BD), leaf proportion, and leaf BD of C₄ grass-based swards.

Forage	Canopy height (cm)	Herbage mass (t ha ⁻¹)	Total BD (kg ha ⁻¹ cm ⁻¹)	Leaf %	Leaf BD (kg ha ⁻¹ cm ⁻¹)
<i>Setaria sphacelata</i> ⁺	13	2.1	162	34	55
<i>Pennisetum polystachyon</i> - <i>Desmodium heterphyllum</i> - <i>Macroptilium atropurpureum</i> [‡]	4-105	1.1-8.8	84-268	22-84	18-225
<i>Setaria sphacelata</i> [']	19	2.1	109	71	75
<i>Digitaria eriantha</i> [']	16	4.0	250	31	77
<i>Hemarthria altissima</i> - <i>Aeschynomene americana</i> ^{&}	18-94	2.5-11.6	71-214	NA	NA
<i>Hemarthria altissima</i> [#]	38	6.8	178	17	30
<i>Cynodon dactylon</i> ⁺⁺	7	1.9	273	37	101
<i>Panicum virgatum</i> ⁺⁺	13	1.6	126	29	37
<i>Pennisetum flaccidum</i> ⁺⁺	13	2.0	154	33	51
<i>Bothriochloa caucasica</i> ^{††}	5-44	1.0-7.6	140-400	10-36	20-90
<i>Bothriochloa ischaemum</i> ^{††}	5-36	1.2-4.8	130-360	6-45	10-110
<i>Cynodon sp.</i> ^{''}	5-20	3.0-7.4	370-610	15-19	65-105

⁺ Chacon and Stobbs (1976); staged setaria Kazungulu to 6 cm in spring; 50 kg N ha⁻¹; live herbage

[‡] Partridge (1979); mission grass-hetero-Siratro mixtures were continuously stocked across a range of stocking rates

['] Ludlow et al. (1982); staged setaria cv. Kazungulu and digitgrass cv. Pangola to 5 cm in winter; 50 kg N ha⁻¹; 9-wk regrowth sampled to ground level

[&] Moore et al. (1987); 24 Floralta limpoglass-common aeschynomene pastures representing a range of attributes; 5-wk rest period, rotational stocking; sampled to ground level

[#] Holderbaum et al. (1992); Floralta limpoglass, rotationally stocked to leave a 20-cm stubble; sampled to 5 cm

⁺⁺ Fisher et al. (1991); bermudagrass cv. Coastal, switchgrass cv. Kanlow, flaccidgrass cv. Carostan; early summer sampling; continuously stocked pastures grazed to similar herbage mass; sampled to 4 cm

^{††} Forbes and Coleman (1993); old world bluestem cv. Caucasian and old world bluestem cv. Plains, multiple sampling dates for a wide range of pastures

^{''} Carnevalli et al. (1999); bermudagrass cv. Tifton 85, continuously stocked, sampled to ground level

Table 2 - Bulk density (BD), crude protein (CP), and in vitro organic matter disappearance (IVOMD) of herbage in the top and bottom halves (by depth) of rotationally stocked (5-wk rest period) limpgrass cv. Floralta swards. Data are adapted from Holderbaum et al. (1992).

Canopy characteristic	Upper half	Lower half
Total BD (kg ha ⁻¹ cm ⁻¹)	100	256
Leaf BD (kg ha ⁻¹ cm ⁻¹)	36	25
Stem BD (kg ha ⁻¹ cm ⁻¹)	74	222
Leaf percentage	33	10
Total CP (g kg ⁻¹ DM)	68	39
Leaf CP (g kg ⁻¹ DM)	107	91
Stem CP (g kg ⁻¹ DM)	47	33
IVOMD (g kg ⁻¹ OM)	577	530
Leaf IVOMD (g kg ⁻¹ OM)	547	539
Stem IVOMD (g kg ⁻¹ OM)	594	529
Total IVDOM:CP ratio	8.5	13.6

Table 3 - Leaf, stem and total herbage (includes dead material) in vitro dry matter disappearance for the top and bottom 5-cm stratum of continuously stocked flaccidgrass, gamagrass, and bermudagrass pastures. Data are from Burns et al. (1992).

Forage	Leaf	Stem	Total
	g kg ⁻¹ dry matter		
Flaccidgrass			
Top	677	646	662
Bottom	665	561	489
Gamagrass			
Top	638	567	629
Bottom	645	639	542
Bermudagrass			
Top	651	620	609
Bottom	599	553	493

Figure 1

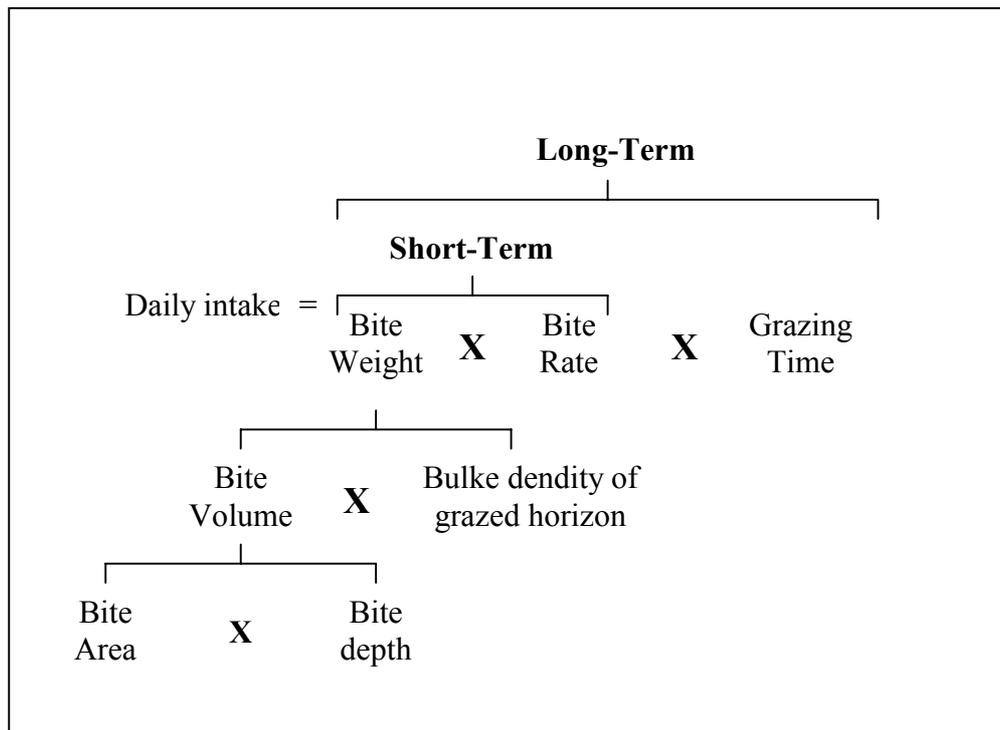
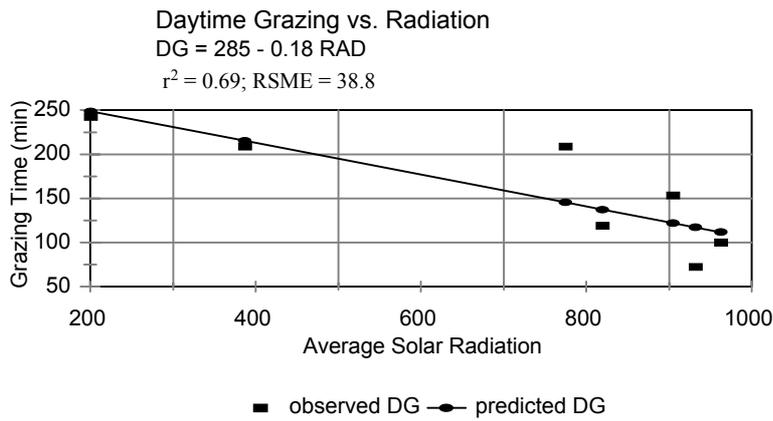
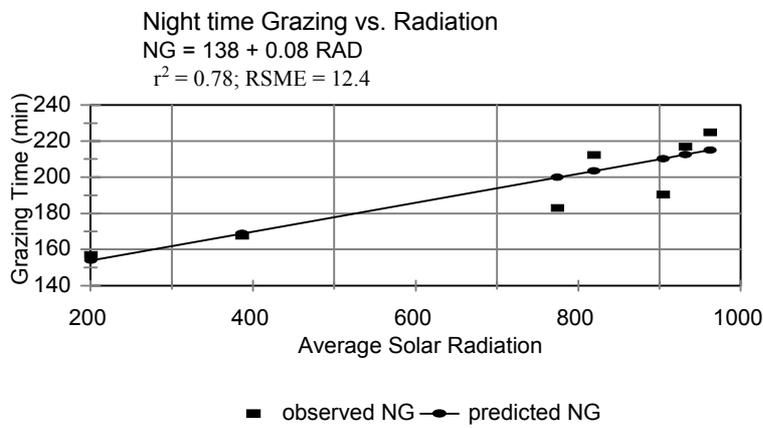


Figure 1. Components of daily herbage intake (adapted from Gordon and Lascano, 1993).

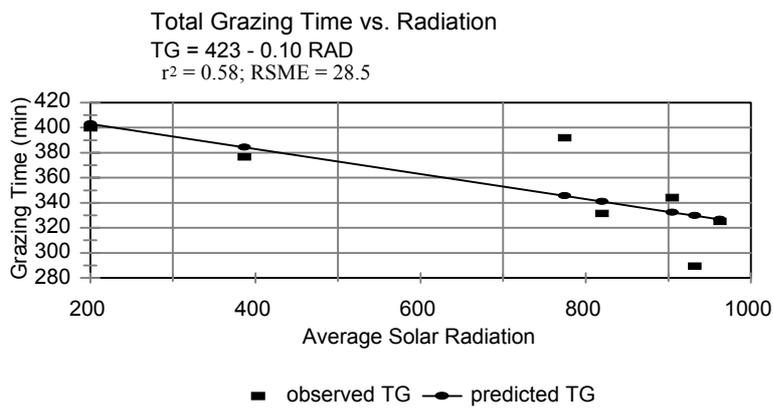
Figure 2



(a)



(b)



(c)

Figure 2. Average solar radiation intensity (RAD; $\mu\text{mol m}^{-2} \text{s}^{-1}$) effects on grazing time during the day (DG; a), grazing time at night (NG; b), and total grazing time (TG; c) of lactating dairy cows during summer in Florida, USA.