Plant and Sward Characteristics to Achieve High Intake in Ruminants

W. J. Wales
PIRVic, Australia

C. R. Stockdale
PRVic, Australia

P. T. Doyle
PRVic, Australia

The XX International Grassland Congress took place in Ireland and the UK in June-July 2005. The main congress took place in Dublin from 26 June to 1 July and was followed by post congress satellite workshops in Aberystwyth, Belfast, Cork, Glasgow and Oxford. The meeting was hosted by the Irish Grassland Association and the British Grassland Society.

Proceedings Editor: D. A. McGilloway

Publisher: Wageningen Academic Publishers, The Netherlands

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W.J. Wales, C.R. Stockdale and P.T. Doyle
Primary Industries Research Victoria (PIRVic), Department of Primary Industries, Kyabram Centre, 120 Cooma Road, Kyabram, Victoria, 3620, Australia
Email:bill.wales@dpi.vic.gov.au

Key points

1. Intake is affected by complex interactions between signals from the digestive tract, intermediary metabolism and energy supply, and behavioural signals associated with learned behaviours or sensory signals.
2. The ideal sward needs to have characteristics that are similar to total mixed rations to achieve high intake and animal performance.
3. Genetic manipulation of plants may offer an accelerated rate of plant improvement, but benefits need to be demonstrated in a systems context.

Keywords: intake, grazing ruminants, herbage mass, herbage allowance, sward height

Introduction

The primary limit to performance of grazing livestock is energy available to the tissues for productive purposes. This occurs because intake at grazing is less than potential intake. Secondary limits to performance appear to occur because the balance and synchrony between energy and amino acid availability to rumen organisms, or to the tissues, leads to inefficiencies in nutrient utilisation. This lack of synchrony between energy and amino acid availability is probably greater in lactating cows fed energy supplements. However, experimental quantification of the implications of poor synchrony in grazing cows is rare. Tertiary limits may be imposed by inadequacies in the supply of other essential nutrients at the rumen or tissue level. The ideal sward would contain plants that enable high rates of intake, long meal duration and optimum supplies and synchrony of energy yielding substrates and essential nutrients for rumen organisms and tissues.

Livestock systems relying on grazed herbage face constraints to animal production from seasonal variations in pasture growth and nutritive characteristics. These constraints limit carrying capacity and individual animal performance. In this review, we have not considered these seasonal constraints in detail, but have focused on the characteristics of vegetative plants and swards that are associated with high intake. For example, the ideal plant for dairy cows would need to provide sufficient metabolisable energy, metabolisable protein, fibre, and other essential nutrients to sustain high yields of milk solids. Currently, total mixed rations (TMR) can be formulated to allow dairy cows to approach their genetic potential for intake and milk production. Cows in early lactation consuming TMR have produced 2.7 kg protein + fat/day; (44.1 kg milk/day; Kolver & Muller 1998), levels of production that cannot be achieved by grazing pasture alone where maximum daily milk yields are only about 30 kg/cow (Doyle *et al*., 2001).

This raises questions as to what limits intake and nutrient supply when animals with the genetic potential for high rates of growth or milk production graze high quality herbage, and are there options to overcome these constraints. To examine these questions, we consider the characteristics of vegetative swards and plants that influence nutrient intake and production by grazing ruminants in relation to theories of intake regulation.

Intake regulation

Herbage intake by grazing animals is affected by the characteristics of the sward, animal factors (physiological state and species), the environment, and interactions between these (Doyle *et al.,* 2000). In all grazing systems, characteristics of swards, such as pasture mass, the spatial distribution of plants and their nutritive characteristics, affect intake. Under strip or small paddock rotation systems that are common in dairy farming, herbage allowance is also a key determinant of herbage intake.

One theory on the regulation of intake has been the concept of limits to intake due to rumen fill, with differences between the capacity of forages to fill the rumen responsible for the observed differences in intake (Mertens, 1987). This concept suggests a key role of the structural and slowly digestible components of plants, generally measured as neutral detergent fibre (NDF), in limiting intake. This concept has been useful when applied to TMR fed to appetite. However, the regulation of intake is more complex and includes interactions between limitations imposed by, or signals from, the digestive tract and intermediary metabolism, involving signals generated by supply of energy and essential nutrients (Weston, 1982). Rumen fill appears to have a key role in intake regulation when digestibility of the diet is less than 75% (Dove, 1996), but vegetative herbages often have digestibility values above this. Ketelaars & Tolkamp (1992) proposed that the intake of highly digestible feeds is physiologically determined, and physical restrictions to intake are less important.

When animals graze vegetative herbage, simple relationships between intake, digestibility and rumen fill do not exist. For example, in cows consuming the same amount of Persian clover (*Trifolium resupinatum)* or perennial ryegrass (*Lolium perenne* L.) with similar digestibility, rumen fill was lower on clover (Williams *et al.,* 2005). In a subsequent study with grazing cows consuming different amounts of Persian clover, rumen fill varied throughout the day with eating bouts, but there were no differences in average rumen fill, DM or NDF loads across the range of intakes (5.5 to 20.4 kg DM/day) (Williams 2003). In contrast to this, rumen fill appeared to have an unexpected role in intake regulation with highly digestible ryegrass. With sheep fed low digestibility forage diets, Doyle *et al*. (1987) indicated rumen fill was not always the major factor limiting intake and that nutrient imbalances were important. However, they suggested that for these types of forage, the setting at which signals associated with fill of the rumen influenced intake might change with type of diet and nutrient supply. It would also seem that with highly digestible herbage or TMR, no single factor such as rumen fill, nutrient supply or deficits to the tissues alone will regulate intake.

At grazing, factors such as the time available for grazing and rumination (Rook, 2000), dietary preferences (Provenza, 1995) and sensory factors such as palatability (Weston, 1985), may also play roles in intake regulation. In mixed swards, animals spend time searching for preferred components, and there are upper limits to the time animals will spend each day ingesting and ruminating feeds. Buckmaster *et al*. (1997) suggested that intake is reduced when grazing time is less than 8 hours per day.

These complexities mean that predicting intake from simple relationships based on single factors, such as digestibility or NDF concentration, will not be universally applicable across the extremes of grazing and TMR feeding systems. Hence, in considering sward and plant characteristics conducive to high intake, an understanding of the complex interactions between signals from the digestive tract and digestive processes, intermediary metabolism and sufficiency of energy and essential nutrients, and behavioural signals associated with learned behaviours or sensory signals is important.

Characteristics of grazed herbage compared with TMR

Conceptually, an ideal sward would have characteristics, nutrient profile and physical attributes similar to a TMR formulated to provide nutrients in relation to requirements while having the physical characteristics necessary to stimulate rumen function and rumination. Because a TMR offers control over the nutritive characteristics of the diet, when offered in sufficient quantities, it allows animals to approach their potential intake and provide the nutrient requirements for high animal performance. Kolver and Muller (1998) compared the nutritive characteristics of a pasture diet based on a mixed grass/clover sward and a TMR consumed by dairy cows in early lactation. Despite both diets having similar digestibilities, there are obvious differences in the concentrations of essential nutrients, as well as pasture having lower DM and non-structural carbohydrate concentrations and higher NDF concentrations. This comparison also does not illustrate the differences in physical characteristics of the diets where clearly the particle sizes in a TMR are conducive to rapid rates of removal from the rumen.

In comparison with TMR, cows consuming grazed pasture even when supplemented with grain, had lower DM intake, milk production, milk protein and fat concentrations, lost more body condition and had lower liveweight (Kolver & Muller, 1998; Bargo *et al*., 2002). In high producing dairy cows, DM intake would need to approach 5% of the cows' liveweight at grazing to achieve similar intakes to that observed by cows consuming TMR. Stockdale (1993) reported that cows grazing Persian clover consumed up to 4.5% of their liveweight, representing one of the highest reported intakes of herbage in the literature. However, Kolver & Muller (1998) concluded that current pasture species are unlikely to provide the nutrients in sufficient quantities to achieve similar milk yields to TMR.

Importantly, at very high water contents, intake of herbage is reduced. For dairy cows, the critical water content was estimated to be about 82%, with a depression of 0.34 kg DM intake for each percentage increase in water content above this level (Verite & Journet, 1970). When water was added to the rumen *per fistulum*, there were no detrimental effects on the intake of forages by sheep (Lloyd Davies, 1962), indicating the effects of water content on herbage intake may be associated with palatability or the large volumes of fresh herbage that need to be processed during ingestion. In cattle, Cabrera Estrada *et al.* (2004) showed that intake and eating rate was restricted by internal water of grass, but not by external water.

Achieving high intake from grazed herbage

To maximise intake, animals need to consume plants that have characteristics that allow rapid consumption and lead to fast rates of passage through the rumen. Intake of herbage has been defined as the product of the rate of eating (R) and the time spent eating (T) (Allden & Whittaker, 1970).

$$\text{Daily intake} = R \times T \qquad (1)$$

This relation has been further refined by Rook (2000), who described rate of eating as the product of bite mass and bite rate, and time spent grazing as the meal duration and number of meals per day.

$$\text{Daily intake} = (\text{bite mass} \times \text{bite rate}) \times (\text{meal duration} \times \text{number of meals}) \qquad (2)$$

Grazing ruminants vary bite dimensions, bite rate and grazing time in response to changes in sward conditions (Hodgson, 1981; Milne *et al.,* 1982; Penning *et al.,* 1991a; Gibb *et al.,* 1997). The animal's mouth size (Taylor *et al.,* 1987; Illius, 1989; Laca *et al.,* 1992), the proximity of the bite to the ground (Hughes *et al.,* 1991; Mitchell, 1995) and the effort required to break the pasture (Hughes *et al.,* 1991) influence bite dimensions and, hence, bite mass.

The complexity of the interactions between factors can be illustrated by examining bite mass. Increases in sward height and bulk density have been shown to increase bite mass (from 0.25 to 4 g DM) for cattle offered micro-swards of lucerne (*Medicago sativa* L.) and paspalum (*Paspalum dilatatum* Poir.) (Ungar, 1996). However, although increasing sward height increases bite depth in sheep (Edwards *et al.,* 1995) and cattle (Laca *et al.,* 1992), increases in bulk density leads to decreases in bite depth, particularly with longer swards (Laca *et al.,* 1992). Bite mass is, therefore, influenced by the height of the sward, its bulk density and the effect of the density on reducing bite depth.

Hughes *et al*. (1991) suggested that the structural strength of accessible pasture components would determine the bite dimensions and bite mass, and that the upper limit to the force ruminants are prepared to exert to sever a bite may be important. Further to this idea, Illius *et al.* (1995) demonstrated that the number of tillers constrains bite mass and is determined by the force required to sever a mouthful. In support, Tharmaraj *et al*. (2003) showed that the bite fracture force, a measure of the resistance to breaking, increased down the sward profile.

Bite rate is related to ease of prehension, herbage shear force, and bite mass, as smaller mouthfuls often lead to an increase in bite rate. It has proven difficult to isolate the individual effects of sward characteristics, such as height, mass, leaf area and nutritive characteristics on ingestive behaviour, since these factors are linked, and experiments that have attempted to vary sward height, for example, have generally varied mass as well. These interrelationships between characteristics of swards lead to confounding when trying to isolate the importance of a particular characteristic.

In short term studies with fasted cows grazing perennial ryegrass, sward height and sward density were shown to have marked effects on hourly intake rate (and presumably potential intake rate) due to differences in bite mass (Mayne *et al.,* 1997). Intake rates were maximised at 3.5 to 4 kg DM/hour when sward heights, measured using a sward stick, were greater than 18 cm. However, intake rates were still very high (3 kg DM/hour) when sward height was 15 cm. With shorter swards, bulk density becomes important, with intake rates varying from 1 to 2.5 kg DM/hour for swards varying in bulk density from 1.7 to 3.1 t DM/ha. Thus, high intake rates by dairy cows may be achieved by grazing tall swards (greater than 15 cm) or by grazing denser short swards (less than 15 cm). However, these high short-term intake rates measured on experimental swards are difficult to translate into grazing systems as swards change during grazing, and utilisation of available herbage is an important consideration.

Where intake rates have been estimated over 24 hours, similar principles apply. For example, Wales *et al*. (1999) reported intake rates of 2.7 kg DM/hour for cows grazing dense, tall swards (12.6 cm using a rising plate meter), but only 1.9 kg DM/hour at the same pasture allowance, but with short (5.6 cm) swards. The grazing time on both swards was not different at 8.3 hours/day.

In many instances, management decisions, such as herbage allowance in strip grazing systems and/or pre-grazing pasture mass, have marked effects on intake (Wales *et al.,* 1998; Wales *et* *al.,* 1999). Curvilinear relationships exist between herbage allowance and intake for grazing dairy cows, with intake increasing with increasing allowance (Stakelum, 1986a; Stakelum, 1986b; Stakelum, 1986c; Holmes, 1987; Stockdale, 2000). In contrast to strip grazing, intake by sheep and cattle in continuous grazing systems is maximised at a green pasture mass between 1.5 and 2.5 t DM/ha, although sheep in particular tend to patch graze when pasture mass exceeds 1.5 t DM/ha (Doyle *et al.,* 1993). Thus, herbage mass, which is influenced by the height of the sward and its bulk density, is a key determinant of diet selection and intake by grazing animals (Kenney & Black, 1984; Black & Kenney, 1984; Laca *et al.,* 1992; Edwards *et al.,* 1995; Gibb *et al.,* 1997; Concha & Nicol, 2000; Pulido & Leaver, 2001). A number of studies have attempted to quantify the effect of herbage mass on intake, with increases in intake by dairy cows under strip grazing of between 1.1 and 2.3 kg DM for each additional t DM/ha (Stockdale, 1985) and between 1.1 and 2.6 kg OM for each additional t OM/ha (Stakelum, 1986b; Stakelum, 1986c).

Meal duration is not only influenced by sward characteristics, but potentially by the capacity of the rumen-reticulum, the need for rumination to breakdown ingested material and the rate of passage of digesta from the rumen. The nutritive characteristics of different plant species are important and studies of the kinetics of digestion at grazing are needed to explore the importance of these characteristics further. For example, Williams *et al*. (2005) found that at the same intakes, perennial ryegrass resulted in higher rumen fill than Persian clover. Cows grazing perennial ryegrass at a high allowance spent less time eating and more time ruminating than those grazing the clover. However, there were no differences in average DM in the rumen for cows grazing Persian clover, with intakes between 5.5 and 20.4 kg DM/day. Although DM in the rumen varied throughout the day as meals were consumed, little time was spent ruminating and it appeared the primary effect of increasing intake was increased passage from the rumen on this herbage type (Williams, 2003).

Relative advantages of legumes and grasses

In general, legumes have characteristics that lead to higher animal performance compared with grasses. An early study in southern Australia (Rogers *et al.,* 1986) highlighted the advantage of white clover (*Trifolium repens*) compared with perennial ryegrass for milk production when intake was not restricted by pasture allowance. Cows consuming the white clover pasture produced more milk (5750 vs. 4740 L) and milk fat (236 vs. 194 kg) and gained more liveweight (85 vs. 80 kg) due to a 30% higher intake (Rogers *et al.,* 1982). More recently, Harris *et al.* (1997) showed that milk yield was increased by 20% when dairy cows consumed a diet with 55 – 65% DM clover, with the balance as perennial ryegrass, compared to a diet with only 20% clover. No further advantage in animal performance was achieved by offering diets with 80% clover. Sheep (Gibb & Treacher, 1983; Penning *et al.,* 1991b) and cattle (Thomson, 1984; Beever *et al.,* 1986b) also eat more and grow faster when consuming diets of pure clover, because of the superior nutritive characteristics of white clover (Beever *et al.,* 2000).

Clover frequently comprises a minor component of mixed white clover/perennial ryegrass swards, particularly in dairy production systems using strip grazing, and given the preference for the legume (Newman *et al.,* 1992), there are likely to be energy costs and restrictions imposed on DM intake as animals search for and select clover. This preference for the clover reduces its presence (Parsons *et al.,* 1994b), which may partly explain why white clover rarely comprises more than 20% of the available herbage for grazing dairy cows (Doyle *et al.*, 2000).

Clovers contain less structural carbohydrate leading to more rapid rates of breakdown of OM, nitrogen (N) and cell walls (Beever & Siddons, 1986; Aitchison *et al*., 1986; Beever *et al*., 1986a) and the retention time is less compared with ryegrass (Ulyatt, 1981). The faster rate of passage of legume compared with grass has been ascribed to differences in particle shape (Troelsen & Campbell, 1968; Moseley & Jones, 1984). The breakdown of grass produces long, thin threadlike structures, while the clover produces more blockish, irregular shapes. Closer examination has shown that grass particles consist of strands of vascular tissue and epidermal sheets, where the fracture lines run longitudinally along the length of the leaves and stems. Clover particles consist largely of epidermal tissue with little evidence of vascular structure, while the fracture lines occur in all planes with equal frequency, giving rise to irregular shaped particles with no dominant axis.

Despite the clear advantages in intake of legumes over grasses, there are other issues that need to be considered. Firstly, the cost of increased prevalence of bloat and the additional costs of maintaining swards need to be addressed. Secondly, while this more rapid breakdown and fermentation is an advantage, it also has some negative consequences. Time spent ruminating by cows consuming clover is low compared with grass (Williams *et al*., 2000), and rumen fluid pH can be below 6.0 for considerable periods on these legume diets (Williams, 2003; Williams *et al*., 2005). Pure clover swards may not provide sufficient NDF for efficient rumen function, with potential negative consequences for milk fat production in dairy cows. Low rumen pH predisposes animals to acidosis when concentrate supplements are fed. Thirdly, associated with the high crude protein concentrations in clovers, rumen ammonia concentrations (up to 500 mg/L) (Stockdale, 1993) can be much higher than microbial requirements. This has energy costs in converting absorbed N into urea for excretion, and has been estimated to be as high as the equivalent amount of energy required to produce 2 kg milk/day for cows grazing irrigated clovers (Cohen, 2001). One possible strategy to improve the utilisation of the excess N is to feed high-energy supplements, but an unintended consequence of this approach is the increased prevalence of sub clinical and clinical acidosis.

An interesting observation is that sheep may show a preference for white clover in the morning, but this preference diminishes through the day in favour of a preference for grass (Parsons *et al.,* 1994a). In theory, this type of preference should lead to increases in DM intake, as rate of intake of clover is faster than grass, and could involve post-ingestive feedback with propionate (Francis, 2002).

Despite the clear advantages of clovers over grass in intake and animal performance, clovers are not an ideal plant from the perspective of rumen function or synchrony of supply of N and energy to the rumen organisms. An alternative approach is to present choices to grazing livestock. This has prompted research into systems where choice is offered to grazing ruminants. When given a choice between grass and clover monocultures, sheep consumed 50 - 70% white clover and 30 - 50% ryegrass (Newman *et al.,* 1992; Parsons *et al.,* 1994b). Cows also prefer 70% of their diet DM as white clover (Cosgrove *et al.,* 1999), and providing them with free choice between perennial ryegrass and white clover has increased milk yield by 10 - 30% compared with a conventional interspersed mixed pasture (Marotti *et al.,* 2001). Offering free choice of pure swards may overcome management and competition issues associated with maintaining optimal amounts of plant species in a mixed sward. However, it also presents challenges in presenting each monoculture in an ideal state (height, density, and nutritive characteristics) for high intake. This may be achieved by offering the alternate pastures at different times of day or using other classes of less productive stock to utilise residual herbage. However, the additional costs and increased level of management complexity may limit the widespread adoption of this approach.

Modification of the nutritive characteristics of legumes and grasses

Plant breeding objectives have expanded from the traditional focus on improving yield and pest and disease resistance to those that have effects on animal health, fertility and characteristics of the animal product (Caradus *et al.,* 2000). For example, techniques to genetically modify the plant have enabled the development of plants with elevated concentrations of ruminal undegraded dietary protein and high-energy yielding compounds, such as starch or triacylglycerides (Spangenberg *et al.,* 2001; Roberts *et al.,* 2002). An alternative to increasing carbohydrates such as starch in leaves, which are readily transported to storage sites, is to introduce the ability to synthesise fructans, storage compounds based on sucrose. Roberts *et al.,* (2002) described research investigating the potential for modifying white clover through the introduction of genes that code for the ability to synthesise fructans from a bacterium and globe artichoke. Their research has indicated that elevated levels of fructans will improve the nutritive value of the herbage. Genetic modification of plants to introduce desirable attributes has the potential to accelerate the selection of plants with desirable animal production traits.

Increasing the digestibility of the herbage is an example of a well-established strategy for increasing intake in ruminants. Stehr & Kirchgessner (1976) demonstrated that herbage intake increased by 5.5 kg for every 10 unit increase in OMD from 64 - 80%. In lambs consuming legumes and grasses, Freer & Jones (1984) reported a linear intake response with OMD over the range 57 to 83%. Grazing animals have demonstrated a strong preference for herbage fractions with high soluble carbohydrate concentrations (Jones & Roberts, 1991; Dove *et al*., 1992; Simpson & Dove, 1994; Ciavarella *et al.,* 2000). Dove & Milne (1994) reported that the efficiency of microbial protein synthesis in sheep grazing perennial ryegrass swards was halved in autumn when water soluble carbohydrate concentrations were lower than in that measured in summer, despite the digestibility of the swards being the same. In zero grazing studies, dairy cows offered pasture with high water soluble carbohydrate concentrations consumed more DM and produced more milk than cows fed grasses with lower concentrations (Miller *et al.,* 1999; Moorby *et al*., 2001).

The benefits of many of these modified cultivars have yet to be demonstrated in animal systems.

Conclusions

Seasonality of pasture growth and of the nutritive characteristics of plants within swards will always present challenges when attempting to provide pastures to achieve intakes near the potential of high producing animals. With vegetative swards, legumes offer significant potential to increase intake of grazed pasture compared with grasses. However, they also present challenges in terms of rumen stability and disposal of excess N. While choice grazing systems (involving legumes and grasses) offer potential to achieve synergistic effects on intake and animal performance, management of such systems will bring complexities, and alternatives that include supplementation or involve partial mixed rations may be more realistic options. Genetic manipulation of plants may offer an accelerated rate of plant improvement, but benefits need to be demonstrated in systems.

Acknowledgments

We would like to acknowledge financial support from the International Grasslands Congress and the Department of Primary Industries, Victoria.

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