
26 Pasture Characteristics and Animal Performance

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Introduction

Forages are extensively used to feed domesticated farm animals, notably cattle and sheep, and comprise a wide variety of plant species. They are predominantly grasses or legumes and can either be fed fresh or conserved. When fed fresh, the harvesting is usually left to the animal. Conserved forages vary from wet silage, through various degrees of wilting to hay.

The bulk component of forages is β -linked polysaccharides. Other components in forages include proteins, soluble sugars, lipids, minerals and vitamins. The β -linkages in the structural carbohydrates cannot be normally split by the hydrolytic enzymes inherently present in the digestive tract of animals. Due to a highly adapted digestive system, with holding and mixing compartments that slow down passage of the feed and accommodate dense populations of microbes, ruminants can use microbes for the breakdown of the structural carbohydrates. Hence, extraction and utilization of nutrients from forages by ruminants uses a three-way interaction between the herbivore, the plant and the microbial population. Important aspects of this interaction are characteristics of the forage and ingestive behaviour of the animal. Success depends on the extent to which this combination can accommodate the microbial population, such that it executes a maximum of activity and provides its host with sufficient quantities of the required nutrients in microbial biomass or in its waste products, the volatile fatty acids (VFA).

This chapter focuses on the utilization of nutrients by farm animals present in forages and the role played by botanical, physical and chemical characteristics of the forage on the one hand and ingestive and digestive behaviour of the animal on the other. Most emphasis will be on freshly fed forages harvested by the animal itself.

Chemical and Biochemical Properties of Forages

The nutritive value of animal feeds is derived from the combination of chemical constituents and their digestibility, in ruminant nutrition often expressed as digestible organic matter and organic matter digestibility (OMD). The OM in forages can be divided, based on its extraction properties, into neutral (ND) and acid detergent (AD) soluble OM. The extraction with ND results in a residue (NDR) not extractable with ND, and the extractable cell contents (NDS). The NDR contains structural carbohydrates (NDF), a small fraction of inorganic matter and some N (NDIN), largely consisting of the protein extensin. The main cell wall polysaccharides are pectic substances, extractable with ND but not with AD (Van Soest, 1994); hemicellulose, extractable with AD; cellulose, extractable with sulphuric acid or with permanganate; and a remaining lignin fraction, a condensed form of phenolics. In some legume species appreciable amounts of other phenolic compounds known as condensed tannins (CT) may occur, which can be further divided into extractable CT, protein-bound CT and fibre-bound CT (Barry and McNabb, 1999). The NDF content of forages ranges between less than 300 and over 750 g/kg DM and is primarily influenced by stage of maturity, whereas the degree of lignification is also influenced by climate, particularly temperature (Van Soest, 1994).

The NDS contain proteins, non-protein N, non-structural carbohydrates, lipids and electrolytes. Between 80% and 90% of the crude protein (CP) in forages is present in the cell contents, while the remaining 10–20% is bound to the cell walls. Of the CP, 25–30% is non-protein N (NPN), a large proportion of which is nitrate. True protein in cell content is usually divided into fraction 1 protein, fraction 2 protein and chloroplast membranes. A major part of fraction 1 is the enzyme complex ribulose-1,5-bisphosphate carboxylase (Rubisco), responsible for the fixation of CO₂. Rubisco comprises some 40% of total leaf protein (Mangan, 1982) and is located in the chloroplasts. The proteins in fraction 2 form about 25% of the total CP and include a wide array of enzymes. The remaining proteins in the cell contents are chloroplast membrane proteins and in ryegrass form 4–5% of the total CP (Boudon and Peyraud, 2001).

The remaining cell contents are soluble sugars (SC), lipids and electrolytes. Sugar content ranges between 100 and 200 g/kg DM, and is usually inversely related to the crude protein content and in grasses is about equally distributed between free sugars and fructosans, the solubility of which depends on their chain length. Their degree of polymerization is usually between 40 and 160 fructose units (Boudon and Peyraud, 2001). The pool of SC is fed by photosynthesis and depleted by oxidation to yield energy for synthetic processes and to provide precursors for these synthetic processes. Photosynthesis depends on light intensity and during daytime, particularly during sunny days, the pool of soluble sugars shows a net growth, whereas during the night, cloudy days or in shade, the pool remains low or even decreases (Parsons and Chapman, 2000). Hence, the SC content changes in the course of the day and is usually highest in the late afternoon and early evening (Van Vuuren *et al.*, 1986). Lipids are usually between 2% and 5% and are primarily present in membranes of the

chloroplasts and in the cover of the cuticular layer. In temperate grasses lipids are extremely rich in linolenic acid.

Grazing Behaviour and Grazing Management

The inter-relationship between pasture and the grazing ruminant is a dynamic, two-way process. As quantitative, qualitative and morphological aspects of the different plant species present in pastures influence the plant material ingested by the grazing animal, that process in turn modifies the plants remaining and their subsequent production and fate. Although differences between forage species, various organs within the plant and changes over the day and throughout their life span affect the dynamics of their digestion, it is aspects of their physical presentation within the sward that largely determine the quantity, quality and temporal pattern of ingested material.

Effects of forage characteristics

The simple model adopted by Allden and Whittaker (1970), in which daily intake was considered as the product of grazing time and intake rate (IR, DM g/min), the latter being the product of bite mass and bite rate, has formed the basis of much research over the intervening decades. Because of the widespread use of intensively managed, temperate, single-species swards or mixed grass/clover swards, much of the research has been within these contexts, although there have been notable exceptions such as that conducted by Stobbs (1973) and Chacon and Stobbs (1977) on tropical pastures. Where mixed-species swards have been investigated, these have mainly been simple two-species mixtures of perennial ryegrass and white clover, rather than more complex multispecies swards. Nevertheless, such work has allowed elucidation of many of the fundamental relationships between sward state and the ingestive processes.

Black and Kenney (1984), using artificially constructed swards grazed by sheep, showed that the relationships between sward height and bite mass, bite rate and IR were modified by tiller density (plants/m²). Such a modifying effect is not surprising since intake per bite (bite mass, g DM per bite) derives from bite volume (i.e. the effective sward volume removed in a single biting action) and the bulk density of the herbage in that volume (Hodgson, 1985). Furthermore, if idealized as rectangular or cylindrical, bite volume may be defined as the product of bite area and bite depth (Milne 1991; Parsons *et al.*, 1994b). Subsequently, Laca *et al.* (1992), using similarly constructed swards offered to beef cattle, were able to demonstrate that height and bulk density are the most important sward features determining bite depth and bite area on green and leafy vegetative swards. Such artificial swards, whilst time-consuming in their construction, have proved invaluable in providing a means of manipulating sward structure and developing conceptual models of the grazing process. However, such artificial swards avoid the possible modification of bite dimensions associated with accumulated plant material in the base of natural

pastures. Thus, we should not be surprised if the precise values obtained under such contrasting scenarios differ.

Various parameters have been used to describe sward state under field conditions, including total herbage mass, green leaf mass (DM, kg/ha) and sward surface height (SSH, cm). Comparing continuous and rotational stocking management systems, Penning *et al.* (1994) showed that green leaf mass or leaf area index, rather than SSH, were a better basis for relating intake and sward state where the ratio of leaf to stem was changing rapidly. Orr *et al.* (1997) have shown both green leaf mass and SSH to be significantly correlated with bite mass ($r = 0.71$ and $r = 0.78$, respectively) and with IR ($r = 0.81$ and $r = 0.78$, respectively). However, since SSH is a principal determinant of bite mass (e.g. McGilloway *et al.*, 1999) and can be more easily determined than green leaf mass, it has received considerable attention and proved to be a useful descriptor of sward state for research purposes (e.g. Hutchings *et al.*, 1992) and in formulating grazing management guidelines (e.g. Mayne, 1991).

Generally, a curvilinear relationship has been shown between SSH and bite mass in sheep (Penning *et al.*, 1991a) and cattle (Gibb *et al.* 1996), with successively smaller increments in bite mass being achieved for each increment in SSH. However, as would be expected from research with sward boards, the precise relationship is sensitive to changes in sward density (Mayne *et al.*, 2000). Such studies have also demonstrated that as bite mass increases, bite rate declines due to a reduction in the proportion of total grazing jaw movements represented by bites, rather than to an increase in the time taken to complete a bite (Penning *et al.*, 1998). The net outcome, however, is a curvilinear relationship between SSH and IR.

Legumes vs. grasses

Non-lactating (dry) (Penning *et al.*, 1991b; Orr *et al.*, 1996a) and lactating (Penning *et al.*, 1995a) ewes take greater bite masses when grazing white clover swards compared with ryegrass swards at the same height. This is accomplished, despite the lower bulk density of herbage within the grazed horizon on the clover, by the ewes having a larger bite area, but of the same depth, compared with that when grazing grass (Edwards, 1994, 1995). Sheep are able to collect herbage from an area larger than their open mouth area, by using their lips to gather material into their mouth before biting it from the sward and Edwards (1994) suggests that this is more easily achieved on clover than grass. However, although the time taken to execute a bite does not differ between clover and ryegrass, fewer non-biting grazing jaw movements are required per unit bite mass of DM on clover (Penning *et al.*, 1995a). Because a large proportion (>50%) of grazing jaw movements by sheep may be non-biting (i.e. manipulative or masticative), they are able to achieve a significant increase in IR on clover compared with ryegrass (Penning *et al.*, 1995a).

In contrast, heifers have similar bite masses on clover as on grass swards (Orr *et al.*, 1996b) and, because a much lower proportion of grazing jaw movements are non-biting movements, any reduction in handling cost on clover has little impact on bite rate (Penning *et al.*, 1998). As a consequence, IR by cattle does not differ significantly between clover and grass swards.

Penning *et al.* (1991b) found that on white clover swards, dry ewes had more meals but of shorter duration and that the total time spent grazing was 165 min/day less than those grazing ryegrass. As a result, daily intakes were the same, although ruminating time on the clover was significantly lower than on the grass swards (100 vs. 259 min/day). Similar results were reported by Rutter *et al.* (2002), where heifers grazed for 100 min/day longer on grass and, although achieving higher daily DM intakes, had similar digestible OM intakes and live-weight gains compared with those on clover swards. Ruminating time was also significantly reduced on the clover (267 vs. 526 min/day) compared with grass swards.

Animals with a higher nutritional demand may, however, benefit from grazing clover. Lactating ewes take advantage of the higher intake rates and low ruminating requirement on clover and extend their grazing time to achieve higher daily DM intakes (0.5 kg) than on grass (Penning *et al.*, 1995a).

Effect of grazing management

The effect of contrasting grazing management systems, such as continuous variable stocking or rotational stocking, on forage production is outside the scope of this chapter. Parsons and Chapman (2000) argue that such differences in management are more imagined than real and that either management system imposes on the individual plant a succession of discrete defoliations, separated by variable periods of uninterrupted growth. However, the physical structure and its rate of change in swards presented to grazing animals under the two systems does affect their grazing behaviour. Under field conditions, irrespective of whether swards are managed under continuous variable stocking or rotational stocking, considerable vertical, horizontal and temporal variability in structure exists.

Continuous variable stocking management

In temperate pastures, under continuous variable stocking management, swards are maintained short, compared with those presented to the grazing animal under rotational stocking, and are kept within a relatively narrow range of SSH (e.g. 4 to 6 cm for sheep and 5 to 8 cm for cattle). Because such sward heights constrain bite mass and consequently IR, sheep and cattle will attempt to compensate by increasing their grazing times (13 and 10.5 h/day, respectively). Although the levels of intake will invariably be below those achievable on taller swards following a period of regrowth under rotational management, the ingested herbage is mainly young leaf material with a high nitrogen content (>3.5% in DM; Penning *et al.*, 1995a; Gibb *et al.*, 2002). Nevertheless, daily intakes cannot match those achievable on tall swards when herbage allowance is not limiting. By keeping SSH more or less constant, herbage production is approximately equal to the herbage consumed, and sward state changes little over the course of the day or from day to day. In this situation, changes in grazing behaviour over the same timescale are relatively minor. Nevertheless, despite the relative constancy in sward structure over the day, similar diurnal

patterns in bite mass, bite rate and IR have been shown by sheep (Orr *et al.*, 1996a) and dairy cows (Gibb *et al.*, 1998) grazing ryegrass swards, where the highest IR (DM, g/min) and bite mass (DM, g/bite) occur in the late afternoon or evening.

Even when maintained with a narrow range of SSH, such swards are generally characterized by a degree of spatial heterogeneity, with a varying proportion of the total area being represented by infrequently grazed patches (Gibb and Ridout, 1986, 1988). In such a grazing environment animals are confronted with a heterogeneous resource from which to select their diet, and the SSH of the frequently grazed areas will be lower than the overall mean SSH of the pasture (Gibb *et al.*, 1999).

Rotational stocking management

Under rotational stocking management the morphology of a grass sward is altered by successive defoliations over the same area over a matter of hours or days, depending upon the grazing pressure applied. This modification of the sward has important consequences for both quantitative and qualitative aspects of herbage ingestion. Firstly, with each successive defoliation of an area the bulk density (kg/ha/cm) of the grazed horizon in the sward increases (Wade *et al.*, 1989), but the reduction in SSH constrains bite depth, to the extent that bite mass and IR are reduced (McGilloway *et al.*, 1999). When sward depletion takes place over several days, inevitably, daily intake progressively declines (Wade *et al.*, 1989). Secondly, as the animal grazes progressively down through the sward, the proportion of lamina material in what is consumed declines and the proportion of pseudostem and senescent material increases, leading to a decline in the digestibility (*in vitro*) of the herbage ingested (Penning *et al.*, 1994). Even when the digestibility of the pseudostem is high, its increasing proportion in the diet may reduce the rate of passage of digesta and limit daily intake (Laredo and Minson, 1973). Although Illius *et al.* (1995) calculated that the majority of energy expended during grazing was in chewing the ingested vegetation, rather than removing plant tissue from the sward, they found that goats would not graze into the pseudostem horizon because of the much increased bite force this would have required. However, they suggested that larger animals would be less constrained by the physical properties of the vegetation than small animals and could, therefore, graze closer to the ground.

The advantage in practice is that rotational stocking management allows a more direct and immediate control of herbage intake by animals, particularly where they are present on paddocks for a period of 1 or 2 days. Daily herbage allowance (DM or OM g/kg live weight) can be regulated by altering the area of the paddock, depending upon herbage mass (DM or OM/ha) and live weight or number of animals. The effect of herbage allowance on daily intake have been demonstrated with dairy cows (e.g. Peyraud *et al.* 1996), calves (Jamieson and Hodgson, 1979), ewes (Gibb and Treacher, 1978) and lambs (Gibb and Treacher, 1976). Although such relationships will be modified to an extent by sward mass (Peyraud *et al.*, 1996), what they have all shown is, to achieve maximum daily intake at pasture, herbage allowance must be equivalent to three to four times daily intake.

Temporal pattern of grazing

The basic temporal pattern of grazing meals, unmodified by depletion of the herbage resource, is demonstrated under continuous variable stocking management. Although animals may increase total grazing time in attempting to compensate for constraints on IR, an underlying pattern of grazing meals is discernible. In temperate climates, this basic pattern is typically of three, possibly four, major periods of grazing activity through the day (Gibb *et al.*, 1997), although the precise timing of the meals will be modified, depending upon events such as removal for milking and times of sunrise and sunset. Similar temporal patterns of grazing meals have been demonstrated with sheep (Penning *et al.*, 1991b).

Daily paddock management

Modifications of this basic temporal pattern are demonstrated under daily paddock stocking management, depending upon the time of introduction to the area of fresh herbage. Orr *et al.* (2001) found that dairy cows provided with equal daily herbage allowances, following either morning milking or afternoon milking, spent the same total time grazing per day but showed different temporal patterns of grazing meals. Cows receiving their fresh allowance in the afternoon, however, spent a greater proportion of their total grazing activity during the late afternoon and evening period, when the sugar content of the grass and short-term intake rate (g DM/min) were higher. As a consequence, they achieved a significantly greater milk yield compared with cows offered the same herbage allowance in the morning.

Restricted access for grazing

Grazing behaviour of dairy cows can be manipulated by time and allocation of the grazing session. Soca *et al.* (1999) showed that, compared with cows given access to pasture for 8 h/day commencing at 06:00 h, cows given access for only 6 h/day commencing at 12:00 h had a longer initial grazing meal (120 vs. 82 min) and were more likely to be found grazing during the first 4 h at pasture (81% vs. 54%), although ruminating and resting time were less. A higher intake rate in the animals that started the grazing session later in the day may be seen as a strategy to optimize intake pattern to adapt to the changes in pasture DM and SC contents (Gibb *et al.*, 1998; Van Vuuren *et al.*, 1986). The incorporation of short-term fasting in grazing and feeding management strategies for cattle has been recently reviewed by Chilbroste *et al.* (2004).

Effect of animal factors on bite mass and intake rate

Size and physiological condition of the animal. Although sward state largely constrains bite mass and IR, Penning *et al.* (1991b) found that larger animals were able to meet their greater maintenance requirements by achieving a greater bite mass, and that bite mass was related to live weight, increasing by 0.66 mg/kg live weight. Although this relationship was independent of incisor arcade width, undoubtedly arcade width and conformation have an effect on bite mass (Gordon *et al.*, 1996). Examining the effect of physiological state,

Penning *et al.* (1995a) found that lactating ewes had a greater bite mass (83 vs. 61 mg DM) and higher IR (4.5 vs. 4.1 g DM/min) than dry ewes, when grazing grass swards of 7 cm. At the same SSH, Gibb *et al.* (1999) recorded higher intake rates by lactating dairy cows than dry cows (23.5 vs. 19.8 g OM/min). Nevertheless, the major means by which ruminants respond to increased nutritional demands is to increase grazing time. For example, Penning *et al.* (1995a) recorded lactating and dry ewes grazing for 582 and 478 min/day, respectively, and Gibb *et al.* (1999) recorded lactating and dry cows grazing for 583 and 451 min/day, respectively, on 7 cm SSH grass swards. Such increases in grazing time may, however, reduce ruminative efficiency by reducing ruminating time per unit of intake (Gibb *et al.*, 1999).

Fasting. Prior fasting increases bite mass by cattle grazing grass (Chacon and Stobbs, 1977; Patterson *et al.*, 1998) and legume swards (Dougherty *et al.*, 1989) and by goats (Illius *et al.* 1995). Likewise, fasting increases IR by sheep grazing grass (Allden and Whittaker, 1970) and legume swards (Newman *et al.*, 1994). The duration of such effects appear to be greater, the longer the period of fasting (Patterson *et al.*, 1998), and fasts of 24 h have affected subsequent meal duration (Newman *et al.*, 1994).

Social structure. There is little evidence to distinguish between the effects of experience or social dominance and size on grazing behaviour. However, examination of the data of Peyraud *et al.* (1996) shows that when forced to compete at restrictive daily herbage allowances in mixed groups, heifers were unable to achieve the same daily intake of herbage as cows, even when expressed relative to their live weight. Only at a relatively high allowance, equivalent to about 80 g OM per kg live weight/day, were intakes similar for heifers and cows. There is evidence from observations with sheep (Penning *et al.*, 1993) and cattle (Rind and Phillips, 1999) that group size can affect social behaviour, grazing time and daily intake possibly due to the requirement for increased vigilance by individuals in small groups.

Environmental factors

Pasture heterogeneity and dietary preference. Grazed swards frequently exhibit heterogeneity in height, morphological and physiological state, and species composition, due to modification of the sward by the presence of grazing animals and, particularly in the case of mixed swards, competition between the different plant species for nutrient resources (Schwinning and Parsons, 1996). Presented with such heterogeneity, grazing animals rarely forage in a non-selective manner, so that the relative proportion of different plant species or plant parts may not reflect their present relative abundance within a sward. Within temperate mixed perennial ryegrass/white clover swards mean partial preferences for clover of about 70% have been demonstrated for sheep (Parsons *et al.*, 1994a; Harvey *et al.*, 2000), heifers (Penning *et al.*, 1995b) and dairy cows (Rutter *et al.*, 1998), although a lower partial preference of 52% has been shown in goats (Penning *et al.*, 1997). Such differences in preference between grazing species not only influence the diet selected, but

ultimately alter sward composition (Penning *et al.*, 1996) and small differences in management, e.g. grazing severity, can affect relative abundance of the different species in the sward (Gibb *et al.*, 1989). However, it must not be assumed that such preferences are constant, either within animal species or in alternative grass/legume mixtures (Norton *et al.*, 1990). Preference may be affected by the height of the different sward components (Harvey *et al.*, 2000), fasting (Newman *et al.*, 1994), previous dietary experience (Newman *et al.*, 1992; Parsons *et al.*, 1994a) and time of day (Newman *et al.*, 1994; Parsons *et al.*, 1994a; Harvey *et al.*, 2000; Rutter *et al.*, 1998).

Forage Ingestion

Feed intake and its regulation, size reduction and passage of feed particles are the subject of Chapters 5 and 23 and here discussion is restricted to aspects specific to forages under grazing conditions. These include aspects of the holding capacity of the rumen, the chewing efficiency as related to particle size reduction and the resulting passage of forage particles.

Holding capacity in the rumen (packing density)

In forage-fed ruminants, the holding capacity of the rumen has long been considered as a constraint to dry matter intake (DMI) (Conrad, 1966). Although this hypothesis has been challenged (Grovm, 1987; Ketelaars and Tolkamp, 1991), rumen fill as constraint to DMI still receives attention (Dado and Allen, 1995).

The first problem to be addressed in assessing the importance of rumen fill as a constraint on DMI is to specify which fraction, if any, properly represents rumen fill. For daily DMI regulation, NDF in the feed has been suggested as the best predictor of rumen fill (Mertens, 1987). Van Soest *et al.* (1991) established that NDF is more closely related to the daily ruminating time, rumen fill and DMI, than other chemical fractions like crude fibre and acid detergent lignin (ADL). Nevertheless when balloons are introduced in the rumen, DM rumen pool has normally been chosen as an indicator of rumen fill (Faverdin *et al.*, 1995). In detailed studies of digestion and particle breakdown kinetics (Bosch, 1991; Van Vuuren, 1993), total rumen content as well as its chemical components have been considered. Table 26.1 shows the positive correlation between total, DM, N, NDF and ADL rumen pool sizes, as observed in grazing lactating dairy cows (Chilibroste, 1999).

For DMI and other animal performance constraints, research has focused primarily on stall-fed animals with conserved forages (either silage or hay) as the fibre source. Less information is available for fresh forages (e.g. Waghorn *et al.*, 1989) and particularly for grazing animals (Chilibroste, 1999). Figure 26.1 shows the relative weights of total, DM and NDF rumen pools measured after the first grazing bout in dairy cows when grazing ryegrass (Chilibroste, 1999) or when fed cut, fresh or wilted lucerne (Danelón *et al.*, 2002), cut ryegrass (Van

Table 26.1. Correlation between rumen pool sizes after grazing for three experiments ($n = 52$) (Chilibröste, 1999).

	DM (kg)	NDF (kg)	ADL (kg)	N (kg)
Total (kg)	0.92***	0.91***	0.81***	0.77***
DM (kg)		0.95***	0.90***	0.88***
NDF (kg)			0.83***	0.71***
ADL (kg)				0.87***

*** $P < 0.01$.

Vuuren *et al.*, 1992), grass silage of different maturity (Bosch *et al.*, 1992), a mixture (50:50) of grass and maize silage plus concentrate (de Visser *et al.*, 1992) or lucerne hay (Hartnell and Satter, 1979). The DM rumen pools after grazing are higher than those observed by Van Vuuren *et al.* (1992) in dairy cows fed fresh ryegrass indoors. They are similar to the figures reported by Waghorn *et al.* (1989) for fresh lucerne and ryegrass, but higher than those found by Danelón *et al.* (2002) for dry cows grazing lucerne, either directly or following cutting and wilting. All observed DM rumen pools are smaller than those reported for diets with high proportions (>40%) of concentrates (Bosch *et al.*, 1992; Dado and Allen, 1995; De Visser *et al.*, 1992; Shaver *et al.*, 1986; 1988). The differences are larger when expressed as DM than NDF rumen pool sizes (Fig. 26.1).

When eating fresh grass cows did not show evidence of having problems to accommodate large volumes of material in the rumen but they failed to pack it properly. The relative differences between plots (a) and (b) of Fig. 26.1 are mediated by the DM percentage of the rumen pool (DMP). Figure 26.2 shows the relationship between DMP and DM rumen pool in the grazing experiments reported by Chilibröste (1999). The model derived from it reaches an asymptote at a DMP of 12%, which means that when a certain DMP threshold is reached, the only alternative for a cow to increase its DM rumen pool is by increasing its volume. No doubt the low DMP of the fresh forages plays an important role in the low-rumen DMP and rumen fill observed. For instance Danelón *et al.* (2002) reported values for total and DM rumen pool of 69.9 and 6.4 g/kg LW for cows grazing strips of fresh lucerne (DM 20.8%) while the values for swath grazing (DM 41.6%), were 88.3 and 9.8 g/kg LW. A close relationship between non-DM grass intake (29.1 ± 10.9 L) and changes in non-DM rumen pool sizes (26.2 ± 12.6 L) has been reported (Waghorn, 1986; Chilibröste *et al.*, 1997, 1998). As DMC of forage increases less herbage manipulation is required, due to a greater fragmentation during chewing and rumination. Because cows are able to reduce chewing during eating to increase intake rate (Parsons *et al.*, 1994b; Laca *et al.*, 1994), especially after a period of fasting, chewing efficiency during grazing seems more influenced by the rate of eating than by the type of feed.

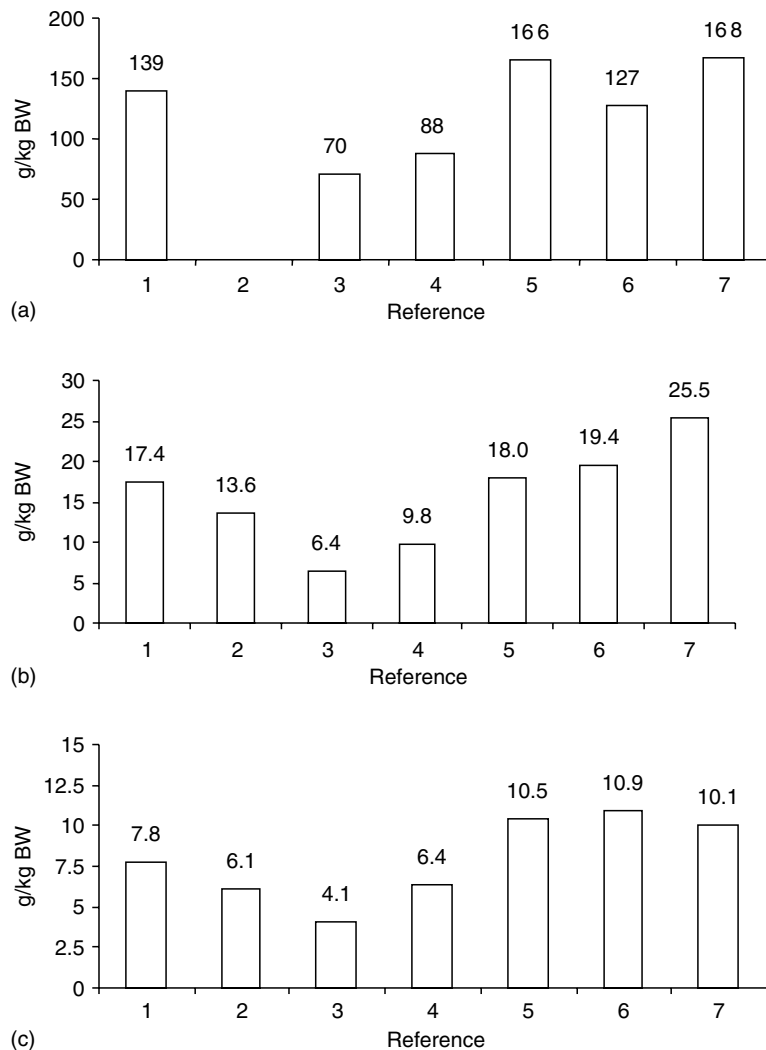


Fig. 26.1. Total (a), DM (b) and NDF (c) rumen pool sizes (g/kg LW). References: 1, Chilibroste (1999) ($n=28$); 2, estimated from Van Vuuren *et al.* (1991); 3 and 4, adapted from Danelón *et al.* (2002); 5, adapted from Bosch *et al.* (1992); 6, adapted from de Visser *et al.* (1992); 7, adapted from Hartnell and Satter (1979).

Particle size reduction

Chewing during eating serves three functions: long forages are reduced to a size small enough to be incorporated in a bolus and swallowed; soluble nutrients are released for fermentation; and the inner structure is damaged, enabling microbes to invade (Ulyatt *et al.* 1986). Many investigations have focused on understanding chewing efficiency during eating and rumination (Ulyatt *et al.*, 1986; Boudon and Peyraud, 2001). However, due to the different methodologies

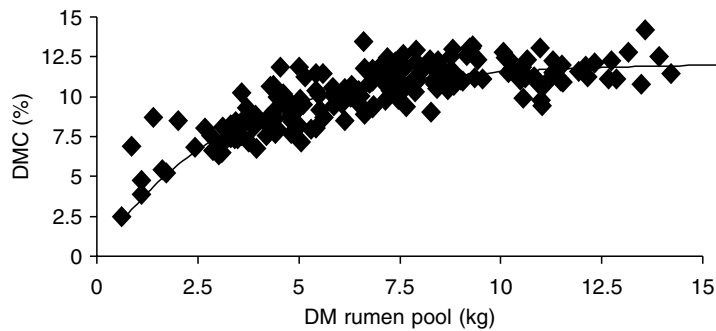


Fig. 26.2. Observed (symbols) and predicted (solid line) DM content (DMC, %) in the DM rumen pool (DMRP, kg) (Chilibröste, 1999). Model: $DMC = 12.05 (\pm 0.189) e^{(-0.32(\pm 0.17)DMRP)}$; RSE = 1.24.

used, comparison of results is difficult. The majority of experiments were conducted with stall-fed animals, using conserved forages as fibre source. Few experiments have used fresh forages (Boudon and Peyraud, 2001; Waghorn *et al.*, 1989) and reports on ingestive mastication under grazing are rare (Chilibröste *et al.*, 1998; Nelson, 1988).

Waghorn (1986) and Waghorn *et al.* (1989) reported a chewing efficiency during eating of 46% for fresh perennial ryegrass and this efficiency was not related to intake rate. With a mix of ryegrass and lucerne, they found that 12%, 32% and 51% of the DM in rumen digesta after eating was retained on 10, 4 and 2 mm sieves, respectively. Boudon and Peyraud (2001) studied the release of intracellular constituents of fresh ryegrass during ingestive mastication in dairy cattle and found that intracellular N and NDS were released at slower rates than total soluble sugars (34% vs. 53%). The release of intracellular constituents as a whole was marginally affected by intake rate. Chilibröste *et al.* (1998) found that after 1 h of grazing, 75% of the newly ingested material was >1.25 mm, but as the grazing session continued and contained a period of rumination, this value declined to 55%. In this study a close and inverse relationship between intake rate and ingestive mastication was observed.

It was assumed by Laca *et al.* (1994) for cattle and by Newman *et al.* (1994) for sheep that the importance of the chewing efficiency during grazing is the response variable exerted by the animal to maximize instantaneous intake rate. Time budgets during grazing have frequently been ascribed to the processes of harvesting the forage (manipulation and biting) and mastication or chewing of the ingested material. However, the functions of these two processes are not mutually exclusive. Research by Laca *et al.* (1994) has shown that cattle are able to bite and chew within the same jaw movement. As result of the overlap between the two processes, time per bite increases linearly with bite weight, while intake rate increases asymptotically. These authors have also shown a linear relationship between chewing per bite and bite mass, which means that the degree of forage comminution decreases with increasing bite

mass. For sheep it has been proposed that the movements for prehension and mastication bites differ (Penning *et al.*, 1984), which suggests no overlap between the two components. Newman *et al.* (1994) suggested that, in addition to bite mass, animals might adjust the degree of mastication, thereby increasing bite rate and intake rate.

Passage rate

Forages are usually rich in insoluble fibre, which immediately after ingestion is in particles that are too large to leave the rumen. Furthermore, they have a low functional specific gravity (FSG) of about 0.8 g/ml (Lechner-Doll *et al.*, 1991) because gases, including air, are present in their internal spaces. These particles form a floating mat on the surface of the liquid in the ventral rumen (Van Soest, 1994).

The amount of gas produced depends on the fermentation pattern and is higher with acetate or butyrate than with propionate production. Fermentation of fibre in forages results in more acetate and more gas than fermentation of cell contents. Removal of gas occurs through rumination and when microbial fermentation of a fibrous forage particle has reached a certain threshold, the removal of gases surpasses its formation. From that moment FSG increases, eventually to a level high enough to let it sink to the reticulum and pass into the omasum. Inverse relationships have been reported between particle size and fractional passage rate and between particle size and specific gravity (Kennedy and Murphy, 1988). In cattle, insoluble matter with FSG above 1.2 and a particle size below 4 mm is prone to pass out of the rumen (Van Soest, 1994). As result of the gradually increasing FSG, a high proportion of what is potentially degradable in the rumen is actually degraded (Tamminga, 1993).

Microbial degradation and synthesis, VFA production (pattern) and absorption

Rumen bacteria are associated with particles (PAB) or free floating (FAB). Adhesion of bacteria to their substrate is advantageous for slow growing bacteria that are exposed to the movement of liquids (saliva, rumen fluid), enabling them to reproduce before being washed away (Pell and Schofield, 1993). For microbes involved in fibre degradation, adhesion is believed to be a prerequisite. The delay in fibre passage caused by a slow fermentation results in a maximum extent of fermentation and ensures that the adhering microbes survive and multiply.

Due to microbial activity after ingestion, forage components are hydrolysed to monomers (sugars, amino acids, long-chain fatty acids) and further degraded to VFA and a varying but usually small proportion of branch-chained fatty acids (BCFA), the latter originating mainly from protein degradation. Degradation of forage simultaneously results in the formation of microbial biomass.

Before hydrolysis starts, FAB have to adhere to their substrate and cell walls need to be disrupted before the cell contents are released. At what point

after ingestion these components become available as nutrients for the microbial population in the rumen or for the animal depends on when the surrounding cell wall is sufficiently damaged to release its contents and on physical and/or biochemical properties that may control their subsequent hydrolysis. Disruption of the cell walls occurs as a result of ingestive mastication and subsequent rumination. The release of cell contents due to ingestive mastication is incomplete. Of the total DM in fresh ryegrass only between 0.15 and 0.20 is released and of the total N between 0.20 and 0.30. Of the components of the cell contents, i.e. free sugars, fructans, protein N, NPN and chlorophyll, proportionally 0.61, 0.42, 0.22, 0.58 and 0.28, respectively, are released. In legumes where SC are solely made up of free sugars, much higher releases of SC of up to 0.80 have been observed (Boudon and Peyraud, 2001).

Protein value and protein degradation in forages were recently reviewed (Tamminga and Südekum, 2000). Based on nylon bag incubation studies, rate of degradation of crude protein in ryegrass was observed to vary between 0.078 and 0.140 per hour and declined with stage of maturity, but increased with level of N fertilization (Van Vuuren *et al.*, 1991). Reported degradation rates of lucerne are usually higher, but white clover shows similar rates (Steg *et al.*, 1994). Rate of hydrolysis also differs between fractions. Rubisco is degraded rapidly in the rumen (Aufreere *et al.*, 1994) with a rate of proteolysis observed to range between 0.04 and 0.47/hour (McNabb *et al.*, 1994; Min *et al.*, 2000), varying with forage species and the presence of CT. Although proteins in fraction 2 may differ in rate of proteolysis in the rumen, their rate of degradation is usually high (Mangan, 1982). Because of its insoluble nature, the degradation of chloroplast constituents like chlorophyll is much slower than that of fractions 1 and 2 (Aufreere *et al.* 1994).

The degradation of SC is very rapid and free sugars are hydrolysed at rates of 3.0 per hour. Degradation of fructosans is slower, but still above 0.20 per hour (A. Boudon, personal communication). Structural carbohydrates are degraded much more slowly. Degradation rate of pectic substances, which are a significant proportion of cell walls in legumes, is highest and usually above 0.10 per hour. The rate of degradation of cellulose and hemicellulose is variable but the rate seldom exceeds 0.10 per hour, and does not clearly differ between the two fractions. The rate declines with an increased NDF content (Sauvant *et al.*, 1996) and both rate and extent of degradation depend on the degree of lignification. The size of the undegradable fraction (INDF) can be estimated from the lignin/NDF ratio (Traxler *et al.*, 1998), with the equation:

$$\text{INDF} = 4.37 \times (\text{lignin/NDF})^{0.84} \quad (26.1)$$

The size of the undegradable fraction of NDF in legumes is usually higher than in grasses, but the rate of degradation of the degradable fraction is higher (Tamminga, 1993; Steg *et al.*, 1994). Degradation of lipids is restricted to hydrolysis followed by partial hydrogenation.

Forage Utilization

Ingestion and distribution of nutrients

Dairy cows with a high milk production potential require high and balanced amounts of nutrients. Van Vuuren (1993) claims that nutrient supply from ingestion in forage-fed dairy cows is insufficient for a daily milk production above 28–30 kg, even when young highly digestible fresh grass is offered. Next to the total supply of nutrients, the ratio in which ketogenic, glucogenic and aminogenic nutrients are supplied is considered important, notably in dairy cows. Sources of nutrients are fed escaping microbial degradation, microbial biomass, fermentation end products and mobilized body reserves.

Ketogenic nutrients originate from acetic acid (HAc), butyric acid (HBu) and long-chain fatty acids (LCFA) from either the feed, microbial biomass or body reserves. Body reserves of protein, potential suppliers of aminogenic nutrients, are small. Hence, these nutrients have to come predominantly from feed protein escaping microbial degradation and from microbial biomass. Glucogenic nutrients come from propionic acid (HPr) and α -linked hexose polymers. The supply of aminogenic nutrients from forage protein escaping degradation is quite variable. In fresh forage it shows a maximum of 113 g/kg DM of protein absorbed from the small intestine (Van Vuuren, 1993). In their review Beever *et al.* (2000) concluded that the efficiency of microbial N yield, expressed as per kg OM apparently digested in the rumen, is highly variable, but on average much lower for ensiled than for fresh forages. The main contributor to the supply of glucogenic nutrients from forages is propionic acid. Other sources of glucogenic nutrients in forage-fed animals are fructans, a proportion of which may escape rumen degradation, and small amounts of α -linked polymers, synthesized by rumen microbes. After passing to the intestine they may contribute to the glucose supply.

Fermentation pattern largely reflects the rate of degradation. High rates yield a high proportion of HPr, whereas at low rates HAc predominates. Variation in rate of degradation of fibre of different sources is small and hence the ratio in which HAc, HPr and HBu, are produced from fibrous forages shows little variation. When expressed as the non-glucogenic/glucogenic ratio [NGR = (HAc + 2HBu)/HPr], in experiments with grass silage the NGR varied in early lactation between 4.6 and 4.8, in late lactation between 4.8 and 5.3 (Bosch, 1991). On stall-fed, grass-based diets variation in NGR was between 4.1 and 4.6 (Van Vuuren, 1993), but on high concentrate diets in early lactation NGR varied between 3.4 and 4.6 (De Visser, 1993).

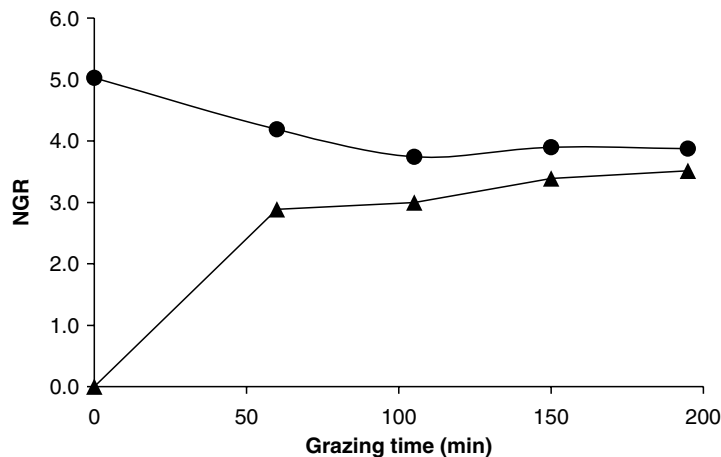
Groot *et al.* (1998) physically separated cell walls (CW) and cell contents (CC) from leaves of Italian ryegrass (*Lolium multiflorum*). Both fractions were subjected to a dynamic *in vitro* fermentation system in which gas production was measured continuously, and also other fermentation end products, notably VFA. The results (Table 26.2) show that fermentation differed between CC and CW and much more HPr was produced when CC was fermented as compared with CW. Both substrates showed a linear increase of the proportion of HAc

Table 26.2. Fermentation profile of cell walls and cell contents of leaves of *Lolium multiflorum* (Groot *et al.*, 1998).

	Cell walls	Cell contents
NDF/OM (g/kg)	771	–
CP/OM (g/kg)	120	258
Total-VFA (mmol/g OM)	5.5	7.7
Hac (% t-VFA)	71	49
HPr (% t-VFA)	23	42
Hbu (% t-VFA)	6	9
NGR (Hac+2*Hbu)/HPr	3.61	1.60

with time of incubation. The NGR was low, even for the fermentation of CW, but this could be expected because very young and leafy material was fermented.

Information on the VFA pattern produced in the rumen of grazing animals is scarce, but its variation may be larger than with forages fed indoors. Grazing animals have better opportunities to select and the level of SC may vary considerably between and within days. Van Vuuren *et al.* (1986) observed the total of SC to vary throughout the day between 130 and 175 g/kg DM in summer and between 80 and 120 g/kg DM in autumn. Highest values were reached in the late afternoon and evening and highest VFA concentrations appeared at midnight and coincided with a low NGR. Chilbroste *et al.* (1998) followed the VFA pattern in the rumen of dairy cows that were allowed to graze for different lengths of time after a long starvation period. The results in Fig. 26.3 show that the NGR in the total VFA pool declined but that the pool of newly added VFA started low (<3.0) and increased with increasing grazing

**Fig. 26.3.** Development of the non-glucogenic/glucogenic ratio in the rumen pools of total VFA (●) and added VFA (▲).

time to a level approaching that reported by Van Vuuren (1993). After a short starvation period no such results were found, but in this experiment (Chilibroste, 1998) the content of non-protein NDS, to which the soluble sugars contribute, was much lower than in the first experiment (172 vs. 318 g/kg DM).

Manipulation of nutrient supply from forages

Factors influencing the chemical composition and digestibility and hence the nutrient supply from forages, are forage species, growing stage, climate, season and forage management, including N fertilization. The effects of climate are complex and depend on temperature, radiation and rainfall.

Forage species and management

Grasses and legumes differ primarily in their protein content, the presence of CT, and the structure of their cell walls. Protein content is usually higher in legumes and the presence of CT is also restricted to legumes. Many tropical legume species contain high amounts of CT, but only a few temperate forages contain significant amounts. Examples are *Lotus pedunculatus*, *Lotus corniculatus*, *Hedysarum coronarium* and *Chicoricum intybus*. Consuming forages with medium concentrations of CT has nutritional advantages for ruminants. At concentrations of over 5 g/kg DM they prevent bloat when animals graze on swards that are rich in soluble proteins. Because they form complexes with forage protein, CT protect protein from degradation in the rumen. Reactivity of CT is pH-dependent and determined by their concentration, structure and molecular mass. Medium concentrations of CT (30–40 g/kg DM) increase intestinal absorption of amino acids and stimulate wool growth, milk protein output and reproduction in grazing sheep, without any negative effect on feed intake, whereas high concentrations of CT (75–100 g/kg DM) depress feed intake and digestion of NDF in the rumen (Barry and McNabb, 1999).

Crude protein content declines with increasing maturity, around 1.4 g/kg DM per day during the growing season. Nitrogen fertilization enhances the growth rate of forage and because it reaches the desired yield in a shorter period, such forages are harvested at a younger stage of maturity with a higher CP content (Van Vuuren, 1993).

Depending on the degree of encrustation of fibre with components such as lignin or silica, a variable proportion of fibre is susceptible to microbial fermentation. Regardless its potential fermentability, 80 to 90% of fibre fermentation takes place in the rumen. The structure of the NDF in legumes differs from that in grasses. It has a higher non-fermentable fraction than grasses, but its fermentable NDF is degraded at a faster rate (Tamminga, 1993). Hot climates enhance both the content of NDF and of lignin, with usually a sharper rise in lignin, resulting in a negative effect on forage quality (Van Soest, 1994).

Forage management can also be used to manipulate nutrient supply to forage-fed animals. Possible approaches are: combinations of different forage

species, the application of N fertilizer, varying the harvesting height (either by cutting or grazing), or varying the harvesting time in the day. In a comparison of two levels of N fertilization (275 and 500 kg N/ha/year) and feeding the resulting grass to dairy cows, Van Vuuren *et al.* (1992) did not observe significant differences in the VFA pattern in the rumen. In an experiment where grazing was allowed on plots with an increasing number of growing days (Chilbroste *et al.*, 2000), NGR both before and after grazing initially declined, to reach a minimum after 16 growing days, after which it increased again (Fig. 26.4).

Grazing management

Increasing the proportion of the daily intake achieved during the afternoon (Orr *et al.*, 2001; Chilbroste *et al.*, 1999, 2004), results in a higher (although not significant) milk yield and a decreased milk fat content. This results from the combined effect of a higher sugar content of forage in the afternoon, a longer initial grazing bout and a faster intake rate that might impair rumen fermentation and hamper fibre digestion rate. Chilbroste *et al.* (2001) found that the milk fat depression previously observed was avoided when a limited amount of dry long fibre (hay from *Setaria italica*) was offered during the starvation time. Increasing the level of water-soluble carbohydrates was recently shown to have a positive effect on grass intake and milk yield (Miller *et al.*, 1999).

Synchronization of rumen fermentation

Productive, i.e. fast growing, grasses need an adequate presence of appropriate enzymes, notably enzymes to capture CO₂. Large amounts of the easily (rumen) degradable enzyme complex Rubisco are therefore needed. Hence, an almost inevitable side effect of the intake of high-quality forage is that its fermentation in the rumen is unbalanced. The ratio between rumen degradable

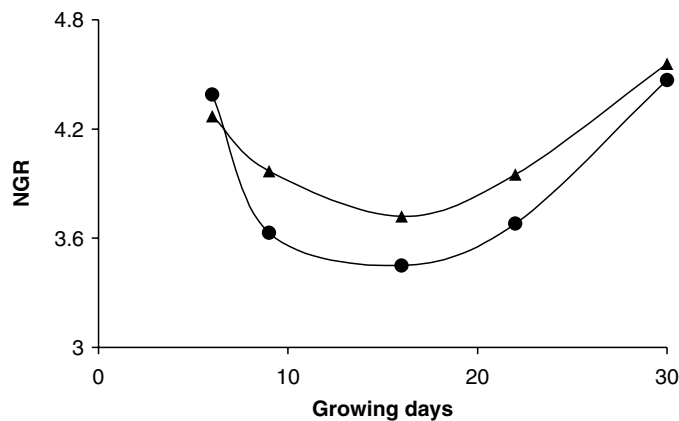


Fig. 26.4. Effect of grass height on NGR of VFA in the rumen before (▲) and after grazing (●).

protein (RDP) and rumen degradable carbohydrates (RDC) usually has a surplus of N, resulting in high urinary N losses (Van Vuuren, 1993). Experiments with animals fed fresh grass indoors have shown that the magnitude of the N surplus as well as other rumen fermentation characteristics depend on composition and intake pattern of the grass. To what extent a better balance and synchronization between RDP and RDC depends on the nature of the RDC (i.e. WSC vs. NDF) in grass is not clearly established yet. Knowledge of the extent to which a better synchronization will result in a more efficient microbial protein synthesis is also scarce. An option may be to reduce the rumen imbalance after the ingestion of high quality, i.e. protein-rich, forages by supplementation. This can be done, either with low-protein forages like maize silage or with concentrates rich in non-structural carbohydrates or rich in rapidly degradable, i.e. pectin-rich, structural carbohydrates such as sugar beet pulp or soy hulls.

Conclusions and Recommendations

Extraction and utilization of nutrients from forages by ruminants involves interaction between the herbivore, the plant and the microbial population. Important aspects of these interactions are characteristics of the forage and ingestive behaviour of the animal. Ruminants have evolved behaviour patterns as distinctive as their anatomy in adapting to their herbivorous life. Nevertheless, far from being rigid, within the grazing environment their ingestive and digestive behaviour patterns show considerable adaptability. The consequences of the behavioural adaptations during grazing on the post-ingestive behaviour by the animal and on the digestive process must be investigated. Advances in scientific understanding can contribute to improvements in grazing and feeding management practices. This chapter attempts to illustrate the nature of herbage variability and some of the adaptive responses by grazing ruminants.

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