FORAGE QUALITY: STRATEGIES FOR INCREASING NUTRITIVE VALUE OF FORAGES

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ABSTRACT

The ruminant animal responds to both the quantity and type of nutrients absorbed. However, in practical terms it is the level of dietary intake which has by far the biggest effect on animal performance. In terms of nutrients, the response by an animal to extra protein is greater when it is accompanied by an increased intake of metabolizable energy (ME). Microbial protein is the major source of absorbed protein for animals consuming forages and the efficiency of microbial crude protein (MCP) production (g/kg digestible organic matter; DOM) varies widely for forage diets, with the concentration of non-structural carbohydrates (NSC) or water soluble carbohydrates (WSC) and dilution rate within the rumen appearing to have most influence on this attribute. C4 plants, in particular, are low in NSC content and are associated with long retention time of digesta within the rumen and low MCP production. In examining the response by animals to various nutrients it is the response of the target tissue (muscle, mammary tissue, epidermal tissue) to specific nutrients which needs to be addressed. There are various strategies by which dietary intake, and hence ME and metabolizable protein (MP) intake, might be increased. Different strategies are suited to different outcomes. For example, reducing protein degradability within the plant is best suited to increasing protein supply from temperate plants. With tropical plants, increasing MCP production appears a more effective strategy to increase protein supply. The inclusion of lowly-degradable protein fractions (eg., sunflower albumin 8; SA8) in the plant, is more suited to a wool production system than for growth or milk production. In an examination of various strategies to improve forage quality, the traditional proposals of legume inclusion and those aimed at increasing intake and digestibility rank highly. Reducing protein degradability was an important strategy for improving protein supply from temperate legumes in particular. However, addressing low efficiency of MCP production was just as effective in improving protein supply and this was sensitive to NSC content, especially in C4 plants. The means by which some of these changes can be delivered may stem from traditional approaches (grazing management, sward structure, legume inclusion, supplements, plant selection) or through molecular approaches (tannin genes, lignin reduction, fibre-degrading bacteria, low-degradable protein fractions, NSC accumulation), and work should proceed on both fronts. The central importance of the rumen in determining the effectiveness of the response to most of these strategies rings a note of caution. Our analysis shows some of these manipulations may not yield the expected response because the rumen microbes are not growing efficiently or are limited in rumen degradable nitrogen, especially in the case of C4 plants.

KEYWORDS

Intake, nutrients, microbial protein, non-structural carbohydrate, rumen fermentation, rumen protein degradability, C4 plants

INTRODUCTION

The response of an animal to forage intake with respect to muscle growth, fat deposition, fibre growth or milk production depends on the quantity and balance of nutrients absorbed. Crampton (1957) used forage quality as a term encompassing intake and nutritive value, but in the passage of time the emphasis has shifted to intake and digestibility, and the nutrients have been forgotten. Ulyatt (1973) outlined a useful approach where feeding value defined the animal response to herbage eaten, whereas nutritive value defined the response per unit of food intake. In general terms nutrients are described as energy and protein but the nutrients contributing to energy utilization are absorbed as volatile fatty acids (VFA), glucose, lipids and amino acids and the form of the energy substrate can be important in defining the response. These features can all be influenced by the plant, its composition and how it is digested.

The characteristics of high feeding value and nutritive value which need to be assessed were ranked in order of importance previously (Ulyatt, 1981; Wheeler and Corbett, 1989) and are summarized as:
- high digestibility
- easy comminution
- high non-structural carbohydrates (NSC)
- high crude protein (CP)
- appropriate tannins
- high sulphur (S)- amino acids
- adequate minerals
- high palatability
- high lipid
- low anti-quality compounds
- erect growth

Some of these issues will be addressed here with emphasis on quantifying the changes which are needed to improve forage quality. There are several strategies for improving the feeding value of forages which primarily relate to increasing energy and protein supply to the animal. Which nutrient has most effect depends on the product (meat, milk, fibre) and on the forage type, for instance whether it is temperate or tropical forage. There may be different strategies which can be used to deliver the same nutrient and these can vary in complexity. The importance of intake and digestion in these considerations is briefly outlined but they have been discussed extensively previously and emphasis in this paper is given to comparing strategies for increasing nutrient supply.

INTAKE AND DIGESTION

Intake has by far the greatest effect on animal performance and whilst it generally has a positive relationship with digestibility, there is considerable variation in this (Reid et al., 1988; Minson, 1990). Intake, digestibility and the efficiency of use of absorbed nutrients are the three components which determine feeding value and animal performance. The key role of intake is best seen in Fig. 1 from Webster (1992).

This shows the relationship between metabolizable protein (MP) supply and milk production. As expected, a positive relationship is demonstrated. In this figure, the response to increasing MP supply on milk protein yield, at different intakes of ME as provided on four separate farms, is examined. Within farms, where MP is increased

and ME is constant, there is still an increase in milk protein production but the efficiency of use of extra MP is low (0.2). This is much less than when ME and MP supply are increased simultaneously (0.68), as indicated by the comparison between farms. The farm with the highest ME intake also delivered the highest milk protein yield. However, the question arises as to whether the animal is responding primarily to energy or protein. The two are interrelated and can never practically be separated. However, in deciding whether to manipulate energy or protein, either through supplementation or manipulation of the plant composition, it is important to determine to which the animal is most sensitive as this influences the strategy to be adopted. The figure illustrates that energy intake is by far the most influential. Black and Griffiths (1975), through infusion studies in lambs, developed a similar response to the above, as did Balch (1967) with dairy heifers fed various supplements and Gerrits et al. (1996) with pre-ruminant calves.

The marked response to an increase in ME intake arises because any strategy that provides an increase in energy intake (higher digestibility, incorporation of legumes, grazing management etc.) results in an increase in both ME and MP intake, since there is always an associated increase in microbial crude protein (MCP) production with the extra intake of fermentable organic matter (OM). Increasing MP supply independent of ME supply results in much smaller increases in production, as shown in Fig. 1. The response is still important but not of the same order as that associated with increased ME intake. Increased intake is the key to improving forage quality. Breeding plants for higher intake is a long-recognized useful goal (Burton, 1969; Anderson et al., 1988) but the greatest improvements to date have come by identifying existing plant species with inherently high intake characteristics, and through incorporating these into production systems. Examples of this approach are the use of legumes, high-intake temperate forages and certain forage crops.

Intake is discussed in this symposium (Illius 1997) but the main feature of a higher intake plant relates to its short retention time in the rumen and this is largely a factor of the rate of breakdown of particles and their passage from the rumen (Poppi et al., 1981). Wilson and Kennedy (1996) have outlined the anatomical features of the plant which influence this, particularly the Kranz anatomy of tropical grass plants, the I girder structures and the sinuous epidermal cell interconnection which inhibit breakdown and hence passage from the rumen. The characteristic leaf vascular pattern and lobed epidermal cells of legumes and other plants enable rapid breakdown to a rounded particle shape which has rapid escape properties.

Breakdown is a feature which can be measured but it is less certain if it can be manipulated within the plant other than through external treatment, eg., ammoniation (Zorilla-Rios et al., 1985). However, isolation of the brown midrib (bmr) mutant gene has raised the possibility of this approach in influencing breakdown. The bmr gene results in less lignin and appears to reduce the cross-linkages associated with tissue types and within cell walls probably enabling greater access by microbes (Lechtenberg et al., 1974; Akin et al., 1986; Cherney et al., 1986; Akin and Chesson, 1989). This results in up to 30% greater intake and up to 33% greater digestibility (Cherney et al., 1991) though increases do not always occur. Thus the use of agronomically suitable plants can be enhanced using this technology. McIntyre et al. (1993) have outlined a lignin reduction approach, using genetic engineering to target various enzymes involved in lignin production and likely to have consequences on cross-linkages within the cell wall and between tissue types. Lignin reduction *per se* may not be as important as reducing cross linkages and increasing the fragility and rate of breakdown of plant particles within the rumen.

This approach is important for tropical plants and perhaps the stems of plants conserved as whole crops.

Factors influencing digestibility have been extensively reviewed in previous symposia and indeed have formed the basis of most discussion on nutritive value. The key features are content of cell wall and digestibility of that cell wall.

Whilst digestibility is important, animals and their tissues respond to the nutrients which are released on digestion. The key nutrient is protein but in order to synthesize protein from absorbed amino acids the cells need ATP which is derived from catabolism of energy substrates: acetate, glucose, lipid and also from amino acids themselves. Tissues vary in which substrates they preferentially catabolize, e.g., muscle cells can use all the above plus branched-chain amino acids, the mammary gland will use glucose, short- and long-chain fatty acids, amino acids and ketone bodies, the gut will also use glutamine whilst the brain will mostly use glucose.

Obviously the quantitative value for digestibility is important as this determines the M/D (MJ ME/kg dry matter (DM)) of the diet where the ME comprises the nutrients: VFA, glucose, lipid and amino acids. However, it is the balance of these nutrients and, most significantly, the needs of the relevant target tissues for specific nutrients, for instance the mammary gland or muscle, fat and epidermal (for fibre growth) cells, which are thought to influence the efficiency of their use (Cant and McBride, 1995a, b).

PROTEIN SUPPLY
Transfer. Protein is considered the key nutrient because it is a component of all animal products, but correcting protein inadequacy in diets is expensive.

The transfer of plant protein to animal product is relatively inefficient with only 11-16% of the ingested protein of high-quality temperate pastures appearing in the final product (Cruickshank et al., 1992). Intensive agronomic efforts (eg., incorporation of legumes into pasture) and expensive protein meal supplements are used to increase protein product formation but they do little to alter this low conversion rate. This inefficiency is of concern from a production perspective but it also contributes to N pollution in intensive systems.

Rumen. The first site of inefficiency of transfer of plant to animal protein is the rumen. Poppi and McLennan (1995) collated a large number of experiments which examined duodenal flow of non-ammonia nitrogen (NAN) and determined that for non-tannin containing plants there was complete net transfer of ingested protein to the intestines in the form of microbial protein (from rumen degraded plant protein), undegraded plant protein and endogenous protein, when the plants contained ca. 210 g CP/kg digestible OM (DOM) or less. Above this threshold there was net loss of protein, with potentially large amounts of ingested protein lost as ammonia (NH_3) across the rumen wall. These losses can be as high as 40% for lucerne (*Medicago sativa*; Cruickshank et al., 1992) and 50% for glen joint vetch (*Aeschynomene americana*; Higgins et al., 1992). Meissner et al. (1993) also recorded high losses of N from the rumen, especially for temperate pastures and suggested that rumen NH_3 levels increased exponentially as N content in the forage exceeded 25 g N/kg DM. This value is similar to those derived by Ulyatt et al. (1988) and Cruickshank et al. (1992) leading to general agreement on the value of 210 g CP/kg DOM above which losses occur. As well as a loss of protein, there is an energy and amino acid cost to the animal by virtue of urea production in the liver (Lobley et al., 1995) Furthermore, absorption of NH_3 from the rumen of animals

consuming high quality temperate pastures approach the maximum values that the liver can detoxify (Beever, 1993) which may in turn contribute to depressed intake because of elevated blood NH_3 levels reaching the brain.

The consequence of these transactions is that N losses can be expected when dietary CP content exceeds ca. 210 g CP/kg DOM, a value which can be translated to various CP contents in the diet DM, as determined by digestibility (Table 1). Many forages exceed these CP contents, especially legumes, so N loss is a feature of many grazed forages. Whilst the CP content of forages can vary considerably, the CP content of the cell contents is reasonably constant, indicating the large effect varying amounts of cell wall content has on determining CP content in the total plant (Table 2). The one exception is the ryegrass (*Lolium perenne*) hay (Laredo and Minson, 1975) and this is probably because of the respiration of NSC during drying (Table 2). These results are consistent with Rubisco being the major soluble plant protein (35-40% of total CP; Mangan, 1982). High Rubisco concentration in the bundle sheath cells of C4 plants most probably accounts for the lower protein content of mesophyll cells in C4 plants compared to C3 plants (Nelson and Moser, 1994).

As Rubisco is the major plant protein, the potential degradability of the plant proteins, in the absence of any complexing compounds such as condensed tannins, is high and probably varies little. Rate of passage therefore has a major influence on its final degradability. Where reliable estimates of degradability of plant proteins are available, the degradability values are high (0.63-0.92; SCA, 1990; Cruickshank et al., 1992; Perez-Maldonado and Norton, 1996a). There is a suggestion with C4 plants that concentration of Rubisco in the bundle sheath cells, which are heavily lignified, might reduce degradability of the plant protein (Hafley et al., 1993; Nelson and Moser, 1994). There is no direct evidence to support this contention but degradability values for a tropical grass protein were quite high (0.92; Chapman and Norton, 1984) and subtropical and temperate forages did not appear to differ in their relationship of rumen NH_3 to N content (Meissner et al., 1993). The incorporation of the bmr gene might influence this as it increases the digestibility of the bundle sheath cells (Buxton and Casler, 1993) and it would be interesting to examine protein degradability in the presence and absence of this gene.

A collation of data relating to the protein degradability of a range of herbaceous legumes and browse plants in Ethiopia, as determined by the *in sacco* method, is given in Table 3 (Bediye, 1995). This indicates the generally high potential for protein degradability (*a* + *b*) but large variation in its fractional degradation rates (*c*). A similar collation for other forages in Africa was done by Erasmus et al. (1990).

Microbial protein. The fact that microbial protein can constitute most of the protein reaching the small intestine (72%; Beever and Siddons, 1986), although it can be as low as 50% (Cruickshank et al., 1992), highlights the importance of rumen transactions and of factors influencing microbial growth. Beever (1993), at the last International Grasslands Congress, stressed the importance of ensuring the nutrient supply to the microbes if effective digestion was to be maintained and microbial protein production maximized, especially for animals on forage diets.

Microbial growth is dependent on the supply of energy and of rumen degradable N (RDN) although peptides and amino acids can enhance this. This principle is encompassed in the AFRC system (1992) which assumes a fixed production of MCP per unit of fermentable OM (or ME), providing the RDN requirements are met, for a given dilution rate as influenced by level of feeding and class of animal, increasing as intake increases. Thus the MCP production is designated as 9, 10, 11 g MCP/MJ fermentable ME (FME) for maintenance, growing cattle and sheep and lactating cattle and sheep, respectively, corresponding to dilution rates of 0.02, 0.05 and 0.08/h.

Not all diets provide adequate RDN (Hafley et al., 1993) and, as was mentioned earlier, some forages produce excess RDN. Values required for forages in the tropical pasture digestibility range are given in Table 4 and these values are probably just within the range expected of tropical pastures at these digestibilities. Any energy supplementation strategy is likely to induce a RDN deficiency. Temperate forages are unlikely to ever have a RDN limitation and usually have excess (Table 4).

The SCA (1990) has collated data for microbial protein production and given values of 100-236 g MCP/kg DOM for forages, with most values in the range 130-170 g MCP/kg DOM. They suggest the maximum efficiency, on theoretical grounds, for fermentation of carbohydrate is 225 g MCP/kg DOM. Whilst DOM does not equate to FME it is a useful approximation as most data do not include an ME or FME value. Metabolisable energy can be estimated from DOM (average 15.83 MJ ME/kg DOM) and the AFRC (1992) uses a constant conversion of approximately 0.93 ME to estimate FME, except for high lipid, undegradable protein sources and silage. The AFRC (1992) values equate to 132, 147 and 162 g MCP/kg DOM at the three dilution rates previously cited. Similarly, NRC (1996) gives a value for forage diets of 130 g MCP/kg TDN or DOM. A collation of experimental data for hays, silages, mixed diets and concentrates give values of 33-206 g MCP/kg DOM (M.J. Bolam personal. communication; Firkins et al., 1986; Merchen et al., 1986; Spicer et al., 1986; Huhtanen, 1988; McAllan et al., 1988; Rooke and Armstrong, 1989; Beever et al., 1990; Hill, 1991; Newbold et al., 1991; Stokes et al., 1991; Chen et al., 1992; Cruickshank et al., 1992; Ferlay et al., 1992; Jaakkola and Huhtanen, 1992; Van Vuuren et al., 1992; Aldrich et al., 1993; Balcells et al., 1993; Cecava and Parker, 1993; Coomer et al., 1993; Dove and Milne, 1994; Osuji and Khalili, 1994; Susmel et al., 1994; Carruthers et al., 1996). The warm season grass species have low values of 60-100 g MCP/kg DOM (rhodes grass (*Chloris gayana*); M.J. Bolam, personal communication), 113 g MCP/kg DOM (bermuda grass, (*Cynodon dactylon*); Hill, 1991), 100-131 g MCP/kg DOM (paspalum (*Paspalum plicatulum*) and kikuyu (*Pennisetum clandestinum*); SCA, 1990), and 86 g MCP/kg DOM for the legume siratro (*Macrotilium atropurpureum*; Chapman and Norton, 1984.

The major points are that there is considerable variation in the value for efficiency of MCP production and that there is considerable scope to enhance MCP supply, in any dietary situation, or to improve the capture of RDN in the rumen, for diets with excess RDN. Synchrony of energy availability and protein degradation is often suggested as being important to enhance both the capture of degraded protein and the efficiency of MCP production, but research findings do not support this (Henning et al., 1993). The animal will respond to the protein arriving at the small intestine (or the MP) and the source of that protein (microbial or plant origin) is of no major relevance as both sources are of similar amino acid composition. Poppi and McLennan (1995) calculated the extra protein needed to increase growth rate of a 200 kg steer by 300 g/d to be 150 g protein arriving at the intestine and speculated on how this might be provided by undegraded fractions or the use of legumes. Improving the efficiency of MCP production from 100 to 170 g MCP/kg DOM increases intestinal protein supply markedly in this scenario. Increasing intake

of DOM by 1 kg will also result in 130-170 g MCP (SCA, 1990). Both of these strategies are at least as effective as incorporating a legume into the pasture and are more effective than condensed tannins or undegraded protein fractions in increasing protein supply. Various strategies are compared in the concluding section.

Another way to enhance MCP supply is through improvement of digestibility as MCP production is directly related to fermentable OM supply. Changes in digestibility can arise through changes in the digestibility of the cell wall or an increase in the cell contents of the plants. Changes in cell wall digestibility with plant maturity and bmr mutants have been well documented. Horn et al. (1989) have indicated that in wheat forage the susceptibility of leaf-tissues to disappearance in the rumen decreased in the following order: mesophyll and parenchyma bundle sheath > phloem > epidermis > sclerenchyma, with virtually no disappearance observed for lignified vascular tissue. This pattern was similar for wheat pasture at the immature stage, when all plants consisted of leaves, or mature stage, when forage samples were collected 7-10 days after anthesis and 80% of plants were in the early stage of seed formation. Leaf blades of immature wheat forage were degraded more rapidly *in sacco* than those of mature forage, but similar tissues were degraded at each maturity stage. Stem material increased in content with plant age and had tissues that were highly lignified. Only small losses of tissues, primarily in the phloem, cortex and part of the parenchyma, were observed in stems.

Changes in digestion of neutral detergent solubles appear to occur as a plant senesces, declining from ca. 80% to ca. 45% (Ballard et al., 1990). Non-structural carbohydrates of various types (fructans, sucrose, glucose, fructose, starch) comprise the majority of the cell contents (Table 5) and altering the total amount and type of carbohydrate may provide a strategy to increase MCP production. Recently Chamberlain et al. (1993) examined MCP production from starch, sucrose, lactose, xylose and fructose. There were differences in the VFA patterns but more importantly large differences in microbial yield (Table 6) with sucrose and lactose being more effective than fructose or xylose, whilst a common storage polysaccharide starch was inexplicably much less effective. These values can be compared to those collated earlier where the range was 33-206 g MCP/kg DOM. Dove and Milne (1994) suggested that efficiency of MCP (g/kg DOM) is influenced by water soluble carbohydrate (WSC) content, which supports the SCA (1990) contention that those plants with WSC content of ca. 90 g/kg DM or less (regrowth temperate and tropical pastures) will have lower efficiency of MCP production. Carruthers et al. (1996) have also observed this in lactating cows consuming ryegrass in two different seasons.

The sugar contents of plants show diurnal variation associated with carbon fixation during the day (Table 7) and with shade (Samarakoon et al., 1990) but this is not as large as the between-species differences. Plant species and plant parts vary in the type of sugar present.

Chatterton et al. (1989) did an extensive study of the leaves of C3 and C4 Gramineae species for the various NSC fractions (Table 5). Growth at high temperature usually reduced total NSC content and that of all its fractions and placed many species in the range where efficiency of microbial protein production (g CP/kg DOM) is likely to be low. Shade caused a similar effect (Samarakoon et al., 1990). Sucrose and starch are the major storage carbohydrates of C4 plants (40 and 41% at 10/5°C (maximum/minimum temperature) and 24 and 51% at 25/15°C respectively) whilst fructan, sucrose and starch are the major storage carbohydrates of C3 plants (37, 19 and 28% at

10/5°C and 11, 22 and 38% at 25/15°C, respectively). Fructan is very sensitive to temperature and declines quite markedly in C3 plants grown at the 25/15°C range (from 115 to 12 g/kg DM; Table 5). The practical significance of this variability in NSC composition, in relation to MCP production, is unclear.

Wilson (1975) showed that in conditions where N was adequate, the NSC content of green panic (*Panicum maximum*) ranged from 73-105 g/kg DM whilst under N deficiency the values were 103-173 g/kg DM. In another study (Wilson and Ford, 1973), green panic had WSC contents of 31-90 g/kg DM whilst values for ryegrass (*L. perenne*) were 55-500 g/kg DM, the variation largely caused by ambient temperature. Similarly, Wilson and Ford (1971) showed that NSC content ranged from 182-237 g/kg DM for two ryegrass varieties whilst the range for green panic was 144-172 and for setaria (*Setaria sphacelata* cv. Nandi) was 181-196 g/kg DM. Variation in plant WSC content has been linked to diet selection (Simpson and Dove, 1994).

Sucrose was the major NSC in four tropical pasture species (Ford and Wilson, 1981) and ranged from 12-34, 10-31, 9-55 and 4-10 g/kg DM for green panic, buffel grass (*Cenchrus ciliaris*), spear grass (*Heteropogon contortus*) and siratro, respectively, over the summer period. Diurnal variation was large for the grasses: 10-25, 10-30, 8-20 g/kg DM for green panic, buffel grass and spear grass respectively, with values of 8-15 g/kg DM for the legume siratro. Hunter et al. (1970) reported NSC values in a group of tropical legumes ranging from 36-389 g/kg DM, and in two grasses (pangola (*Digitaria eriantha*) and setaria) from 60-68 g/kg DM.

The major conclusion from this collation of data is that the C4 grasses have low levels of WSC and NSC such that efficiency of microbial protein production is low and below what feeding tables would predict was theoretically possible according to the level of fermentable OM present in the plant. On the other hand, temperate pastures usually, but not always, have adequate levels of these nutrients to maximize efficiency of microbial protein production. Dove and Milne (1994) have suggested that levels in ryegrass are too low in autumn. In some instances, the level of fermentable OM in temperate pastures is inadequate in relation to the amount of protein which is solubilized and degraded. As OM digestibility of grazed temperate pasture is usually around 80% there is little scope to increase the total supply of fermentable OM, and really the problem becomes one of quantity and degradability of the protein in these plants, and their content of NSC as is markedly affected by season.

Moore et al. (1993), in a selection program with switchgrass (*Panicum virgatum* L.) based on *in vitro* DM digestibility, increased DM digestibility (57.4 to 60.4%) and neutral detergent fibre (NDF) digestibility (30.9 to 33.1%), without changing NDF content or the concentration of cell solubles (26.9%). Non-structural carbohydrate content will be ca. 100 g/kg DM, if it is assumed that the plant has CP content of ca. 100 g/kg DM, and this is about the minimum NSC value below which efficiency of microbial protein production is reduced (SCA, 1990). Consequently, NSC content should perhaps be targetted specifically in plant breeding exercises rather than just DM digestibility in those plants (usually C4) with low NSC composition. Targetting this aspect of plants has been largely ignored but it appears potentially of equal or greater value than targetting protein fractions in an attempt to improve protein supply to animals.

One easy way to modify NSC supply is to add supplements to the diet. A recent experiment examining response curves of MCP production to increasing level of supplement illustrates this (Fig. 2, M.J. Bolam, M. Connors, S.R. McLennan and D.P. Poppi,

unpublished observations). All four supplement types (protein meal, starch of high or low rumen degradability, and sugar) increased the efficiency of MCP production (g/kg DOM) and total MCP production (g/d). Increasing NSC supply is thus a useful goal and these results suggest the form of this carbohydrate is of lesser importance than the total amount. Sorghum is a little different because it has a lower degree of rumen digestion of its starch compared to barley. The confusing aspect of these results is that supplements fed at 0.5% of body weight, especially molasses, should have easily satisfied a requirement for WSC and hence should have increased the efficiency of MCP production more rapidly. This may be largely a product of the low rumen dilution rates associated with these forages. Thus C4 plants in particular may have low efficiency of MCP production because of low NSC content and also low dilution rates in the rumen. Low dilution rates are associated with slow rate and extent of digestion, and long retention time of particles, in the rumen.

Undegradable protein fractions. The protein of most plants is highly degradable as Rubisco comprises 35-40% of the total protein (Mangan, 1982). This fraction is rapidly degraded. Animals require more protein than can be derived from MCP production for certain physiological states such as rapid growth and early/mid lactation, based on current feeding standards of efficiency at 130-170 g MCP/kg DOM. Broderick (1995) indicates a ruminal escape of 35% of ingested protein is needed in lactating cows, and steers increase liveweight gain in response to extra undegradable protein (Hafley et al., 1993; Mbongo et al., 1994). The various feeding standards enable more precise estimates of these values, e.g., Uribe et al. (1996). Klopfenstein (1996) has outlined the situations where escape protein is needed in growth and lactation phases for beef cattle, based on an average MCP yield of 130 g MCP/kg DOM, providing results similar to Mbongo et al. (1994) and Bolam et al. (1996a).

There are a number of strategies to alter the undegradable protein fraction such as the use of legumes, condensed tannins, albumin fractions and specific peptides. Rubisco in C4 plants may also be partially protected although there is no conclusive evidence of this.

Legumes have been assigned high nutritive value characteristics because of their high intake and high CP content. However the degradability of non-tannin containing legumes is similar to grasses and their incorporation into grass-based diets is unlikely to significantly alter protein flow to the intestines unless they also increase intake (Poppi and McLennan, 1995).

Condensed tannins offer the best form of protection of protein but the protein can be irreversibly bound if the level of tannin is too high. However, Lotus (*Lotus pedunculatus*), sainfoin (*Onobrychis viciifolia*) and leucaena (*Leucaena leucocephala*) offer examples of the substantial increases in protein flow which can occur by virtue of tannin inclusion (Bamualim et al., 1984; Barry et al., 1986; Waghorn et al., 1987). Poppi and McLennan (1995) calculated that, second to an increase in intake, this was the most effective strategy to alter protein supply in plants. Perez-Maldonado and Norton (1996a) have shown that inclusion of legumes with condensed tannin (Desmodium (*Desmodium intortum*) and Calliandra (*Calliandra calothyrsus*)) in the diet increased undegraded protein flow to the intestines but there was no overall beneficial effect on animal production. There was substantial metabolism and disappearance of condensed tannins and its various forms within the gastro-intestinal tract (Perez-Maldonado and Norton, 1996b). The role of the various molecular weight phenolic compounds in the binding and release of protein in the intestines has yet to be fully characterized.

Protein fractions such as sunflower albumin 8 (SA8) have received a lot of attention recently as they are of low degradability and the genes for their production can be incorporated into plants (McNabb et al., 1993). These fractions are high in S-amino acids and where these are particularly limiting, for instance in silage-based diets for dairy cows and for wool production in sheep, inclusion of S-amino acids has led to significant increases in production. Thus inclusion of SA8 into legume plants such as subclover (*Trifolium subterraneum*) to enhance wool production is likely to be beneficial. However, inclusion of SA8 into legumes to enhance muscle growth or milk production is less likely to succeed as the amounts which are needed require high levels of expression (in the order of 16-50% of the protein in the leaf depending on the level of intake of legume in relation to grass; Poppi and McLennan, 1995). This may not be biologically possible (Tabe et al., 1995). Inclusion of SA8 into the basal diet alone at a level required to theoretically increase LWG by 300 g/d, i.e. 150 g/d of extra protein or its six amino acid equivalent still requires at least an expression of 19% of the CP in the grass leaf (Poppi and McLennan, 1995).

ENERGY SUPPLY

Energy substrates. Fig. 1 outlined the overriding importance of ME supply over MP supply for improving production. Increasing MP supply independent of ME supply results in a low efficiency of use of the extra protein, estimated at ca. 0.15-0.2 (Fraser et al., 1991; Cruickshank et al., 1992; Webster, 1992). Increasing ME supply, with its associated MP supply, results in an efficiency of use of the extra protein of ca. 0.59 for growth and 0.68 for lactation (AFRC, 1992) or 0.49-0.66 for growth and 0.65 for lactation (NRC, 1996). This occurs because of the nature of the response curve. The protein/energy ratio of most temperate forages varies between 180-220 g intestinal CP/kg DOM (Poppi, 1990) and extra protein is unlikely to be efficiently used because the response curve is reaching a plateau at that point (Black and Griffiths, 1975). Webster's analysis clearly shows that this usually occurs with production diets. Hence, in order to assess strategies to increase production, ME intake needs to be revisited.

As stated earlier, DM intake has by far the greatest effect on performance. ME intake can be increased by increasing digestibility or intake. The strategies to do this have been discussed in previous symposia but in this review we discuss the importance of the form and source of ME.

ME is available to the cells as acetate (butyrate contributes as a C2 equivalent), glucose (propionate and glucogenic amino acids contribute to this), lipid and amino acids. The yield of ATP from glucose, acetate or lipid varies, but not greatly. Differences in VFA patterns have traditionally been used to explain differences in efficiency of use of ME (Armstrong and Blaxter, 1957) but in the growth studies reported by Orskov et al. (1979) the pattern had no influence on ME used for growth. What does seem apparent is that VFA pattern is important when animals are approaching maturity and laying down fat such that glucogenic substrate supply is important (MacRae and Lobley, 1986), whereas it appears to have little effect in the early growth phase. This latter growth phase is characterized by protein synthesis with a primary need for ATP and all energy substrates are similar in their ATP yield. Bolam et al. (1996b) could find no difference between acetate or glucose as an energy substrate for improving N retention in lambs. Muscle cells may use different substrates preferentially and this changes under exercise (grazing) or high energy demand (Pethick, 1993). Increasing energy supply into the cell may occur by virtue of having an array of substrates presented to the cell for transport into the cell rather than

concentrating increasingly on one type and its transporter system. Lipids in plants may be important here as lipid supplements have well-recognized positive effects on growth and milk production when incorporated at levels not exceeding 5% of DM (De Peters and Cant, 1992). Most pasture species are usually low in lipids but certain forage crops, e.g. soybean, can provide significant amounts of lipid if grazed when pods are present. Recently trans unsaturated fatty acids have been implicated in low milk fat (Gaynor et al., 1994) and inhibition of fat synthesis in mammary and adipose tissues (Teter et al., 1990; Atal et al., 1994). Plants do not appear to have trans-fatty acids but animals with a high unsaturated fatty acid intake will produce trans-fatty acids within the rumen (J.P. Cant, personal communication).

Branched-chain amino acids are also used as an energy substrate by muscle cells and can regulate metabolism (Lobley, 1990, 1992). It is difficult to determine what degree of change in supply of branched-chain amino acids would be useful, if at all, at this stage but in the development of undegradable protein fractions ensuring the supply of branched-chain amino acids would be sensible. With similar reasoning the supply of phenylalanine + tyrosine is important for the efficient use of other essential amino acids in milk protein synthesis (Cant and McBride, 1995b).

Recently Cant and McBride (1995a) proposed that blood flow and delivery of nutrients to a tissue bed was a most important factor influencing synthesis and use of nutrients within the tissue bed. In modelling metabolism within the mammary gland and examining experimental data they found that increasing lipid content in the diet could lead to depressed yield and content of milk protein through the effect of the lipid on adenylate charge within the cell leading, in turn, to a negative feedback on blood flow to the mammary tissue bed (Cant and McBride, 1995b). This is a most exciting development providing a mechanism by which nutrient balance and specific nutrient supply might influence production responses.

Supplements. Supplements are one way in which ME intake, and as a consequence the MP supply to the animal, is increased. The developers of forage-based systems are often reluctant to use supplements as it appears to highlight a limitation of the plant. However, the key to the sustainable use of a pasture-based system is the agronomic competitiveness of the plant. Supplementation seems an appropriate strategy to utilise those competitive plants and enhance animal productivity or overcome problems.

The response of animals to protein supplements was collated by Poppi and McLennan (1995; see Fig. 3 b), and Fig. 3 (a) outlines a similar collation of data for energy supplements of various types. The data are drawn from a wide array of experiments, primarily using young growing cattle but with considerable variability in the nature of the basal diet, the type of energy supplement used, and the level of inclusion of N in the supplement which has important implications for the response achieved. The data show that the extent of the response varies with the quality of the basal diet, as defined by the liveweight gain achieved from the basal diet unsupplemented. The higher the quality, the lower the response (Fig. 3 a). It is interesting to compare the protein and energy response figures (Figs. 3 a, b). It should be stressed that neither supplement group provides just energy or just protein. The estimated supply of MP and ME from cottonseed meal and barley are given in Table 8 showing that both supplements provide both MP and ME, albeit it in different proportions. With lower quality forages, the response above the control is substantial and linear for energy supplements and, although a linear relationship is plotted for the protein supplements, the data appear to follow a curvilinear relationship for protein supplements, as indicated by the

high positive intercept if the line is extrapolated to zero intake. The maximum increment is about 0.9 kg/d with the protein supplements. Of particular interest is the response to supplementation up to the 0.5% W level of feeding, as it is unlikely that any manipulation of the plant could alter nutrients beyond this level. For high quality forages, the response curve is essentially flat with a growth response of *ca.* 0.16 kg/d for protein and 0.12 kg/d for energy supplements. Considerably higher responses were recorded for lower quality forages. These observations can be viewed as a response to the supplement or considered in relation to the necessary change in nutrient level and type which would have to be made within the plant for a similar increase in growth rate. However, it is clear that considerable changes need to be made for a significant increase in liveweight gain. Substitution (of supplement for basal diet) is a major factor influencing the response to supplements, and thereby both jeopardising attainment of significant increases in growth rate and of providing a cost-effective management strategy, especially with high quality forage (Fig. 3). This phenomenon has been well recognised for a long time but is no closer to being resolved. If Weston's model of intake is taken to its logical conclusion (Weston, 1985, 1996; Gherardi and Black, 1989), there may be no way around this substitution problem although there are differences between supplement types in the extent to which substitution occurs (Minson, 1990).

A further issue highlighted by these data is whether the form of the energy substrate influences the response. Use of various supplements will shift the substrate form towards acetate, glucose, amino acids or lipid (the pattern shifts - there is never just one substrate increased). Fermentable fibre (soybean hulls and pulps such as sugarbeet) would be expected to cause a shift towards acetate, degradable starch (barley) towards propionate, less degradable starch (corn) towards glucose, and oilseed meals (whole cottonseed, copra meal etc.) towards lipid. The collated data provided no evidence of differences in energy substrate utilization even though there are theoretical reasons why differences should occur (Black et al., 1987). Most experiments reported were not designed to test this factor, which really should be resolved to provide directions for carbohydrate manipulation of plants, especially relating to the storage of highly fermentable sugars and starch, the latter of which may have variable rumen fermentation.

Physical structure and metabolically active tissue. Diet types (concentrate, roughage, plant species) differ in their effect on metabolically active tissues in the animal (Huntington, 1990). The gut and liver are metabolically active tissues accounting for ca. 50% of the energy expenditure but only 10% of the weight of animals (Lobley, 1990). Any feature of a plant which increases the size of these tissues will influence energy expenditure. Animals consuming grasses are known to have larger amounts of gut tissue and this influences energy expenditure thereby reducing energy available for protein and fat synthesis in the animal.

Extensive protein degradation in the rumen with subsequent high amounts of NH_3 needing to be processed by the liver, is a characteristic of temperate legumes and some grasses. There is both an energy demand to do this as well as increased catabolism of amino acids within the liver which reduces their supply to peripheral tissues (Lobley et al., 1995).

The point is that there are costs involved in processing different amounts of plant material, either in terms of the amount of physical bulk material or the amounts and imbalances of nutrients that arise from digestion. In examining differences in animal production from

plants these hidden costs need to be examined and in some cases strategies used to reduce them. For example, NH_3 load can be reduced by increasing the fermentable OM supply or by feeding a diet which contains condensed tannins.

STRATEGIES TO IMPROVE FORAGE QUALITY

Of all the forage quality attributes of a plant, voluntary intake has by far the greatest effect on animal performance. Attempts to alter the voluntary intake potential of a plant through plant breeding have met with moderate success. Equally successful strategies have been those directed towards better grazing management and improved sward structure. Most successful is the identification of existing plants with high intake potential which is largely related to their physical characteristics, tissue distribution, anatomy and leaf yield, and hence particle breakdown within the rumen. Changes in these characteristics can promote large differences in voluntary intake.

Given that certain plant species have agronomic advantages in a pasture-based system, then by virtue of the intake potential of that plant the animal production level is set according to that intake. Manipulation of nutrient supply around that intake is the next strategy for increasing animal production level and the opportunities for doing this increasingly lie with molecular technologies. The question is: "what parameters should we manipulate?"

The ranking of parameters in importance varies with the digestibility of the plant. With tropical plants and those of digestibility less than approximately 0.7, decreasing lignin or lignin cross-linkages offers the best prospect for substantial improvement in voluntary intake and digestibility. This manipulation can result from using the bmr mutants, ribozyme or antisense technologies. Alternatively, directing microbial activity towards the lignin cross-linkages has also been a focus. A further strategy is to increase protein supply to animals. This can come from the plant or by enhancing microbial protein supply. Ensuring adequate WSC is necessary as there is evidence that efficiency of microbial protein production is often low and could be improved in these plants by improving WSC or NSC content and rumen dilution rates (see earlier). These pasture plants often have a low protein content and targetting protein degradation is not likely to be of major benefit. However, some tropical legumes are high in protein and a program directed at reducing their protein degradability would be very useful. The leucaena model shows what can be achieved. Increased incorporation of protein fractions of low degradability would have little role in these systems because the amounts needed for meaningful increases in meat and milk production appear too high to be achieved. However, it is a strategy of relevance for increasing wool production. Lipids may also be beneficial as a means of increasing the energy density of forage and the range of energy substrates.

Plants of high digestibility and these include most used in the current temperate pasture systems, have little scope for changes in lignin or its cross-linkages but they would benefit from any program aimed specifically at increasing voluntary intake. The grasses are the obvious candidates for change through targetting an increased rate of physical breakdown. The maintenance of an appropriate sward structure is also important in achieving high pasture intake. Most of these temperate plants are characterized by inefficient transfer of protein through the rumen and reducing protein degradation and increasing microbial growth are perhaps of highest priority. Whilst protein degradation is the highest priority, improving WSC and NSC content as well as lipids are also important.

The new manipulation strategies offer long term hope to improve the nutritional characteristics of plants but in the meantime many of the changes needed can be delivered by strategic use of supplements, and this may be just as effective a strategy where agronomically competitive plants are available. Closer examination of supplement experiments will indicate the extent to which manipulation of a nutrient(s) will enhance animal performance.

The relative advantages and consequences of various manipulations are examined in Table 9 using a tropical grass (signal grass (*Brachiaria decumbens*); Higgins et al., 1992) and a temperate grass (ryegrass; Ulyatt et al., 1988). These grasses were chosen because specific data were available but also to illustrate clearly the consequences of certain approaches with both tropical and temperate grasses and legumes. The table should also be compared to Table 9 of Poppi and McLennan (1995) where the consequences of legume incorporation were evaluated. In that study, legume incorporation with no increase in intake had little effect on intestinal protein supply but where it increased total intake by 30%, this strategy supplied an extra 140 g CP/d to the animal. Similarly, reduction in degradability of the legume protein was only a viable strategy where it was accompanied by an increase in intake. The approach used here is to examine the merits of various strategies for increasing the intestinal protein supply by 150 g CP/d for a 200 kg weaner steer, an amount which is required to increase liveweight gain by about 300 g/d (Table 9).

For the tropical grass:

- A change in efficiency of MCP production from 100 to 162 g MCP/kg DOM increases intestinal protein supply by 149 g/d. This change in efficiency could be effected by targetting WSC content and rumen dilution rates. However, such a shift in efficiency increases the rumen degradable crude protein (RDCP) requirements, and consequently the level of CP necessary in the plant, to meet microbial needs. The corollary is that achievement of high efficiency is jeopardised by low RDCP supply.
- The protein degradability value also has a major bearing on the CP content needed in the plant. A degradability of 0.65, with the higher RDCP requirement at higher efficiency of MCP production, sets a CP level in excess of that usually found in tropical grasses, but at 0.8 the CP contents are possible.
- A change in OM digestibility of 5% units through manipulation of WSC content, coupled with an increase in intake, gives the biggest increase in intestinal protein supply (230 g above control) and, as this is linked with an increase in ME intake, it would also promote higher efficiency of use of absorbed protein. Unfortunately, this strategy will require CP content in the plant to increase to 164 or 133 g/kg OM (at degradabilities of 0.65 and 0.80 respectively) to meet the needs for RDCP. Only the latter scenario is possible.
- Changing OM digestibility, and hence intake, by altering the digestibility of the NDF fraction alone (plant selection, bmr gene or similar, genetically-modified microbes) would increase intestinal supply of CP by 50 g/d compared to the previously discussed strategies aimed at increasing efficiency of MCP production (149 g/d) and increasing OM digestibility by changing WSC content (230 g/d). However, this approach does not put a major demand on RDCP requirement which is easily met under currently recorded CP levels in plants, but its effect is less than anticipated because it does not improve the low efficiency of MCP production from tropical grasses.
- Changing the degradability of the protein in grass to supply this additional 150 g CP in the intestines is not a useful approach. Degradability would need to be 0.29-0.44 for the undegradable fraction to supply 150 g CP and this would induce a marked RDCP

deficiency, thereby reducing the MCP supply post-ruminally.

- The legume inclusion (Table 9 of Poppi and McLennan, 1995) is more promising especially if legumes of high CP content and low degradability are used, but these legumes must increase total intake by 20-30%.
- Supplementation would also be an appropriate strategy but where high energy supplements are used attention must be paid to RDCP requirements. Supplements must include sufficient RDCP to balance the fermentable OM therein supplied but if, as is likely, they increase the efficiency of MCP production, then they will need to supply even more RDCP to meet this need which is beyond the capacity of the plant to satisfy.

For a temperate grass:
- Increasing the efficiency of MCP production to 162 g MCP/kg DOM, from often observed values of 130 g MCP/kg DOM (e.g., Cruickshank et al., 1992) will deliver an extra 178 g MCP and easily meet the target of an additional 150 g intestinal CP supply. This is clearly a fruitful area to pursue.
- Increasing digestibility is not really an option as digestibility is already high but appropriate grazing management strategies need to be used to keep it at this high level.
- Increasing intake (10%) with no change in digestibility leads to an extra 106 g/d intestinal CP as it increases both MCP (72 g/d) and UDP (34 g/d) supply. This higher intake accounts for much of the difference between temperate grasses and legumes.
- Reducing degradability down to 0.56 or 0.71, depending on the initial value, will provide an extra 150 g/d of UDP without inducing an RDCP deficiency, in marked contrast to the situation with tropical grass. This is clearly an important strategy and degradability values close to this (0.63) have been recorded (Cruickshank et al., 1992).
- Inclusion of a legume will also provide the additional nutrients, especially if it has low degradability.
- Supplementation to capture the excess RDCP would also be appropriate and less attention needs to be given to RDCP in the formulation of supplements for temperate compared with tropical pastures. This strategy is as useful an approach as changing MCP efficiency and degradability.

CONCLUSIONS
Digestibility and protein considerations have dominated plant manipulations in the past but in this review we have identified manipulation of lignin, WSC and NSC content as being worthy of similar efforts in the future. The animal responds to nutrient supply and, in seeking to enhance animal performance, the strategies of improved grazing management and strategic use of supplements appear just as effective as the high technology approaches currently being explored.

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Table 1

Dietary CP levels above which losses in net transfer of ingested protein to intestinal protein occur, for diets of varying digestibility (from Poppi and McLennan, 1995)

OM digestibility of diet	CP (g/kg DM)
0.80	151
0.70	132
0.60	113
0.50	94

Table 2

The CP content of ash-free neutral detergent solubles (NDS) of some temperate and tropical pastures varying in ash-free NDF and CP content

	NDF (g/kg DM)	CP (g/kg DM)	CP (g/kg NDS)
Oesophageal extrusa of lambs grazing spring temperate pasture (Cruickshank et al., 1992)			
Prairie grass[z]	361	206	414
	496	175	497
Ryegrass[z]	312	281	530
	375	225	458
White Clover[z]	187	306	447
	200	275	414
Lucerne[z]	198	306	466
	180	325	475
Hay of temperate grass leaf fractions (Laredo and Minson, 1975)			
Ryegrass leaf	540	238	711
	568	212	685
Hay of tropical grass leaf fractions (Laredo and Minson, 1973; Poppi et al., 1981)			
Pangola leaf	622-677	72-133	310-508
Rhodes grass leaf	654-730	62-108	357-473
Kikuyu leaf	650-695	81-126	418-524
Setaria leaf	604-659	80-131	345-455
Panicum leaf	634-686	54-120	265-467
Hay of tropical legume leaf (Hendricksen et al., 1981)			
Dolichos lab lab leaf	373	175	345

[z] Values are g/kg OM of extrusa

Table 3

Protein degradability parameters (*a* and *b*, %; *c*, /h) of herbaceous legumes (top group) and browse species (bottom group) as determined by the *in sacco* method (Bediye, 1995)

	Range		
Species	a	b	c
Centrosema sp.	60.5-68.3	22.8-30.8	0.062-0.079
Desmodium intortum	28.5	62.3	0.043
Lotus corniculatus	54.4	38.1	0.070
Medicago sativa	60.5	30.8	0.095
Stylosanthes sp.	38.0-61.5	31.7-56.7	0.065-0.072
Trifolium sp.	35.9-50.5	39.9-58.1	0.061-0.074
Vicia sp.	40.9-61.5	37.8-50.4	0.072-0.093
Cajanus cajan	32.6	58.6	0.049
Chaemacytisus palmensis	29.1	62.3	0.069
Gliricidia sepium	42.0	47.8	0.075
Leucaena sp.	25.6-44.6	41.9-62.2	0.022-0.039
Sesbania sp.	33.6-50.4	40.2-64.6	0.059-0.091

Table 4
The CP content required in forage to meet the degradable nitrogen requirements of rumen microbes for a microbial CP production rate of 9 g /MJ fermentable ME, when degradabilities of the plant protein are 0.7 or 0.9 at varying DM digestibilities

DM digestibility	CP required in diet (g/kg DM) for degradability of:	
	0.7	0.9
0.45	75	58
0.50	86	67
0.55	98	76
0.60	109	85
0.65	120	94
0.70	132	102

Table 5
Concentrations of total and of various types of nonstructural carbohydrates (g/kg DM) in leaves of C3 or C4 *Gramineae* species grown at two temperature regimes (maximum/minimum) (from Chatterton et al., 1989)

	Total	Fructans	Sucrose	Glucose	Fructose	Starch
Cool season grasses (C3)						
10/5 ºC						
Mean	312	115	58	29	24	86
Range	82-771	0-455	9-177	7-72	0-68	29-211
25/15 ºC						
Mean	107	12	23	18	14	41
Range	41-341	0-123	0-83	6-52	0-42	15-110
Warm season grasses (C4)						
10/5 ºC						
Mean	166	3	66	22	14	68
Range	35-290	0-15	16-172	6-83	0-91	10-184
25/15 ºC						
Mean	92	4	22	13	8	47
Range	32-312	0-18	1-94	4-86	0-110	12-134

Table 6
Yields of microbial CP (MCP) from various carbohydrate sources for sheep consuming a silage diet (Chamberlain et al., 1993)

	Sucrose	Lactose	Xylose	Starch	Fructose
MCP yield (g/kg carbohydrate)	144	128	90	53	110

Table 7
Diurnal variation in content of water soluble carbohydrate (WSC) and non-structural carbohydrate (NSC) (g/kg DM) content

	WSC		NSC		
	0600 h	1800 h	0600 h	1800 h	
Grasses	52	80	115	138	Holt and Hirst (1969)
Legumes	70	82	95	135	" "
Alfalfa	110	130	170	210	Lechtenberg et al. (1971)
Festuca	120	140	210	240	Lechtenberg et al. (1972)

Table 8

Estimated metabolizable energy and metabolizable protein supply derived from supplements of cottonseed meal or barley (per kg of supplement) and the resultant protein/energy ratio of the end-products of digestion (calculated from AFRC, 1992)

Level of feeding......	Cottonseed meal		Barley	
	Maintenance	Growing steer	Maintenance	Growing steer
Fractional outflow rate (h^{-1})	0.02	0.05	0.02	0.05
Metabolizable energy				
(ME; MJ/kg DM)	11.1	11.1	12.8	12.8
Crude protein (CP; g/kg DM)	375	375	114	114
Digestible undegraded protein				
(DUP; g/kg DM)	51	92	9	14
Microbial CP (MCP; g/kg DM)^z	79	88	111	123
Metabolizable CP				
(g/kg DM) = (0.6375 MCP +DUP)	101	148	80	92
(g/MJ ME)	9.1	13.3	6.2	7.2
(g/MJ non-protein ME)^y	11.6	19.5	7.3	8.7

^{z} Assuming effective rumen degradable N (ERDN) requirements are met, if not from supplement itself, then from a urea-based supplement. In the case of cottonseed meal, ERDN supply is greater than microbial requirement but with barley it is less than microbial requirement and urea will have to be added at the levels of 7.0 and 14.8 g urea/kg DM at fractional outflow rates of 0.02 and 0.05, respectively.
^{y} By subtracting the gross energy of metabolizable protein from ME.

Figure 1

Observed and theoretical relationships between metabolizable protein (MP) intake and yield of milk protein (Yp). The four lines are the observed regressions at farms a, b, c and d when MP was increased with little change in metabolisable energy (ME) intake. The dashed line kl (efficiency of use of MP based on efficiency of use of ME) relates Yp to MP when CP concentration = 160 g/kg on the assumption that milk yield is determined by ME intake. (Modified from Webster (1992) and reproduced with permission from Butterworth and Heinemann, UK).
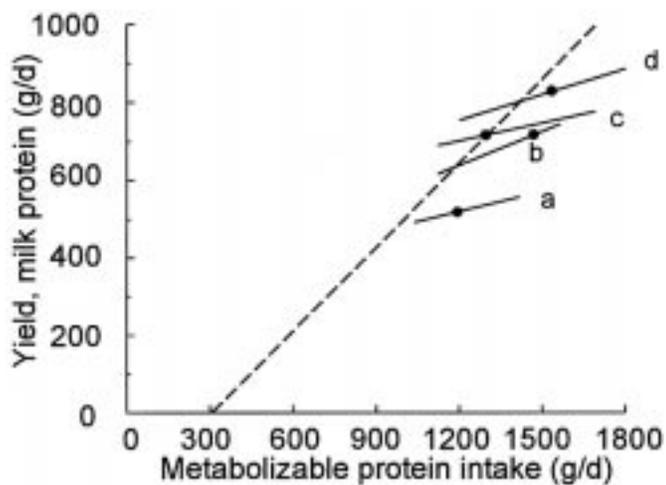
Figure 2

Effect of intake (relative to animal liveweight (W)) of supplements of cottonseed meal (CSM), molasses, grain sorghum and barley on the efficiency of production of microbial crude protein (MCP), expressed in relation to intake of digestible organic matter (DOM), for weaner steers given a basal diet of low quality Rhodes grass (Chloris gayana) hay ad libitum. Efficiencies at nil supplement intake are those for steers receiving hay alone during the relevant run of the experiment (M.J. Bolam, M. Connors, S.R. McLennan and D.P. Poppi, unpublished observations).
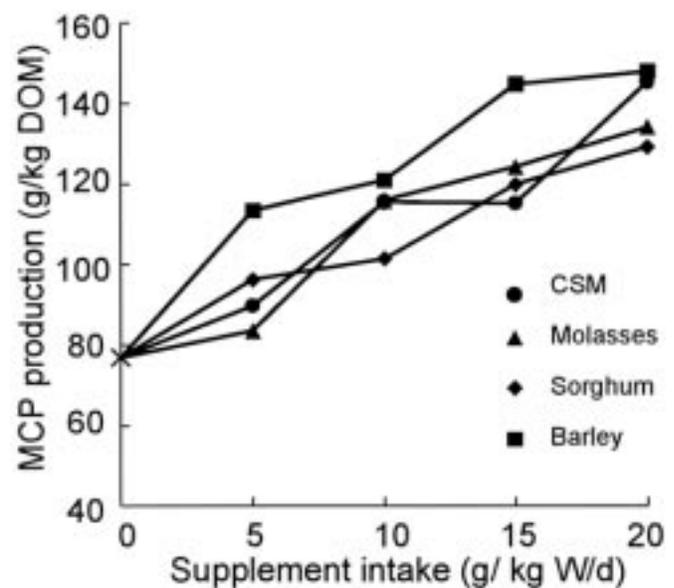
Table 9

The effectiveness and consequences of various strategies to increase CP supply to the intestines by 150 g/d for a 200 kg weaner steer consuming either tropical or temperate grass. Values for intake, digestion and CP content for (tropical) signal grass (*Brachiaria decumbens*; Higgins et al., 1992) and (temperate) ryegrass (*Lolium perenne;* Ulyatt et al., 1988) were used and manipulations involving MCP production efficiencies of 100 (SCA, 1990), 130 and 162 (SCA, 1990; AFRC, 1992; NRC, 1996) g/kg DOM, protein degradabilities of 0.65 and 0.80 (range of values observed; SCA, 1990) and predicted intake change, through altering digestibility (SCA, 1990), were examined

	A. Tropical grass	B. Temperate grass
OM intake (kg/d)	4.0	6.6
OM digestibility	0.60	0.84
DOM intake (kg/d)	2.4	5.54
CP (g/kg OM)	104	255
RDCP (g/d) @ 0.65	272	1092
@ 0.80	332	1344

Strategy 1: alter efficiency of MCP production

A. Tropical grass

	Efficiency of MCP production (g/kg DOM)		
	100 (control)	130	162
MCP production (g/d)	240	312	389
MCP production above control (g/d))	0	72	149
RDCP adequate @ dg 0.65?	yes	no	no
@ dg 0.80?	yes	yes	no
Level of CP (g/kg OM) needed to meet RDCP requirements @ dg 0.65	92	120	150
@ dg 0.80	75	98	122

B. Temperate grass

	Efficiency of MCP production (g/kg DOM)	
	130 (control)	162
MCP production (g/d)	720	898
MCP production above control (g/d))	0	178
RDCP adequate @ dg 0.65 or 0.80?	yes	yes
Level of CP (g/kg OM) needed to meet RDCP requirements @ dg 0.65	168	210
@ dg 0.80	137	170

Strategy 2: change degradability to deliver extra 150 g/d undegraded dietary protein (UDP)

A. Tropical grass (@ 4.0 kg/d OM intake)

	Initial protein degradability	
	0.65	0.80
Initial UDP (g/d)	146	83
Final UDP, after increase (g/d)	296	233
New dg to meet increase in UDP	0.29	0.44
RDCP from this new dg (g/d)	120	183
RDCP adequate for efficiency of 100 g microbial CP/kg DOM at new dg?	no	no

B. Temperate grass (@ 6.6 kg/d OM intake)

	Initial protein degradability	
	0.65	0.80
Initial UDP (g/d)	588	336
Final UDP, after increase (g/d)	738	486
New dg to meet increase in UDP	0.56	0.71
RDCP from this new dg (g/d)	941	1193
RDCP adequate for efficiencies of 130 and 162 g microbial CP/kg DOM at new dg?	yes	yes

Strategy 3: change OM digestibility

Tropical grass (OM digestibility increased from 0.60 to 0.65)

OM intake (kg/d)	4.4
OM digestibility	0.65
DOM intake (kg/d)	2.9
RDCP (g/d) @ 0.65	299
@ 0.80	368

	Efficiency of MCP production (g/kg DOM)	
	100 (change in cell wall digestibility only)	162 (change in WSC content)
MCP production (g/d)	290	470
MCP production above control (g/d))	50	230
RDCP adequate @ dg 0.65?	yes	no
@ dg 0.80?	yes	no
Level of CP (g/kg OM) needed to meet RDCP requirements		
@ dg 0.65	101	164
@ dg 0.80	82	133

Strategy 4: increase intake but no change in digestibility

Temperate grass (OM intake increased from 6.6 to 7.25 kg/d)

OM intake (kg/d)	7.25
DOM intake (kg/d)	6.09
MCP production @ efficiency of 130 g/kg DOM (g/d)	792
MCP production above control (g/d)	72

CP - crude protein;
MCP - microbial CP;
OM - organic matter;
DOM - digestible OM;
RDCP - rumen degradable CP;
dg - protein degradability
WSC - water soluble carbohydrate.

Figure 3

Effect of intake of various high-energy concentrates, including cereal grains, molasses and readily-fermentable, high-fibre sources (**Fig. 3 a**), and of protein meals (**Fig. 3 b**), on the liveweight gain response (kg/d above unsupplemented control animals) for young growing cattle receiving either high quality forage basal diets (closed symbols) or lower quality forage diets (open symbols), in pens or at grazing. Delineation of high and lower quality diets is based on the growth rate of unsupplemented animals being greater (high quality) or equal or lower than 0.8 kg/d (lower quality). For Fig. 3 (a), the relationships between intake and liveweight response were : $Y = 0.062 + 0.069X$, ($R^2 = 14.6\%$), and $Y = 0.057 + 0.288X$, ($R^2 = 58.4\%$), for the high and lower quality diets, respectively. Data have been extracted and calculated from S.R. McLennan (unpublished observations), Beames (1959), Dodsworth and Ball (1962), Bryant et al. (1965), Musangi et al. (1965), Forbes et al. (1966, 1967), Morris and Gulbransen (1970), Perry et al. (1971a, b), Tayler and Wilkinson (1972), Bond and Rumsey (1973), Gulbransen (1974, 1976a, b), Lake et al. (1974), Lowrey et al. (1976a, b), Utley and McCormick (1976), Winks et al. (1980), McLennan et al. (1984, 1989), Goetsch et al. (1991), Brown (1993), Forster et al. (1993), Galloway et al. (1993), de Figueiredo et al. (1994), Grundy et al. (1994), Rowe et al. (1994), Horn et al. (1995) and Hess et al. (1996). Fig. 3 (b) has been modified from data collated by Poppi and McLennan (1995).