Physical Constraints on Voluntary Intake of Forages by Ruminants

Michael S. Allen
Department of Animal Science, Michigan State University, East Lansing 48824-1225

ABSTRACT: Voluntary dry matter intake (VDMI) of forages by ruminants may be limited by distention resulting from restricted flow of digesta through the gastrointestinal tract. An animal’s capacity for fill depends on the weight and volume of digesta that causes distention and the flow rate of digesta from the organ in which distention occurs. The reticulorumen is generally regarded as the site in the gastrointestinal tract for which distention limits VDMI with high-fill diets, although evidence suggests that distention of the abomasum may also limit VDMI. Linear decreases in VDMI have been noted with increasing amounts of inert fill inserted into the reticulorumen, but results have not been consistent across several experiments. Reduction in VDMI depends on the extent to which intake is limited by fill before insertion of inert fill; hence animals with high energy requirements consuming relatively low-energy, high-fill diets are affected to the greatest extent. Because NDF generally ferments and passes from the reticulorumen more slowly than other dietary constituents, it has a greater filling effect over time than non-fibrous feed components and has been found to be the best single chemical predictor of VDMI. However, many other factors affect fill, including particle size, chewing frequency and effectiveness, particle fragility, indigestible NDF fraction, rate of fermentation of the potentially digestible NDF, and characteristics of reticular contractions. These factors are only partially accounted for in models that have been developed to predict VDMI. Increased accuracy of prediction of VDMI is expected as models continue to evolve.

Key Words: Ruminants, Forage, Voluntary Intake, Physical Fill

Introduction

Productivity of ruminants depends on their ability to consume and extract usable energy from available feeds. Pregastric fermentation allows ruminants to extract much more energy from roughages than is possible by mammalian enzymes alone and to convert nonprotein nitrogen to microbial protein with high biological value. However, voluntary dry matter intake (VDMI) may be limited for ruminants consuming forages as a result of restricted flow of digesta through the gastrointestinal tract. Restricted flow may result in distention of one or more segments of the gastrointestinal tract, resulting in decreased intake. Lehman (1941) suggested that ballast of undigested feed residues in the gastrointestinal tract may limit intake, and evidence in support of this theory has been presented since then (Campling, 1970; Forbes, 1995).

Balch and Campling (1962) reported that intake varies inversely with the filling capacity of forages, which is represented by fiber mass. Van Soest (1965) found that VDMI of forages by sheep was more highly related to NDF than to other chemical measures. This finding was affirmed by Waldo (1986), who suggested that NDF is the best single chemical predictor of VDMI by ruminants. Although NDF has been used as the only feed characteristic to predict the filling effects of forages (Mertens, 1987, 1994a), there is substantial evidence that NDF alone is inadequate; its filling effect varies with differences in initial particle size, particle fragility, and rate and extent of NDF digestion. A fill-unit system has been developed (Jarrige et al., 1986) in which forages are assigned fill values to predict VDMI based on intake experiments with sheep and dairy cattle. Although fill-unit systems have the advantage of integrating factors affecting VDMI for a particular forage, their usefulness depends on the ability to match the forage of interest with a reference forage and the similarity of the animal of interest to the reference animal.

Mechanistic models hold the promise of increasing prediction accuracy further. Several mechanistic models that predict VDMI as a function of fill in the reticulorumen have evolved from the simple model of...
cellulose digestion developed by Waldo et al. (1972) based on the kinetics of digestion and passage from the reticulorumen. However, progress made in the prediction of VDMI by these models has been disappointing, primarily because of an inadequate understanding of the mechanisms that affect flow from the reticulorumen and insufficient data with which to develop and validate models. The objectives of this review are to evaluate evidence of physical constraints to forage intake, to discuss dietary and animal factors limiting flow through the gastrointestinal tract, and to identify limitations of models that predict VDMI and research needed to improve them.

Evidence of Physical Constraint to Voluntary Dry Matter Intake

As a result of diverse supporting evidence, the theory that physical distention in the gastrointestinal tract limits VDMI has been widely accepted (Campling, 1970; Baile and Forbes, 1974; Grovum, 1987; Forbes, 1995). The relationship between digestibility of forages and VDMI is well established (Blaxter et al., 1961; Blaxter and Wilson, 1962; Van Soest, 1965). This relationship is not linear, with a decreased response in VDMI as digestibility increases (Blaxter et al., 1961). Voluntary DMI of low digestibility feeds is thought to be limited by physical distention in the gastrointestinal tract, which presumably diminishes as digestibility increases. Conrad et al. (1964) suggested that there is a breakpoint in digestibility at which limitation of VDMI by physical fill in the gastrointestinal tract is replaced by limitation by satisfaction of energy demand. However, this breakpoint is likely a convenient mathematical simplification because VDMI is thought to be controlled by the integration of multiple stimulatory and inhibitory inputs to the brain (Forbes, 1986), and the effect of fill on VDMI gradually diminishes as digestibility increases. Van Soest (1965) observed that NDF content and DM digestibility explained similar variation in VDMI of forages and that VDMI decreases with an increasingly negative slope as forage NDF content increases, noting that such a decrease is consistent with the theory that fiber mass in the gastrointestinal tract may inhibit VDMI.

The reticulorumen is generally regarded as the site in the gastrointestinal tract at which distention limits intake with high-fill diets (Campling, 1970; Baile and Forbes, 1974). Tension receptors located primarily in the reticulum and cranial sac respond to distention (Leek, 1986). Decreasing particle size of forages by grinding and pelleting generally increases VDMI (Minson, 1963) as a result of a reduction of initial volume and retention time in the reticulorumen (Moore, 1964). A greater intake response is obtained by pelleting low-quality forages than high-quality forages (Minson, 1963) because VDMI is limited by fill to a greater extent for forages with low digestibility and high fiber contents. Chopping silage more finely just before feeding resulted in increased VDMI by sheep (Dulphy and Demarquilly, 1973; Dulphy et al., 1975; Deswysen et al., 1978), probably because of decreased retention time in the reticulorumen (Deswysen et al., 1978). The inverse relationship between retention time in the reticulorumen and VDMI has been noted in many experiments (Campling et al., 1961; Freer and Campling, 1963; Thornton and Minson, 1972, 1973; Laredo and Minson, 1975). For example, Laredo and Minson (1975) offered chopped or pelleted leaf and stem fractions of three tropical forages to sheep. Mean retention time in the reticulorumen decreased 23.2 and 25.4% with increased VDMI of 88 and 60% for pelleted vs chopped leaf and stem fractions, respectively.

Welch (1967) observed a 30% decrease in VDMI of chopped alfalfa hay by sheep when 150 g of 7-cm long polypropylene fibers were inserted into the reticulorumen. Intake decreased immediately after insertion of the fibers and gradually increased as the fibers were reduced in size by rumination and passed from the digestive tract. Insertion of the same weight of 30-cm long fibers resulted in a 75% decrease in VDMI. Although VDMI partially recovered, it did not regain its pre-treatment level and 95% of the particles inserted into the reticulorumen were recovered from the reticulorumen after 27 d. When the same weight of ground polypropylene fibers were inserted into the reticulorumen, no effect on VDMI of chopped hay was observed.

Inert Fill in the Reticulorumen. Decreased VDMI with insertion of inert fill into the reticulorumen via permanent cannulas has been reported (Campling and Balch, 1961; Davies, 1962; Mowat, 1963; Egan, 1972; Baumont et al., 1990; Johnson and Combs, 1991; Dado and Allen, 1995). However, the effects of distention of the reticulorumen with inert fill have been inconsistent, with no effect on VDMI observed in several experiments (Carr and Jacobson, 1967; Waybright and Varga, 1991, Johnson and Combs, 1992). Failure to achieve a depression in VDMI by inserting inert fill into the reticulorumen is likely a result of a reserve capacity for fill because of reserve volume and flow from the reticulorumen (Dado and Allen, 1995). In the experiments in which added fill had relatively little effect, ruminal fill was probably not a significant factor affecting VDMI. Ruminal capacity and ruminal DM disappearance must both be limiting before a maximum decrease in intake is observed.

Several experiments have observed a dose-dependent response to long-term addition of inert fill. Regression analysis of treatment means showed a linear or nearly linear decrease in VDMI with added fill for most experiments (Table 1). Campling and Balch (1961) evaluated the effect of addition of inert fill as water-filled bladders on VDMI of long hay by
Table 1. Effect of inert fill added to the reticulorumen on voluntary dry matter intake (VMDI) by cattle and sheep

<table>
<thead>
<tr>
<th>Reference</th>
<th>Displacement, L</th>
<th>n&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Linear effect</th>
<th>Response, g of VMDI/L</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baumont, 1990&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0 to 2</td>
<td>3</td>
<td>.97</td>
<td>.11</td>
</tr>
<tr>
<td>Baumont, 1990&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0 to 2</td>
<td>3</td>
<td>.95</td>
<td>.14</td>
</tr>
<tr>
<td>Campling and Balch, 1961&lt;sup&gt;d&lt;/sup&gt;</td>
<td>0 to 34</td>
<td>3</td>
<td>.998</td>
<td>*</td>
</tr>
<tr>
<td>Campling and Balch, 1961&lt;sup&gt;d&lt;/sup&gt;</td>
<td>0, 46</td>
<td>2</td>
<td>NA&lt;sup&gt;1&lt;/sup&gt;</td>
<td>NA</td>
</tr>
<tr>
<td>Carr and Jacobson, 1967&lt;sup&gt;e&lt;/sup&gt;</td>
<td>0, 1.7</td>
<td>2</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Carr and Jacobson, 1967&lt;sup&gt;f&lt;/sup&gt;</td>
<td>0, 5.2</td>
<td>2</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Carr and Jacobson, 1967&lt;sup&gt;f&lt;/sup&gt;</td>
<td>0, 8.7</td>
<td>2</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Egan, 1972&lt;sup&gt;g&lt;/sup&gt;</td>
<td>0 to 3</td>
<td>4</td>
<td>.81</td>
<td>.10</td>
</tr>
<tr>
<td>Egan, 1972&lt;sup&gt;h&lt;/sup&gt;</td>
<td>0 to 3</td>
<td>4</td>
<td>.98</td>
<td>**</td>
</tr>
<tr>
<td>Mowat, 1963&lt;sup&gt;i&lt;/sup&gt;</td>
<td>0 to 48</td>
<td>4</td>
<td>.97</td>
<td>*</td>
</tr>
<tr>
<td>Mowat, 1963&lt;sup&gt;j&lt;/sup&gt;</td>
<td>0 to 24</td>
<td>4</td>
<td>.98</td>
<td>**</td>
</tr>
<tr>
<td>Waybright and Varga, 1991&lt;sup&gt;k&lt;/sup&gt;</td>
<td>0 to 6.5</td>
<td>4</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

<sup>a</sup> = number of levels of displacement.
<sup>b</sup>Sheep fed 70% NDF timothy hay, polystyrene cubes.
<sup>c</sup>Sheep fed 51% NDF alfalfa hay, polystyrene cubes.
<sup>d</sup>Non-lactating cows fed hay, water-filled bladders.
<sup>e</sup>500-kg cattle fed chopped alfalfa hay, polyethylene cubes.
<sup>f</sup>500-kg cattle fed chopped alfalfa hay, water-filled bladders.
<sup>g</sup>Sheep fed pellets (50% alfalfa, 50% barley), water-filled bladders.
<sup>h</sup>Sheep fed chopped wheat straw, water-filled bladders.
<sup>i</sup>295-kg steers fed 29% crude fiber hay, water-filled bladders.
<sup>j</sup>227-kg steers fed 38% crude fiber hay, air-filled bladders.
<sup>k</sup>Sheep fed 22% NDF total mixed ration composed of 75% grain and 25% forage, water-filled garbage bags.
<sup>l</sup>NA = not applicable, less than three levels.
<sup>m</sup>NS = not significant (P > .05).
<sup>*</sup>P ≤ .05.
<sup>**</sup>P ≤ .01.

nonlactating, nonpregnant cows. They observed a linear decrease in VDMI of 54 g/L with added fill in one experiment with 14-d periods and a significant decrease in VDMI, again of 54 g/L, with addition of 46 L of added fill in a second experiment with 10-d periods. Mowat (1963) reported a decrease in VDMI with inert fill in the form of water- or air-filled bladders added to the reticulorumen of steers fed chopped hay during 7-d periods. In one experiment, addition of inert fill as water-filled bladders resulted in a linear decrease in VDMI of 93 g/L, and in a second experiment, addition of inert fill as air-filled bladders resulted in a linear decrease in VDMI of 111 g/L. Direct comparison of the two experiments (air- vs water-filled bladders) should be avoided; although a greater reduction in VDMI per liter was observed in the experiment with air-filled bladders, the steers had lower BW and were offered hay with a higher crude fiber content (Table 1).

Carr and Jacobson (1967), in three different experiments, found no effect of long-term insertion of inert fill into the rumen of cattle consuming chopped alfalfa hay when added fill was in the form of polyethylene cubes or water-filled bladders. However, it is likely that the energy requirement of their animals was met by the chopped alfalfa hay, and VDMI was probably not limited by physical fill. Only 1.7 L of polyethylene cubes was inserted in one experiment and only 5.2 and 8.7 L of water in bladders in the other two experiments; hence a decrease in VDMI was not likely because the animals probably had reserve reticulorumen volume and flow to easily accommodate the added fill.

Several experiments with sheep also resulted in a decreased VDMI with insertion of inert fill into the reticulorumen. Egan (1972) inserted inert fill into the reticulorumen of sheep that were offered pellets (50% alfalfa, 50% barley) and chopped wheat hay in two different experiments. Insertion of inert fill resulted in decreases in VDMI of 115 and 213 g/L for the sheep consuming the pellets and the chopped wheat straw, respectively. Although the two diets were offered in different experiments, a greater decrease in VDMI was observed for the sheep consuming the higher fill (wheat straw) diet. The sheep consuming chopped wheat straw may have had VDMI limited by physical fill before addition of the inert fill, whereas the sheep consuming the pellets may have had more reserve capacity for fill volume and flow from the reticulorumen.

Baumont et al. (1990) reported a decreased VDMI resulting from addition of polystyrene cubes in two experiments with sheep fed orchardgrass hay (70% NDF) and alfalfa hay (51% NDF) during 5-wk periods. Addition of inert fill to the rumen resulted in average decreases in VDMI of 175 and 210 g/L for sheep consuming orchardgrass and alfalfa hays, respectively. Although the same sheep were used in
Table 2. Effect of inert fill added to the reticulorumen on voluntary dry matter intake by lactating dairy cattle

<table>
<thead>
<tr>
<th>Reference</th>
<th>Displacement^a</th>
<th>DIM^b</th>
<th>EB^c</th>
<th>NDF^d</th>
<th>Response^e</th>
</tr>
</thead>
<tbody>
<tr>
<td>Johnson and Combs, 1991</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exp. 1</td>
<td>24.2</td>
<td>49</td>
<td>+2.4</td>
<td>26</td>
<td>99*</td>
</tr>
<tr>
<td>Exp. 2</td>
<td>21.6</td>
<td>73</td>
<td>+1.6</td>
<td>27</td>
<td>122**</td>
</tr>
<tr>
<td>Johnson and Combs, 1992</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exp. 1</td>
<td>19.5</td>
<td>250</td>
<td>+6.6</td>
<td>29</td>
<td>NS</td>
</tr>
<tr>
<td>Exp. 2</td>
<td>22</td>
<td>227</td>
<td>+3.8</td>
<td>27</td>
<td>NS</td>
</tr>
<tr>
<td>Exp. 2</td>
<td>23</td>
<td>227</td>
<td>+10.1</td>
<td>33</td>
<td>NS</td>
</tr>
<tr>
<td>Dado and Allen, 1995</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>22.2</td>
<td>59</td>
<td>+5.3</td>
<td>26</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>22.2</td>
<td>59</td>
<td>−1.4</td>
<td>35</td>
<td>95*</td>
</tr>
</tbody>
</table>

^aInert fill added to reticulorumen, L.
^bDays in milk.
^cEnergy balance, Mcal of NE\textsubscript{L}/d.
^dDietary NDF, %.
^eReduction in VDMI resulting from inert fill, g/L.

*P ≤ .05.
**P ≤ .01.

Both experiments, the effect of adding inert fill was less for the higher fill forage, the opposite of the results observed by Egan (1972). This inconsistency can be explained if VDMI was limited by fill before insertion of inert fill for sheep consuming both forages in the experiments by Baumont et al. (1990) and for sheep consuming wheat straw only in the experiments by Egan (1972). When physical limitations to intake exist, displacement of reticulorumen contents by inert fill should result in a greater decrease in VDMI for forages with lower fill factors as a percentage of DM, such as alfalfa hay compared with orchardgrass hay. In the experiments of Baumont et al. (1990), sheep offered alfalfa hay had much higher VDMI (1,757 g/d) than those offered orchardgrass hay (1,099 g/d), which was expected because of differences in NDF content. Higher NDF intake observed for alfalfa hay (896 vs 769 g/d) was probably a result of a lower filling effect of the alfalfa NDF due to a faster rate of digestion and passage from the reticulorumen (Jung and Allen, 1995). In the experiments conducted by Egan (1972), a greater decrease in VDMI of the low fill diet would not be expected until the reserve capacity for fill was eliminated. This reserve capacity for fill may explain the data of Waybright and Varga (1991), who observed no effect of addition of up to 6.5 L as water-filled bags to the reticulorumen on VDMI of sheep offered very low fill diets of 75% concentrate and 25% forage. The sheep in this study were offered the diet at 2.3% of pretrial BW and were in positive energy balance (1.8 times maintenance) throughout the experiment.

Recent experiments with lactating dairy cows demonstrate the relationship between response to inert fill added to the reticulorumen and energy balance. Johnson and Combs (1991, 1992) reported decreased VDMI when inert fill was inserted into the reticulorumen in two different experiments with dairy cows in early lactation that were in slightly positive energy balance (Johnson and Combs, 1991), but observed no effect on VDMI in two different experiments (Johnson and Combs, 1992) with dairy cows in late lactation that were in greater positive energy balance (Table 2). Intake limitation by fill in early lactation is often assumed because dairy cattle in early lactation are generally unable to consume enough energy to meet their requirements. This may be partially a result of the diminished volume of the reticulorumen before parturition; weight of reticulorumen contents of lactating dairy cattle gradually increased by more than 40% in the first 2 mo of lactation (Remond, 1988). Dado and Allen (1995) reported that VDMI by dairy cows in early lactation (59 d in milk) was decreased by insertion of inert fill (22.2 L) into the reticulorumen for cows offered a high-fill diet (81% forage, 35% NDF) but not by cows offered a low-fill diet (45% forage, 25% NDF). Energy balance of the cows offered the two diets without addition of inert fill were calculated as +5.3 and −1.4 Mcal of NE\textsubscript{L}/d for the low- and high-fill diets, respectively. Hence, response to inert fill inserted into the reticulorumen depends on the energy requirement of the animal, the caloric density and filling effect of the diet, the capacity of the reticulorumen, and the ability of the animal to alter flow from the reticulorumen.

Reticulum vs Rumen. Grovum (1979) reported a linear decrease in VDMI of meals 30 min after feeding by sheep offered ground and pelleted alfalfa hay (40% ADF) of 211 g/L due to distention of the reticulum with volumes up to 800 mL. Compensatory feeding was observed when the source of distention was removed. No effect of distention of the rumen with a balloon containing 800 mL of water was observed on
VDMI over 30 min. The difference in response to site of distention was attributed to the much higher density of tension receptors in the reticulum and cranial sac than in the rumen (Iggo, 1955; Leek, 1969). It is likely that a decrease in VDMI by distention in the rumen would have been observed by addition of a greater amount of inert fill or by offering a diet with higher fill than pelleted alfalfa hay, even though the response may be mediated by distention in the reticulum or cranial sac. Although it may not have been a factor in these experiments because the reticulum was distended for only short periods of time, balloons added to the reticulum may cause a further increase in fill by decreasing flow of particulate matter from the reticulum; insertion of a 500-g weight into the reticulum of sheep has dramatically increased the mean retention time of dense particles in the reticulum by interfering with the mechanism of their removal (Kaske and Midasch, 1994).

**Short-Term vs Long-Term Effects.** Short-term (Anil et al., 1993) and long-term (Dado and Allen, 1995) distention of the reticulum resulted in opposite effects on VDMI by lactating dairy cows during the 3 h following feeding. Anil et al. (1993) reported a linear decrease in VDMI of 70 g/L when inert fill was added to the reticulum by balloons inflated with water at feeding. However, Dado and Allen (1995) reported that when inert fill was inserted into the reticulum for 21-d periods, VDMI increased over the 3 h following feeding in spite of a lower daily VDMI. Sensory stimuli may have caused the animals to eat to a greater level of mechanoreceptor stimulation in the reticulum, resulting in decreased intake in subsequent meals. A greater understanding of the interactions of stimuli affecting VDMI is needed.

**Other Sites of Restricted Flow.** Mertens (1994a) suggested that distention of the reticulum, and not flow capacity of undigested feed residues through the abomasum or intestines, limits intake, with the observation that when low-quality, high-fiber forages are pelleted, intake and fecal output are increased. However, post-ruminal flow of undigested residues may have limited VDMI of the pelleted forages. Grovum and Phillips (1978) reported a decreased VDMI of 28% for sheep offered alfalfa hay when methylcellulose was infused into the abomasum at a rate of 544 g/d, with increases in the dry and wet fecal outputs of 50% and 223%, respectively. Although this demonstrated that post-omasal flow was not limiting before infusion, it ultimately limited VDMI. Although distention may have occurred at either the abomasum or the intestines, it is more likely that distention of the abomasum may limit intake. Grovum (1979) distended the abomasum of sheep with water-filled bladders of up to 1 L and observed a linear decrease in VDMI of .11 g/mL over a 30-min period. Harding and Leek (1972) described mechanoreceptors in the abomasal epithelium that resulted in continuous discharge with sufficient stimulus. Additional evidence was reported by Malbert and Ruckebush (1989), who found that VDMI by sheep offered alfalfa hay (51% NDF) increased 54% following pyloroplasty and 27% following pyloroplasty (removal of circular muscle coat of about 1/3 the circumference of the sphincter muscle). The authors concluded that the increase in VDMI observed was a result of the increased abomasal emptying rate with suppression of the pyloric gate. The extent to which distention of the various organs in the digestive tract limits VDMI should continue to be evaluated.

**Alternative Theories.** Dissatisfied with evidence for physiological regulation of VDMI of forages by ruminants, Ketelaars and Tolkamp proposed a new theory of feed intake regulation in ruminants, with the hypothesis that feed intake is adjusted by the animal to maximize efficiency of oxygen utilization (Tolkamp and Ketelaars, 1992; Ketelaars and Tolkamp, 1992b). However, their criticism of data supporting the theory of physical limitation to VDMI (Ketelaars and Tolkamp, 1992a) is unconvincing. They observed that intake of indigestible matter and reticulum fill begin to fall once feed digestibility is greater than 70%, whereas OM intake and digestible OM intake continue to rise. However, this observation only provides evidence against a breakpoint at which limitation to VDMI resulting from physical fill is replaced by limitation resulting from satisfaction of energy requirements; identification of other factors limiting VDMI of forages does not exclude physical limitations. The authors discount the experiments in which VDMI decreased with insertion of inert fill into the reticulum, doubting the relevancy to normal feeding conditions. However, the presence of tension receptors in the reticulum and cranial sac, and the linear decreases in VDMI with increasing levels of inert fill added to the reticulum for both short- and long-term experiments discussed previously, are convincing evidence that VDMI can be limited by distention. Much more difficult to understand is the mechanism by which an animal regulates intake to maximize efficiency of oxygen utilization. The authors suggest that maximization of efficiency of oxygen utilization benefits the animal over a lifetime by minimizing damage to tissues caused by excess oxygen consumption. However, animals have evolved without a constant food supply, and maximization of VDMI of low-quality forages is probably a more beneficial strategy for survival than maximization of efficiency of oxygen utilization when an adequate supply of nutrients in the future is uncertain.

**Capacity of the Reticulum**

The first model to calculate gut fill was that of Blaxter et al. (1956), who calculated the weight of DM in the gastrointestinal tract of sheep. Most subsequent models have assumed that the reticulum is the primary control point for physical limitation to intake (Illius and Allen, 1994), with capacity...
determined as a linear function of BW. Gut contents has been reported to be highly related to BW for herbivores ranging from less than .1 to over 1,000 kg of BW (Demment and Van Soest, 1983). This relationship also holds well for ruminants; Illius and Gordon (1991) reported that the DM in the rumen was highly related (r² = .98) with BW for 18 species of ruminants ranging from 3.7 to 720 kg of BW. However, the relationship between maximum volume or weight of reticulorumen contents (with fill limiting conditions) and BW within species or breed is not known; it is expected to be much less than observed across species that vary in BW by over two orders of magnitude. Physiological state of animals also affects their capacity for fill in the reticulorumen. Forbes (1969) reported that volume of ruminal contents of sheep offered hay decreases as pregnancy progresses, with a decline in volume of .39 L/L of incompressible abdominal contents. Remond (1988) reported that the weight of reticulorumen contents increases by about 20% during the first 2 mo of lactation, which is related to increased VDMI at 3 kg/kg of DMI. However, capacity may not have been limiting VDMI following calving; the increase in ruminal fill may have been a result of the increase in DMI and not the reverse. Stanley et al. (1993) reported that although VDMI and fill weight in the reticulorumen increased for Hereford × Angus cows from 8 to 22 d after calving, capacity of the reticulorumen measured by water-holding capacity did not.

Models developed to predict VDMI by fill volume (Mertens and Ely, 1979; Bywater, 1984) have used the weight of NDF rather than DM in the reticulorumen as a proxy for volume. Mertens (1994b) recently developed a model in which the filling effect of a diet is represented entirely by weight of NDF of large particles, and suggested that fluid and small particles contribute little to the filling effect of the diet and that volume, not weight, is the important determinant of fill. The experiment conducted by Mowat (1963) with air-filled bladders (Table 1) demonstrated the importance of volume of fill in the reticulorumen on VDMI. However, both weight and volume of reticulorumen contents affect fill because tension receptors are stimulated by their combined effects. Dado and Allen (1995) reported a reserve volume of more than 16 L in the reticulorumen of dairy cattle consuming a fill-limiting diet with addition of 22.2 L of inert fill, indicating that additional capacity may exist for volume even when distension in the reticulorumen limits VDMI. Most other models that have predicted VDMI from physical constraints have predicted fill as the weight of DM in the reticulorumen (Illius and Allen, 1994). However, wet digesta weight may not be adequately predicted by DM weight as DM content of the reticulorumen varies. Although water added directly to the reticulorumen has been reported to have no effect on VDMI (Campling and Balch, 1961; Davies, 1962) because of rapid removal, the lag time required for moisture in feed to exchange with the free water pool in the reticulorumen increases fill weight. Observations that VDMI of fresh forage (Davies, 1962) is limited by moisture content support the concept that weight is an important determinant of fill. Similar observations have been made for VDMI of ensiled forages (Hawkins et al., 1970; Coppock, 1978), although the effect of moisture may be a result of undesirable fermentation products in higher moisture silages. Variation in water-holding capacity of digesta (McBurney et al., 1985) should also be considered when predicting the weight of digesta in the reticulorumen.

**Limitations to Flow From the Reticulorumen**

**Regulation of Flow by the Animal.** Fractional passage rate from the reticulorumen increases as DMI increases (Riewe and Lippke, 1970) and during cold stress (Kennedy et al., 1976). Stanley et al. (1993) found that as VDMI increased for Hereford × Angus cows consuming chopped alfalfa hay from 61 to 6 d before calving, fill in the reticulorumen decreased, and fractional passage rate of indigestible ADF increased by 87%. Deswysen and Ellis (1988) reported that the efficiency of digesta flow per contraction increased at higher intakes. Okine and Mathison (1991b) concluded that duration of reticular contractions could be the primary determinant of flow of digesta from the reticulorumen, because flow of NDF from the duodenum with increasing DMI was related to duration and amplitude but not frequency of reticular contractions. However, distension of the reticulorumen with added inert fill resulted in an increased rate of reticular contraction and a 34% increase in fractional passage rate of NDF from the reticulorumen (Dado and Allen, 1995). It is likely that interactions among the diet and the animal affect the specific mechanism by which flow through the reticulo-omasal orifice is regulated. When VDMI is limited by distention in the reticulorumen, the limitation results from both the load of digesta in, and flow of digesta from, the reticulorumen. Although intake and retention time in the reticulorumen are negatively related, no fill model increases fractional rate of passage from the reticulorumen with increased VDMI, resulting in an underestimate (bias) of VDMI at higher VDMI by these models. In addition, such models are unable to predict the depression in digestibility of feeds as DMI increases, which is one of their most useful potential benefits (Illius and Allen, 1994).

**Particle Size.** Reduction of large particles is a requisite to flow from the reticulorumen (Ewing and Wright, 1918). Large particle breakdown in the reticulorumen is primarily a result of rumination (Kennedy, 1985) and primary mastication, with
relatively little breakdown directly resulting from digestion and detritus (McLeod and Minson, 1988). Little or no further reduction occurs after particles leave the reticulorumen (Poppi et al., 1980; Okine and Mathison, 1991a). Although fermentation has little direct effect on particle size reduction alone (Murphy and Nicoletti, 1984; Wilson et al., 1989b), it affects rate of particle size reduction during chewing by increasing tissue fragility (Chai et al., 1984). Resistance to flow from the reticulorumen increases with increasing particle size (Poppi et al., 1980; Dixon and Milligan, 1985). A threshold sieve aperture size has been reported for sheep and cattle in which resistance to escape increases dramatically for particles retained on a sieve aperture of 1.18 mm (Poppi et al., 1985). However, higher threshold sieve aperture sizes in the range of 3 to 4 mm have been reported for steers (Dixon and Milligan, 1985) and dairy cattle (Cardoza and Mertens, 1986). The concept of a threshold size has been used to describe flow from the reticulorumen by most models of rumen function (Illius and Allen, 1994). However, Van Soest et al. (1988) suggested that the threshold is variable due to physical form and DMI (Van Soest, 1966), as well as dietary NDF content (Cardoza and Mertens, 1986).

The effect of DMI on rate of particle size breakdown is not clear. Decreased ruminating time per gram of NDF as DMI increases has been reported in several experiments with cattle (Welch and Smith, 1969; Luginbuhl et al., 1989a) and sheep (Ba et al., 1979a), although no effect was observed in an experiment with steers reported by Okine and Mathison (1991a). Welch and Smith (1969) suggested that as DMI increases, rumination may become more efficient in reducing particle size, microbial digestion could become more important at particle size reduction, larger particles may flow from the reticulorumen, or that fill in the reticulorumen may increase. Evidence suggests that higher DMI results in greater fecal particle size (Van Soest, 1966; Luginbuhl et al., 1990; Okine and Mathison, 1991a) and fill in the reticulorumen (Okine and Mathison, 1991b). The proportion of large particles in the reticulorumen has also been found to increase with higher DMI in an experiment in which intake was restricted at several levels (Okine and Mathison, 1991a). However, results from experiments with restricted feeding must be used with caution for prediction of VDMI; in another experiment, restricted feeding was found to decrease particle size reduction during ingestive mastication because of an increased rate of intake (Luginbuhl et al., 1989b), resulting in no effect of DMI on mean particle size of reticulorumen contents (Luginbuhl et al., 1990). None of the models reviewed by Illius and Allen (1994) adjust the rate of particle size reduction for DMI. Rate of particle size breakdown is probably related to animal size, because ruminating time per gram of NDF decreases exponentially with BW (Welch, 1982); this fact was recognized by Illius and Gordon (1991), who scaled rate of breakdown by BW$^{27}$, which was found to be common across other time-related physiological variables (Taylor, 1980).

Differences in fragility of forage particles affect rate of particle size breakdown and retention time in the reticulorumen (Poppi et al., 1981a; McLeod and Minson, 1988). Poppi et al. (1981b) reported that initial mastication resulted in a greater reduction in particle size for both stems and leaves as maturity of Pangola grass and Rhodes grass increased. Ulyatt (1983) reported a greater reduction in particle size by chewing for mature ryegrass with higher cell wall content and lower digestibility than for a less mature ryegrass and suggested that “brittleness” increased as the ryegrass matured. Although there are limited data on the relationship between maturity and(or) chemical composition and rate of particle size reduction, it is clear that differences in fragility exist among forages and must be accounted for in models that predict flow of digesta from the reticulorumen. At least two models have varied rate of breakdown of large particles by feed characteristics; Bywater (1984) predicted rate of breakdown as a quadratic function of cell wall content, and Illius and Gordon (1991) estimated rate of breakdown of large particles as a function of indigestible NDF. A greater understanding of factors related to particle fragility is needed.

Particle Density. Although particle size reduction is clearly a requisite to flow from the reticulorumen, it may not always be a constraint. It has been observed that most of the particulate matter in the reticulorumen is smaller (Evans et al., 1973; Welch and Smith, 1978; Poppi et al., 1981b; Ulyatt et al., 1986) and the diameter of the reticulolaral orifice is much larger (Bueno and Ruckebusch, 1974; McBride et al., 1983) than the maximum particle size in feces. Okine et al. (1993) found no relationship between flow of digesta from the reticulorumen and characteristics of reticular contractions after adjusting for differences in DMI, and they concluded that other factors were responsible for differences in flow. Flow must then depend on the quantity of particles eligible to pass from the reticulorumen that are in close proximity to the reticulo-omalis orifice at the second phase of reticular contraction (Allen and Mertens, 1988), which is clearly dependent on particle density. A negative relationship between particle density and retention time in the reticulorumen has been established with experiments with inert particles (Balch and Kelly, 1951; King and Moore, 1957; desBordes and Welch, 1984; Murphy et al., 1989) or labeled indigestible cell walls (Ehle, 1984; Ehle and Stern, 1986). The relationship between particle density and retention time in the reticulorumen was reported to be nearly linear, with retention time decreasing from 91 to 19 h as density increased from 0.9 to 1.5 g/mL for experiments with inert particles of different densities (Lechner-Doll et al., 1991). Small, dense particles fall to the ventral rumen where they flow with the ventral...
These particles are presented to the reticulo-omasal orifice as it opens at the second reticular contraction in which the reticular contents are expelled (Midasch et al., 1994). Particles that are less dense have a lower rate of passage from the reticulorumen either because of entrapment by the raft (Faichney, 1986) or because they are propelled further away from the reticulo-omasal orifice than denser particles when the reticulum contracts (Lechner-Doll et al., 1991). Inhibition of the ability of the reticulum to expel its contents by insertion of the 500-g weight into the reticulum of sheep resulted in an increase in retention time of dense (1.44 g/mL) particles from 9 to 37 h and a decrease in retention time of less dense (1.03 g/mL) particles from 33 to 24 h in the reticulorumen (Kaske and Midasch, 1994), supporting the mechanism proposed by Lechner-Doll et al. (1991).

Resistance to flow of large particles observed by Poppi et al. (1981b, 1985) is partly a result of the inverse relationship between density and particle size observed by Sutherland (1988). Kaske et al. (1992) reported that when sedimentation of particles in the reticulorumen was prevented, the outflow of 10-mm plastic particles was approximately 40% of the outflow of 1-mm particles of the same density for sheep. Kaske and Von Englehardt (1990) reported that particle density and particle size accounted for 59 and 28% of the total variation in mean retention time of plastic particles in the reticulorumen.

Most digesta particles in the reticulorumen are buoyant (Sutherland, 1988) in spite of a true specific gravity of 1.3 to 1.5 (Siciliano-Jones and Murphy, 1991). Air trapped within the void spaces of forage particles that are swallowed eventually dissolves, and particle density is determined by the retention of carbon dioxide and methane produced by particle-associated microbes. As fermentation proceeds, potentially fermentable OM diminishes, resulting in a lower rate of gas production and an increase in density (Figure 1). Density is then a function of rate of fermentation of potentially fermentable fiber and the fraction of fiber that is potentially fermentable (Jung and Allen, 1995). Grasses generally have higher fractions of potentially fermentable fiber, as well as lower rates of fermentation, than legumes (Smith et al., 1972), tending to make them buoyant for a longer time (Figure 2). Mertens (1973) reported positive relationships between in vitro rate of NDF digestion and VDMI of forages (r = .55). The greater correlation observed for grasses (r = .66) than for legumes (r = .26) may be a result of the higher potentially digestible fraction for grasses. However, results of experiments comparing rate of change in density of grasses and legumes over time of fermentation have been inconsistent (Jung and Allen, 1995), which may be a result of differences in anatomical structure that affect the ability of particles to retain gases (Wilson et al., 1989a). The effect of forage maturity on buoyancy is probably less than that of the differences between grasses and legumes. Advancing maturity generally increases the indigestible fraction and decreases rate of digestion of forage NDF (Smith et al., 1972), which will have counteracting effects on the length of time a particle is buoyant (Jung and Allen, 1995).

The suggestion by Ulyatt et al. (1986) that particle size reduction is not the rate-limiting step in clearance from the reticulorumen may underestimate the importance of particle size reduction. The concept of a single rate-limiting step for flow from the reticulorumen is invalid; reduction of forage particle size by chewing increases rate of fermentation by increasing surface area (Cherney et al., 1988) and decreases the ability of the particle to retain gases, both of which affect particle density. Rate of particle size breakdown may also be an important determinant of fill when limitations resulting from volume occur.

**Limitations of Models: Needed Research**

Limited accuracy of prediction of VDMI by empirical models based on forage fiber content or digestibility results from their inability to account for interaction among animal and forage characteristics. Several models have been developed to integrate animal and forage factors to predict VDMI (Illius and Allen, 1994). Accuracy of prediction of VDMI by these...
PHYSICAL CONSTRAINTS ON VOLUNTARY INTAKE 3071

Figure 2. Enrichment of the indigestible NDF fraction of forage particles over time of fermentation in the reticulorumen. Simulated curves are plotted for typical legume NDF (50% of NDF indigestible, 5%/h rate of NDF fermentation, solid line) and grass NDF (30% of NDF indigestible, 4%/h rate of NDF fermentation, broken line). Gases produced from fermentation of OM decrease density and increase particle buoyancy. Depletion of potentially fermentable fiber decreases gas production and buoyancy. A positive relationship between the fraction that is indigestible over time and particle density is proposed. Dashed vertical lines represent the retention time at which 75% of the particulate DM is indigestible, demonstrating the effects of digestion kinetics on retention time of particles in the reticulorumen. Grass particles may be buoyant for a greater length of time as gas production from fermentation of NDF is extended because of the slower rate of fermentation and greater potentially digestible fraction.

Models, however, has been disappointing. A major limitation of these models is the assumption of a threshold level of fill weight in the reticulorumen that limits VDMI; this threshold has been implemented as a linear function of body weight. Several models predict VDMI based upon this threshold alone (Mertens and Ely, 1979; Pienaar et al., 1980; Poppi et al., 1981b; Illius and Gordon, 1991; Hyer et al., 1991a), whereas others predict VDMI as the first limitation by this threshold, or meeting energy demand (Conrad et al., 1964; Forbes, 1980; Bywater, 1984; Mertens, 1987), or by several different mechanisms (Poppi et al., 1994). Although distention in the reticulorumen is clearly an important factor affecting VDMI, prediction of VDMI using a threshold fill alone will result in an overprediction of VDMI for high-quality forages, and it is clear that other mechanisms must be accounted for.

In addition, the use of a threshold fill limitation to VDMI must be questioned given evidence of additive effects of physical and chemical stimuli (Mbanya et al., 1993). A greater understanding of the additivity of feedback signals is required to integrate mechanisms controlling VDMI.

By ignoring differences in the filling effects of NDF, the model developed by Mertens (1987) has the distinct advantage of ease of implementation because of readily available model inputs but at a cost of decreased accuracy. Dramatic differences in VDMI have been observed for fill-limiting diets of the same NDF content, indicating that the filling effect of NDF is variable. Among these observations are a 29% greater VDMI by lambs consuming corn stover silage with similar NDF content but 20% higher NDF digestibility than the control silage (Muller et al., 1972), a 34% greater VDMI of leaf compared with stem fractions of three tropical grasses with similar NDF content and digestibility (Laredo and Minson, 1975), and a 26% greater VDMI of grazed immature compared with mature coastal bermudagrass for which the NDF contents of the ingested boli were 68% and 70%, respectively (Pond et al., 1987).

Models have been developed to account for differences in filling characteristics of forages by considering kinetics of digestion and passage from the reticulorumen. The performance of these models has been reviewed by Illius and Allen (1994), but the results of few models have been compared with experimental data. The model of Mertens and Ely (1982) underpredicted low DMI, overpredicted high DMI, and explained only 26% of the variation in VDMI of 166 forages fed to sheep. The authors suggested that overprediction at high VDMI was probably a result of observed intakes that were limited by energy demand, and bias at low VDMI was a result of low rate of passage, increased ruminal capacity, or low rates of digestion. Predicted VDMI was also biased for the model of Hyer et al. (1991b) with underprediction for low-digestibility forages and overprediction for high-digestibility forages. The authors suggested that ruminal fill does not limit VDMI for high-digestibility forages. Illius and Gordon (1991) reported a good agreement between VDMI predicted with their model and data from the literature, with 61% of the variation explained and no bias observed. The increased variation in VDMI explained by this model was a result of inclusion of animal factors by scaling large particle breakdown rate, small particle passage rate, and capacity by BW.27. Omitting size-scaled phenomena from this model reduced variation explained to 25% (Illius and Allen, 1994). Although inclusion of animal factors in integrated models is an important contribution, further refinement of these models is needed to accurately predict VDMI; the root mean square error for prediction of VDMI was 8.5 with a mean VDMI of about 55 g/kg of BW.73 for the model of Illius and Gordon (1991).

There are several common factors among models for which future improvements might be made. Rates of
digestion determined in vitro or in situ with ground forages may overestimate VDMI and digestibility because digestion rates increase as grind size decreases (Cherney et al., 1988). Because most models use digestion rates determined with ground forages as inputs, the relationship between rates of digestion of ground and as-fed forages must be evaluated. It is clear that retention time in the rumen is related to particle density. Although this has been modeled at an aggregated level (Allen and Mertens, 1988; Kennedy and Murphy, 1988) it has not been accounted for in models predicting VDMI. The bias observed for underestimation for low-digestibility forages and overestimation for high-digestibility forages (Mertens and Ely, 1982; Illius and Gordon, 1991) may be a result of longer retention times of grasses compared with legumes because of greater buoyancy over time, as discussed previously. Accuracy of prediction of VDMI should increase by inclusion of this mechanism for particle flow from the reticulorumen. Particle size reduction decreases fill volume and is a requisite for flow from the reticulorumen. Although it is clear that particle fragility varies for forages, only two models vary rate of particle size breakdown by forage characteristics. Factors affecting particle fragility need to be elucidated and included in models to predict VDMI. It is also clear that flow of digesta from the reticulorumen is affected by level of DMI, yet no model adjusts fractional rate of small particle passage or rate of breakdown of large particles for level of DMI.

The relative importance of various factors affecting VDMI by distention of the reticulorumen is difficult to determine. Sensitivity of predictions to changes in model parameters has been used (Mertens, 1993), but sensitivity is highly influenced by the structure of the model, and results may be misleading. For instance, Illius and Gordon (1991) reported that VDMI is more than seven times as sensitive to changes in small particle passage rate as to changes in rate of cell wall digestion, yet rate of small particle passage may be partly determined by rate of digestion because of its effect on particle buoyancy. Because this relationship was not included in the model, the importance of rate of digestion was probably underestimated. Influence of model structure should be considered when evaluating the relative importance of factors influencing VDMI by sensitivity analysis.

Implications

The prediction of voluntary dry matter intake (VDMI) is important to the assessment of forage quality. Differences in VDMI account for more than 50% of the variation in digestible nutrient consumption by ruminants. Distention resulting from restricted flow of digesta through the gastrointestinal tract is an important limitation on VDMI, particularly as forage quality decreases. A better understanding of the additive nature of feedback mechanisms, as well as mechanisms affecting flow of digesta from the reticulorumen, will lead to more accurate predictions of VDMI, which will result in improved evaluation of forage quality and superior prediction of performance by ruminants consuming forages.

Literature Cited


