Options for efficient utilisation of high fibre feed resources in low input ruminant production systems in a changing climate: A review

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Abstract

One of the major effects of climate change is disruption in normal weather patterns, especially an increase in long-term annual temperature, and more frequent and intense droughts and floods. These changes have impact on the natural resource base that includes plants, animals and biodiversity. Consequently, this diminishes feed and water resources which livestock depend on to survive and therefore impacting negatively on food security and household incomes of smallholder livestock producers and pastoralists, the majority of whom are found in the tropics. Efficient utilization of available feed resource by ruminants, most of it being high in fibre and low in protein content is often constrained by low digestibility and inefficient metabolism of absorbed nutrients at the tissue metabolic level. The low digestibility of high fibre forage in ruminants is mainly attributed to a high level of lignification and a deficiency of essential nutrients, especially nitrogen (N) and sulphur (S) that are required by rumen microbes for optimal growth. Furthermore, the absorbed nutrients also tend to be imbalanced in the ratio of protein to energy and/or acetogenic to glucogenic substrates. As a result the intake of high fibre forages in ruminants is often associated with a significant loss of feed energy as heat increment and methane (CH_4) gas production, with the later also contributing significantly to global warming through greenhouse gas emissions.

This review gives an overview of the various strategies in the form of treatment and supplementation that have been shown to improve digestion and intake of high fibre forages in ruminants, and also reducing CH_4 gas production. The role of rumen degradable nutrients as well as by-pass nutrients in enhancing digestion and absorption of nutrients that are balanced in protein: energy ratio and/or acetogenic: glucogenic substrates is also reviewed and suggested as one way of increasing metabolic efficiency of absorbed nutrients at the tissue level to reduce heat increment. The role of glucogenic substrates such as propionate and protein/amino acids in ensuring an adequate supply of reducing equivalents in the form of reduced nicotinamide adenine dinucleotide phosphate (NADPH) that is required for the conservation of excess acetate as fat in the adipose tissue and also for regeneration of oxaloacetate for efficient VFA energy metabolism in the body tissues is also reviewed. It is concluded that a multipronged approach combining treatment with supplementation with cheap and locally available rumen degradable nutrients (e.g. molasses-urea liquid mixture and the urea-molasses-mineral based multi-nutrient block) and bypass nutrients that are compatible with low input ruminant production systems holds the key to increasing efficiency in the utilization of high fibre-low protein forage in ruminants. This can play a major role in increasing the capacity of smallholder livestock producers and pastoralists in most parts of the tropics to adapt and therefore mitigate the adverse effects of climate change.

Keywords: adaptation, climate change, forage, greenhouse gases, mitigation

Introduction

Mitigating the effects of greenhouse gases such as methane, carbon dioxide, nitrous oxide and chlorofluorocarbon (CFCs) responsible for the changing climate is attracting attention in low input livestock production systems in the tropics. It is predicted that changing climate will be characterized by extreme and sometimes unpredictable weather events that include: more frequent and intense drought, rising mean ambient temperatures leading to heat stress in plants, livestock and humans, and a higher than average rainfall in some wet seasons, which will lead to massive floods in some areas. Furthermore, in some regions long term mean rainfall data shows irregular peaks and troughs which in an environment often characterised by higher mean ambient temperature translates into decreasing available moisture for plant growth and therefore low crop yields and pastures (Ndathi et al 2011). Various models have been proposed to predict the magnitude and severity of the negative effects of global warming depending on the mitigation measures that will be put in place at the present time to check the rate of green house gas emission. For example, a 2.5^{o}C increase in global temperature above the levels prevailing before industrialisation will result in major losses with about 20-30 of plant and animal species being at risk (IPCC 2007). This is likely to greatly affect the quantity and quality of plant biomass including pastures and crop residues on which ruminant livestock depend for survival, a scenario that is likely to have disastrous consequence on animal production performance (Devendara and Leng 2011; Ndathi et al 2011). Besides the indirect effect on both quantity and quality of feed resources available, high ambient temperature and humidity do also negatively affect animals productivity by reducing production potential of modern breeds by between one half and one third (Parson et al 2001). The fertility and health and to some extent even longevity are also seriously compromised (King et al 2006). At the moment there is some evidence of what is likely to happen in the near future if no mitigation measures are put in place to check the effects of accelerated emission of greenhouse gases. These effects are in the form of decreasing natural resource base, especially pastures, water resources and even species biodiversity with the indigenous animal genetic resources being worst affected (FAO 2007a,b).

All these aspects of climate change will impact negatively on smallholder livestock producers in the agro-pastoral areas and pastoralists in arid and semi-arid areas (ASALs) with disastrous consequences on food security, biomass fuel availability and household income which will inevitably lead to increasing levels of poverty, especially among the vulnerable groups in the rural areas (IPCC 2007; Ndathi et al 2011). This is likely to impact negatively on the achievement of noble goals such as the millennium development goals (MDG) and even Kenya's Vision 2030. From a global perspective the impact is likely to be felt more and with devastating effects in the tropics where the majority of the vulnerable world population live and the home of the largest proportion of world ruminant livestock (FAO 2007b). Incidentally the tropic is also the region where ensuring adequate nutrition, especially in animal protein for the majority of the human population has always been a major challenge (FAO 2007b). For example, it is projected that by 2050 the per capita meat and milk consumption will be 44 kg and 78 kg in developing countries while that of developed countries for the same products will be 94 kg and 216 kg respectively (Rosegrant et al 2009) indicating a huge global demand for animal protein which will be a major challenge to supply. Therefore, any decrease in animal productivity is not tenable as available evidence suggests that the demand for animal protein in the tropics is on the increase due to the rapidly changing demographic factors such as growing human population, urbanization, improved per capita income and changes in lifestyle (FAO 2007a,b; Rosegrant et al 2009).

Furthermore, the increasing rate at which available resources such as arable land, biological resources (plants & animals), water, fossil fuels and even some minerals for fertiliser manufacture (N, P, K & S) are being depleted and the predicted effects of climate change will lead to spiralling food costs and financial crises most likely with devastating consequences on the livelihoods of many households (Leng 2009a,b; Devendra and Leng 2011). There are reports that the predicted climate change is expected to put 49 million additional people at risk of hunger by 2020, and 132 million by 2050 (IFAD 2009) with a relatively high proportion of these people being located in poor countries majority of them being in the tropics. This situation is likely to adversely affect the livelihood of most smallholder livestock producers and pastoralists in the tropics unless they are assisted in increasing their adaptive capacity to mitigate the effects of predicted climate change. This can be achieved through multipronged strategies that include the up scaling of time-tested indigenous coping mechanisms and the development and promotion of the adoption of specific coping strategies in their livestock production systems. Agro-pastoral areas are known to produce large quantities of crop residues which in addition to natural pastures and biomass from failed cereal crop represent a significant proportion of feed resource (Ndathi et al 2011). An efficient use of these feed resources can go a long way in reducing hunger and therefore assist in ameliorating the predicted effects of climate change, especially among the vulnerable groups.

A wide range of crop residues, agro-industrial by-products and to some extent even non-conventional feed resources are readily available in many parts of developing countries in Latin America, Asia and Africa and their intensive use as a feed resource may be one way to increase supply of animal protein from ruminant production in a sustainable low-cost production system (Devendra and Leng 2011). Globally it is conservatively estimated that about one billion metric tonne of crop residues are produced annually mostly in the form of cereal straw and stover, and the bulk of it is used to sustain ruminant livestock in developing countries (Sansoucy 1995; Devendra and Leng 2011). Quantitatively it is estimated that the yield of grain to straw in most cereals is in the ratio of 1:1 and therefore, any expansion in grain production locally or globally to feed the increasing human population is likely to result in an equally large output of straw (Leng 1992). Fibrous crop residue is therefore an important feed resource that cannot be ignored, especially in developing countries where there is an urgent need to increase ruminant production in the face of increasing human population and diminishing resources, a situation likely to be worsened by the predicted changes in climate.

It is proposed in this review that an intensive and efficient utilization of locally available fibrous crop residues, most of which are deficient in protein nitrogen could be one practical way in which ruminant livestock producers in the agro-pastoral and pastoral areas in the tropics could be assisted in adapting to and therefore mitigate the effects of the predicted change in climate. Their abundant supply notwithstanding, an efficient utilisation of these fibrous feed resources by ruminants is often hampered by various constraints. This occurs even when many reports indicate that inadequate feeding and nutrition is a major factor limiting growth in ruminant production in many parts of the tropics (Devendra et al 1997; Devendra and Leng 2011).

Heat increment in ruminant herbivores and its implication on feed utilisation efficiency

High fibre forages most of which are also low in protein form an important feed resource for ruminant herbivores in the tropics, especially cattle and buffalo and to some extent sheep and goats (Egan 1989; Devendra and Leng 2011). In some cases they may be the only feed resources available to smallholder producers to sustain ruminant livestock during the dry period and prolonged drought. However, in spite being abundantly available these feed resources are largely under-utilized by ruminants, mainly because of their low digestibility, leading to low rate of digesta clearance from the gut and therefore low voluntary intake which generally translates into low animal productivity (Lechner-Doll et al 1991). The two major causes of low digestibility and therefore low voluntary intake of fibrous forages have been identified as the high cell wall content and low contents of protein and sulphur (Egan 1989). Furthermore, when these high-fibre forages are digested in the rumen the absorbable end-products of microbial fermentation mainly in the form of volatile fatty acids (VFA) and microbial amino acids are normally imbalanced both in the ratios of protein: energy and glucogenic: acetogenic substrates. This nutrient imbalance inevitably leads to an inefficient metabolism of acetate at the tissue metabolism level given that this is a major VFA accounting for over 60 to 70% the total energy absorbed in the gut during fibre digestion in ruminants. It is widely accepted that it is partly due to this inefficient metabolism of absorbed acetate in the body tissues that ultimately leads to a high heat increment that is normally associated with high fibre basal diets and which results in the animal experiencing heat stress. This contributes to low voluntary feed intake and ultimately low animal productivity, especially under tropical conditions that are often characterized by high ambient temperatures and intense solar radiation (Preston and Leng 1987; Leng 1990), a situation likely to worsen with climate change.

A high ambient temperature occasioned by the predicted climate change is likely to exacerbate the detrimental effects of heat increment normally associated with consumption of fibrous forages in herbivores resulting in a further depression in voluntary intake. It is has been known for a long time that consumption of high fibre forage in ruminant herbivores has normally been associated with high heat increment compared to those fed on concentrates (McClymont 1952; Armstrong and Blaxter, 1961). The initial though simplistic explanation at that time was that most of the heat was generated by the animal doing “more work” during mastication and peristalsis when digesting fibrous forage (McClymont 1952; Armstrong and Blaxter, 1961). However, this view was not convincing enough and was challenged later as more information became available. In fact a more plausible explanation was to come far much later after more advanced tools of studying rumen microbial fermentation and tissue metabolism of absorbed digestion products became available to ruminant nutritionists, and especially the intricate details of tissue metabolism (Egan 1977; Cronje et al 1987; Leng 1990; Cronje et al 1991). The work of these authors among others gave the first clear indication that the high heat increment produced by ruminants subsisting on high fibre-low protein basal diets was not just from "more work" being done by the animal during the digestion process but most of the heat emanated mostly from an inefficient metabolism of VFA at the tissue level. This in particular was in relation to metabolism of absorbed acetogenic substrates, mainly acetate when glucogenic substrates such as propionate and amino acids are limiting. It therefore logically follows that any attempt to increase the ruminant's capacity to utilize high fibre forage in an environment characterized by increasing ambient temperatures due to the predicted effects of climate change must of necessity include strategies that focus on ways and means of reducing heat increment by increasing efficiency of forage digestion in the rumen and complemented with an equally efficient metabolism of absorbed acetate at the tissue metabolism level.

Production of methane from enteric fermentation in ruminant herbivores

While the use of fibrous crop residues as a cheap feed for ruminant herbivores appears to be an obvious choice for many ruminant producers in low cost crop-livestock production systems, it incidentally also comes with an extra baggage in the form of methane (CH_4) gas production mainly due to the inefficiency inherent to enteric fermentation. It is currently estimated that approximately 80 to 115 million tonnes of methane which is equivalent to 15 to 20 % of the total anthropogenic methane gas production emanates from enteric fermentation in herbivores (LEDI 2005). The strategies for increasing efficiency in the digestibility of forage in the rumen therefore needs to incorporate measures that can also reduce methane gas production. Such a strategy has the dual benefit of not only releasing more feed energy to the host animal for metabolism but also helps to reduce the greenhouse gas emissions that have been blamed for the predicted changes in climate particularly, the global warming. This is crucial given that enteric fermentation of high fibre forages in the rumen of foregut fermentation results in approximately 4-12% of feed gross energy being lost as CH_4 (Wittenberg and Boadi 2001; Alford et al 2006). However, there are concerns in some quarters that from a global perspective, the proportion of greenhouse gases emanating from ruminants has often been exaggerated when compared to that produced by transport and mining industries. In spite of the differences in opinion on the proportional source of greenhouse gases, there is general consensus among ruminant nutritionists on the need to urgently reduce CH_4 gas production from ruminant herbivores at least to reduce losses in feed gross energy and in the process releasing more energy for use by the animal. This will also have an added benefit of reducing greenhouse gases emission to the environment.

It is therefore proposed that strategies to assist vulnerable livestock producers to cope with the effects of predicted changes in climate must be holistic, practical and mainly focusing on increasing feed utilization efficiency by reducing the proportion of feed gross energy lost as heat and CH_4 gas production. The adaptive or coping strategies that can be used to help smallholder livestock producers and pastoralists in low input production systems in the tropics can assume various forms focussing on dietary manipulation and other complementary management approaches that enhance livestock productivity under a changing climate. Such measures are necessary to avoid loss in body condition, low live weight and ultimately low animal production performance.

The objective of this review is to highlight the various constraints that hinder realization of the nutritional potential of high fibre-low protein basal roughages, especially fibrous crop residues while at the same time exploring the options that are available and their possible role in enhancing efficient use these forages as feed for ruminant herbivores in the tropics. This is while taking into consideration low input ruminant production systems that are widely practised in many parts of the tropics and within the context of the effects of the predicted changes in climate. This is crucial because technological packages that are considered successful are those that are widely accepted and able to contribute to household food security, increased income, and can be up scaled for adoption by other farmers due to their positive contribution to improved animal production. This review therefore explores the various intervention strategies that are reported in the literature and which focus on stimulating efficient rumen microbial fermentation and reduced enteric methane gas production. The review also revisits the classical explanation of the sources of high heat increment in ruminants subsisting on high fibre basal diets, while shedding more light on the more recent explanation based on advances made in tissue metabolism of absorbed nutrients. Attempts have also been made to review practical approaches that can be used to reduce heat increment and CH_4 gas production in ruminants subsisting on high fibre basal diets.

Constraints to efficient utilization of high fibre forage by ruminants

Low digestibility

It is widely acknowledged that low digestibility is a major factor constraining voluntary intake of high-fibre low-protein roughage in ruminants. In an attempt to address this constraint, most attention has focused on a number of factors thought to contribute significantly to low digestibility and therefore low voluntary intake. These are the high cell wall contents and the low content of rumen degradable nutrients, especially nitrogen (N) and sulphur (S) and also low content of micro and macro minerals (Preston and Leng 1987, 1990; Leng 2009a). Major advances in plant science and biochemistry have contributed significantly to a better understanding of the physical and chemical architecture of major components of high fibre forages, especially cellulose, hemicellulose and lignin. In particular the relationship between the amorphous and crystalline portions of the cellulose and the association between the structural carbohydrates and the lignin. This knowledge has made it possible to identify specific interventions in the form of both physical and chemical treatments that can be used to treat fibrous crop residues to complement rumination in the animal in a bid to increase the rate of reduction of the particle size of the refractory parts of the forage. Besides increasing the rate and extent of fibre digestion in the rumen this ultimately translates to a higher voluntary intake of the forage which increases animal productivity.

A high lignin content in the forage is likely to form a major obstacle to the digestion of fibrous crop residues in the rumen unless physical and/ or chemical treatments are effected to disrupt this ligno-cellulosic linkage in the forage. The use of strong and weak alkalis such as sodium hydroxide, ammoniation and urea-ammonia treatment that have been widely applied in parts of the world with varying degrees of success is aimed at achieving similar results (Sundstol et al 1993; Devendra et al 1997; Leng 2004; Devendra and Leng 2011). Among the chemical treatments, the use of urea-ammonia has been the most successfully applied in many low-input low-output ruminant production systems in developing countries, especially in Asia where significant increases in both growth and milk production have been realised (Sansoucy 1995; Leng 2004). Even better results in animal productivity have been realised when chemical treatments has been complemented with supplementation with by-pass nutrients, especially agro-industrial by-products such as cotton seed cake (Sansoucy 1995). The effectiveness of these treatments in increasing digestibility lies in making the ingested forage material more susceptible to degradation by rumen microbes.

At the moment our understanding of how the ingested plant material is comminuted to particle sizes that are small and dense enough to be cleared from the rumen to the lower gut through the reticulo-omasal orifice is now better than before and especially the roles of rumination and microbial fermentation (Fahey and Merchen 1987; Lechner-Doll et al 1991). Indeed various models have been proposed to explain the dynamics of particle size reduction and digesta movement in and out of the various compartments in the gastro-intestinal tract of the ruminant, and especially the rumen (Lechner-Doll et al 1991). It is apparent from these models that the rate of digesta clearance from the rumen to lower parts of the gut and which to a large extent influences intake to a large extent depends on the proportion of the completely indigestible material in the roughage (Lechner-Doll et al 1991). There are indeed opportunities for the use of low cost shredding machines at the farm level for shredding crop residues so as to reduce particle sizes prior to feeding the refractory forage material to ruminants. Such an intervention at the farm level in agro-pastoral areas can be quite successful, especially where institutional support from the both public and private sector is available.

Opportunities for reduction of methane gas emission from enteric fermentation

It is recognized that during the enteric microbial fermentation of high fibre forages in the rumen of foregut fermenters, an average of 4-12% of gross energy (GE) in the feed is lost as methane gas (Wittenberg and Boadi 2001). This, however, varies with quality of the roughage and the level of concentrate supplementation. This represents a significant loss of feed energy besides contributing to greenhouse gas emission. For example, steers fed high quality forage produced 50% less CH_4 gas compared to those on mature pastures that is high in fibre and therefore of low digestibility (Boadi et al 2000). This implies that ruminants subsisting on poor quality mature forage that is normally high in fibre are likely to waste more feed GE as CH_4 gas compared to those subsisting on high quality forage of fairly high digestibility index. Besides loss of feed energy as CH_4 gas, further energy loss as heat increment is also incurred during intense mastication that is normally associated with high fibre forages. It is therefore apparent that mastication of forage harvested/grazed at the prime stage of growth when it is not yet highly lignified requires lower energy during mastication and therefore a saving on energy used during digestion. This suggests that there are opportunities for efficient utilization these roughages when they are harvested and conserved at their prime stage of growth or alternatively allowing the animals to graze on them before their quality starts to deteriorate. It has been reported that cattle grazing pastures in rotation wasted only about 7.1% of GE as CH_4 compared to a higher level of 9.5% when on a system of continuous grazing (McCaughey et al 1999). This suggests that grazing grass pastures at their prime stage of growth or on grass/legume mixtures or legumes alone can reduce significantly wastage of feed GE as CH_4 gas. Besides, this will simultaneously contribute to a reduction in greenhouse gas emission in the environment. While this strategy is practical in pasture-based production systems such as those practised by pastoralists, it may not be a viable option in most agro-pastoral crop-livestock mixed production systems in medium to high potential areas where crop residue is used as the main source of forage for ruminant herbivores during the dry season when high quality forage is normally scarce.

Use of feed additives

Other options for reducing methane gas production from enteric microbial fermentation and therefore releasing more feed GE to the animal have been proposed, though their practical application have been questioned. Most of these options aim at stimulating fermentation patterns that utilize excess reducing power (hydrogen) in the rumen and conserving it in form of volatile fatty acids (VFA), especially propionate. For example, the use of ionophores such as monensin and lasolocid as feed additives has been reported to reduce methane gas emission in dairy cows by as much as 28% (Kinsman et al 1997). This is achieved through selective suppression of some strains of cellulolytic bacteria that favour acetate-producing fermentation pathways (acetate type) rather than a propionate type of fermentation. The latter type of fermentation pattern conserves more feed GE as VFA when compared to the former type of fermentation (Kinsman et al 1997), with an added benefit of lower greenhouse gas emission in form of methane. Unfortunately, the benefits are normally short-lived mainly due to the rumen microbes adapting to the ionophores (Wittenberg and Boadi 2001). Besides there is also the cost considerations of the ionophores that may be way beyond the reach of resource constrained smallholder livestock producers in agro-pastoral areas and pastoralists who incidentally are also some of the targeted beneficiaries of this mitigation strategy. This suggests that economic viability notwithstanding, the sustainability of this approach as a strategy to reducing CH_4 gas production in ruminants is in doubt. Recent studies have also shown that nitrite (NO_2^-) supplementation to ruminants on high fibre diets may also be beneficial in supplying rumen microbes with degradable N while also acting as a sink for the hydrogen in the rumen and therefore reducing methane gas production (Hulshof et al 2012).

Use of unsaturated fat/oils

Similarly, the use of moderate quantities of unsaturated fats/oils that act as a sink for excess hydrogen in the rumen has been reported to reduce CH_4 gas production by as much as 33% (Boadi et al 2004, Beauchemin et al 2009). However, caution is required in this approach given that besides the issue of the high cost of fats/oils that may be prohibitive, any fat or oil level higher than 6-7% in the basal diet is likely to depress fibrolytic activity in the rumen and therefore negatively affect the digestibility of the basal forage diet (Mathison et al 1997, Bauman et al 2003). Depression of fibrolytic activity in the rumen is likely to deny the ruminant animal a vital source of cheap energy from the basal forage. Furthermore, there are also reports that the presence of significant content of oil in the rumen may interfere with mobility of protozoa and therefore depressing their activity and population (Demeyer and Van Nevel 1996). While such a development that may suppress fibrolytic activity in the rumen, it may also have a potential benefit in the host animal by reducing nitrogen recycling in the rumen and therefore increasing microbial protein flow to the small intestines. Protozoa are associated with recycling of N in the rumen and therefore reducing efficiency of microbial protein production which denies the ruminant a crucial source of protein (Koening et al 2000). This suggests that in rural communities where the use of ram-press oil-extracted oilseed cake known to contain high contents of residual oil (e.g. sunflower cake) is being popularised as protein supplement for cattle subsisting on high fibre basal forage, there is a need to conduct validation studies to clearly establish the real net benefit of the cake. Such validation studies are crucial before up-scaling the widespread use of these cakes among agro-pastoral communities keeping ruminant livestock. Moreover, for ruminants subsisting on high fibre forage that are normally protein-deficient and whose main protein source is likely to be microbial protein, the potential benefit of natural defaunation arising from the residual oil in ram-press oil-extracted cake need to be explored further and validated under *in-vivo* conditions. Such a validation process is crucial given the preliminary *in vitro* results that suggest potential natural defaunating properties of the cake (Demeyer and Van Nevel 1996). Detailed *in vivo* studies can assist in establishing the net benefit of manipulating rumen microbial fermentation through the residual oil inherent in ram-press oil-extracted cake. However, for smallholder livestock producers using crop residues, the use of various forms of treatments, and nutrient supplementation remains the most viable and practical option to increase digestion and efficiency of metabolism of absorbed nutrients in the tissues.

Role of treatment in improving digestibility and intake

Various forms of physical, chemical and even biological treatments have been reported as being variably successful in improving digestibility and intake of high fibre forage in ruminants (Sansoucy 1995; Zadrazil et al 1995; Osafo et al 1997). Examples include various forms of physical treatments such as chopping, grinding with/without pelleting and shredding have been used though there are limitations (FAO 2010). For example, chopping does not always increase intake with the response depending on the extent of particle size reduction effected by the method used with sufficient particle size reduction to increase intake only achieved by grinding (FAO 2010). Such an increase voluntary intake may somehow compensate the reduction in digestibility occasioned by higher rate of passage of fibre particles from the rumen and therefore lower mean retention time. Overall the animal ends up with a higher intake of digestible energy and therefore making the process of grinding/shredding beneficial. In recent times, shredding in particular has been receiving increased attention due to the fact that unlike fine grinding it does not compromise digestibility through increased rate of passage through the rumen. Initiatives in the local fabrication of portable machines capable of shredding highly refractory fibrous roughage such as cereal stover, especially that from maize is already receiving support in a number of developing countries where such materials are readily available. It is, however, well known that some of the limitations to digestibility are due to the chemical nature of the fibrous roughage making physical treatments on their own to be largely inadequate in surmounting the low digestibility hurdle. This has over the years lead to an intense search for other viable options to complement physical treatments with a view of further improving digestibility. It is in this regard that various forms of chemical treatments such as the use of strong and weak alkali among others have been explored with various degrees of success.

The success of various forms of treatments in increasing digestibility and intake of basal roughage has been attributed to their effect in reducing particle size of the refractory material and/or increasing the susceptibility of the ingested roughage to microbial degradation in the rumen (Lam et al 1992; Lowry and Kennedy 1996). When digestibility increases, the intake of forage organic matter is also increased mainly because a higher rate of reduction of the roughage to particle size and density allows faster clearance of digesta from the rumen to the lower parts in the gastro-intestinal tract (Lechner-Doll et al 1995). Besides increasing digestibility, some forms of physical treatment such as grinding and pelleting have been reported to reduce CH_4 gas production in cattle by as much as 20 to 40% (Wittenberg and Boadi 2001). Such a reduction in CH_4 production is likely to translate into higher VFA absorption in the gut and therefore more energy being available to the animal. However, these treatments on their own are generally inadequate in achieving digestibility and intake levels that can guarantee adequate intake of digestible nutrients to meet maintenance requirements and a reasonable production level. This is mainly due to the fact that most fibrous roughage is also normally deficient in key degradable nutrients such as nitrogen and sulphur that are required by the cellulolytic microbes in the rumen for optimal growth (Preston and Leng 1987; Leng 1990). Supplementing animals subsisting on high fibre basal forages with these limiting nutrients is considered critical for optimal growth of rumen microbes. Furthermore, this is a necessary prerequisite for an efficient fibre digestion in the rumen to ensure absorption and delivery of adequate quantities of volatile fatty acids (energy) and microbial amino acid supply to the body tissues.

Supplementation of rumen degradable nutrients as a strategy for improving digestibility

Numerous opportunities exist for manipulating rumen microbial fermentation and intestinal digestion in ruminants subsisting on high fibre forages to increase digestibility and intake. This can be achieved through strategic supplementation of key nutrients such as rumen degradable nitrogen (N), sulphur (S), by-pass protein and even carbohydrates. Supplementation with rumen degradable N in particular ensures adequate supply of ammonia N (NH_3-N) to the cellulolytic microbes for efficient fibre degradation in the rumen. It has been known for a long time that cellulolytic bacteria have a specific requirement for ammonia N for optimal growth (Bryant 1973) due to a lack of an efficient mechanism to transfer amino acid N across their cell membrane into the cell protoplasm (Russell et al 1990). On the other hand Sulphur is specifically required by anaerobic fungi in the rumen for their proliferation, especially formation of fruiting bodies (sporangium) and subsequent release of zoospores (Phillips and Gordon 1991). This is considered important because rumen anaerobic fungi are known to play a major role in the initial colonization of refractory fibrous material, a process that helps in opening it up to secondary invasion and solubilisation by the cellulolytic bacteria (Gordon 1985; Phillips and Gordon 1991; Gordon and Phillips 1995). Presumably, sulphur supplementation may also be crucial in ruminants receiving a commercial yeast supplement (*Sacchromyeces cerevisciae*) in a bid to boost fibre digestion in the rumen of ruminants subsisting on fibrous forages such as crop residues.

Supplementation with rumen degradable nutrients and sulphur is done with a view of increasing digestibility and ultimately stimulating higher absorption of acetogenic and glucogenic substrates (propionate and microbial amino acids) from the gut so as to deliver a more balanced ratio of absorbed nutrients for efficient tissue metabolism. There are indeed many reports on the use of various supplements to increase digestibility in ruminants fed high fibre roughage among them being urea, preformed protein such as cotton seed cake (Preston and Leng 1984; Iwanyanwu et al 1990; Sansoucy 1995) and even carbohydrates (Ørskov 1986; Lee et al 1987; Fonseca et al 2001; Royes et al 2001). However, issues of practical application of some of these supplementation strategies often arise, given the resource constraints facing many smallholder livestock producers and pastoralists practicing low input ruminant production systems in the tropics. Furthermore, the level of sophistication of some supplementation strategies may require a skill base that is not compatible with low education levels of the majority of these end users and viable practical options must be explored.

One such practical supplementation strategy that has been pre-tested for adoption among smallholder ruminant livestock producers is the use of molasses-urea liquid mixture (MULM) supplementation on chopped or shredded cereal crop residues, such as maize stover (Migwi et al 2003) or when the MULM lick is offered to ruminants grazing on standing hay, a situation common in many parts of Australia, South Africa and even Brazil and Argentina in South America. An example of a MULM formulation on maize stover that was used with success in an on-farm technology transfer project for smallholder dairy producers in Nakuru County, Kenya is shown in Table 1. This formulation was adequate to meet the maintenance requirements of one mature cross-bred dairy cow (Exotic x Zebu) with a live weight of approximately 450 kg and concentrates being added depending on lactation performance.

Table 1. Ingredients in molasses urea liquid (MULM) mixture for feeding one mature dry cow per day for maintenance.

Ingredient	**Amount**
Chopped/shredded maize stover	10 Kg DM
Molasses	2 Kg
Urea	150 g
Defluorinated Ruminant salt (mostly Sodium Chloride)	200 g
Water (As solvent)	2-3 Litres
Complete Mineral Supplement (offered separately)	*Ad libitum*

(Source: Migwi et al 2003).

The use of urea-molasses licks and multi-nutrient block in ruminants grazing on standing hay or feeding on crop residues is based on the same approach and the success of this technology in many parts in Asia, especially in China and India is well documented (Sansoucy 1995; FAO 2010). Overall these supplementation strategies tend to have incremental effects on rumen microbial fermentation resulting in a higher absorption of VFA from the gut and consequently better animal production performance (Sansoucy 1995; Fonseca et al 2001; Royes et al 2001).

Use of protein rich forages including herbaceous legumes and multipurpose trees

The use of protein rich forages such as lucerne, Dolichos lablab, vetch, desmodium and even sweet potato vines as supplements to high fibre-low protein roughages such as crop residues has great potential given that most of these forages are easy to grow in most agro-pastoral areas. Equally important are the multipurpose trees (MPTs) legumes such as lucaena (*Leucaena leucocephala*), calliadra (*Calliandra calothyrus*) and gliricidia (*Gliricidia sepium*). The MPTs have unique qualities in that they remain green even during the dry period due to their deep root system that can access subterranean water. They can therefore provide protein rich forage to the animals during dry period or even drought when other feed sources are in short supply. However, the use of these supplements is not without challenges such as unavailability of planting materials for the various agro-ecological zones and even pest attack such as in the case of gliricidia.

Use of yeast culture supplementation to improve crop residue nutritive value

In recent years, yeast culture *(Saccharomyces cerevisiae)* has been used to improve the nutritive value and utilisation efficiency of low-quality roughages such as crop residues (Tang et al 2008). There are reports that dietary supplementation of yeast culture increases the percentage ruminal cellulolytic and proteolytic bacteria (Galip 2006). It has also been reported to increase dry matter intake in ruminants: For example, Williams et al 1991 reported an increase of 1.2kg/day while Moallem et al 2009 indicated an increase of 2.5% in dry matter intake due to addition of live yeast in basal roughage diet. There are suggestions that addition of yeast culture in the rumen increases the number of fibre digesting bacteria possibly by assisting in hydrogen transfer during the metabolic processes associated with fibrolysis. There is also a possibility that yeast culture provides soluble growth factors that stimulate growth of ruminal bacteria that utilize lactate and digest cellulose (Hossain and Haque 2009). All these studies suggest that there is a potential to utilize yeast culture in boosting utilization efficiency of low quality roughage such as crop residues, especially when complemented with strategic supplementation of limiting nutrients such as nitrogen and sulphur given than that the later is required for growth of most rumen anaerobic fungi (Phillips and Gordon 1991). However, the packaging of this technology must be appropriate to most smallholder livestock producers, especially those in crop-livestock mixed farming systems where crop residues form an important feed resource for cattle.

Complementary effects of treatment and supplementation

There are, however, situations when the beneficial effects of some treatments and/ or supplementation are way beyond their individual additive effects on intake and animal production performance which suggests a multiplier effect. Among chemicals that have both treatment and nutrient supplementation effects are urea-ammoniation (Cloete and Kritzler 1984) which besides having a treatment effect also supplies rumen microbes with NH_3-N. Similarly, a combination of ammoniation and sulphur dioxide also tends to have a treatment effect while simultaneously supplying rumen microbes with both N and S (Dryden 1986). Such treatments therefore tend to have a multiplier effect in increasing digestibility and intake of roughage to levels that cannot entirely be attributed to treatment alone. Also positive associative effect has been reported when some protein nitrogen is used as a supplement in high fibre basal roughage (Sansoucy 1995). Negative associative effect has also been known to occur when rapidly fermentable carbohydrates rich such as sugars and starch are used as supplements resulting in depression of both digestibility and intake of basal forage. It is however, noteworthy that surmounting hurdles related to rumen microbial fermentation and total tract digestion does not always translate to an automatic increase in voluntary intake. This is primarily because rumen or even gut functions do not work in isolation from tissue metabolism as the two are closely interrelated in the regulation of feed intake in herbivores (Woyengo et al 2004). It has long been known that constraints associated with inefficient metabolism in the body tissues of absorbed nutrients, especially acetate do impact negatively on voluntary intake via negative feedback (Egan 1965a, 1965b, 1977). These constraints at the tissue metabolism level therefore need to be addressed along those of digestibility if voluntary intake is to be enhanced in ruminants. A model illustrating the interaction between enteric microbial fermentation in the rumen, intestinal digestion and nutrient metabolism at the tissue level and their effect on voluntary intake is shown below (Figure 1).

Figure 1. A model depicting the interaction between rumen digestion, intestinal digestion, tissue metabolism of absorbed nutrients and their influence on voluntary intake in ruminants (Adapted from: Migwi 2006).

Limitation of intake at the tissue metabolism level

It is now well established fact that most of the energy and amino acids available to the ruminant herbivore are absorbed as VFAs from the rumen and microbial protein N digested in the small intestines (Preston and Leng 1987; Leng 1990). For a long time it has been presumed that once the low digestibility hurdle at rumen metabolism level has been overcome by use of various treatments and/ or supplementation with rumen degradable nutrients such as N and S, voluntary intake would improve automatically. Presumably this would lead to delivery of a higher VFA energy and other absorbed nutrients such as amino acids to the body tissues. This however, did not always happen, especially in ruminant herbivores subsisting on high fibre forages in the tropical environment, a fact that puzzled many ruminant nutritionists (Leng 1990).

In an attempt to understand this scenario attention has over the years been directed to the inefficient metabolism of absorbed nutrients at the tissue level as a possible constraint to increased intake of roughage in ruminants. In particular, attention has been given to the issue related to imbalance of absorbed nutrients with two factors being of particular concern; the inadequacy of protein relative to energy (P: E) in the body tissues (Illius and Jessop 1996), and the proportion of glucogenic to acetogenic substrates in the digestion products absorbed from the gut (Leng 1989, 1990; Cronje et al 1991). Most of the early work by Egan (1965a,b; 1977) among others showed that, when the amino acid supply in the body tissues of sheep fed low quality roughage was improved through post-ruminal infusion (abomasal) of protein in the form of casein, voluntary intake was significantly increased. These findings led to the conclusion that it was not just low digestibility alone that constrained voluntary intake of roughage in ruminants but also the inability by the animal to efficiently metabolise the absorbed nutrients at the tissue metabolism level. This was attributed to an imbalance of P: E and /or glucogenic to acetogenic substrates available for metabolism at the tissue level.

Egan (1977) further argued that provided that the body tissues are well supplied with balanced nutrients, especially the ratio of P to E and glucose or glucogenic substrates such as propionate and amino acids, the body tissues could be in a better position to metabolise most of the absorbed acetogenic substrates mainly acetate. Acetate is considered to be a major product of fibre digestion absorbed in the rumen (Cridland, 1983). Furthermore, it has been argued that ruminants could somehow circumvent the low digestibility hurdle by tolerating additional gut distension to accommodate a higher digesta load (Egan 1977). This is in spite of the discomfort such a distension is likely to cause in the animal. Presumably a higher digesta load in the rumen combined with a longer mean retention time is likely to translate into a higher absorption of acetate which would be metabolised efficiently.

Acetate metabolism and implications on intake of high fibre forages in ruminants

Ruminants require energy and other nutrients for both maintenance and production functions such as growth and lactation. Most of the energy is absorbed from the gut in the form of VFA, mainly acetate, while the protein is sourced mainly from microbial protein digested and absorbed from the small intestines. Compared to propionate that is highly glucogenic, acetate is a non-glucogenic substrate and is therefore considered to be primarily an acetogenic substrate as it enters the tricarboxylic acid cycle through the acetyl Coenzyme A pathway. It follows, therefore that any absorbed acetate that is in excess of the quantity required for immediate adenosine triphosphate (ATP) requirements by the animal has to be either converted to long chain fatty acids (LCFA) and stored in the adipose tissue as fat or alternatively it is wastefully oxidized to heat otherwise it will depress appetite and possibly disrupt the pH homeostasis in the body (Berg et al 2002). There are reports that excessive acetate availability in the body tissues relative to glucogenic substrates could result in changes in cell membrane permeability to Na^+ and K^+ ions which results in elevation of ATPase activity in body cells to restore the ionic balance, with the extra ATP generated from acetate metabolism being dissipated as heat (Jessop and Leng 1993). It is hypothesised that the disposal of excess acetate as heat may further exacerbate the already grim situation, and may reduce the animals' capacity to cope with the predicted increase in ambient temperatures arising from the predicted global warming due to greenhouse gas emission. However, the effect may be lower than predicted given that some ruminant herbivores may somehow compensate for this effect by shifting their feeding and rumination patterns to coincide with night time when ambient temperatures are normally cooler.

The synthesis of LCFA from the excess acetate requires a source of reducing equivalents mainly in the form of reduced nicotinamide adenine dinucleotide phosphate (NADPH) which is mostly sourced from oxidation of glucose through the pentose-phosphate pathway (Cronje et al 1987, 1991). If the forage diet or body tissue is inadequate in glucose or glucogenic substrate such as propionate and/or protein that can act as source of reducing equivalents (i.e. hydrogen) to conserve acetate as fat, then most of the excess acetate absorbed from the gut has to be wastefully oxidized to heat via what has often been referred to as the "futile" or "substrate cycle". It is this wasteful oxidation of acetate as heat that has been suggested to be the main source of high heat increment in animals feeding on high-fibre low-protein forage (Cronje et al 1987; Leng 1990; Cronje et al 1991). However, the exact mechanism through which this heat is produced has been open to speculation.

While the exact mechanism through which acetate is wastefully oxidized to heat is still not well understood, several theories have been proposed. One theory proposes that the conversion of acetate to acetyl-CoA through an ATP consuming activation process, and then Acetyl-CoA to acetate again, generates some ATP that is dissipated as heat (Berg et al 2002). According to this theory, the amplification of the forward reaction that involves acetylation could generate even more heat from the oxidation of ATP (Berg et al 2002). This proposition is partly supported by the observation that sheep fed basal roughage (a high acetate output feedstuff) tend to have in their adipose tissue a higher activity of enzymes similar to those involved in the putative futile cycle, when compared to those fed concentrates (low acetate output feedstuff) (Scollan et al 1988). Similarly, the hepatocytes of sheep fed high roughage diets have been reported to have a high substrate cycle activity (Jessop et al 1990), presumably for metabolizing the excess acetate to heat, its benefit to ruminants in the tropics notwithstanding.

While the heat generated from wasteful oxidation of acetate may be useful to ruminants in temperate areas where ambient temperatures are generally low, it may pose a serious challenge for those animals in the tropics, as it is likely to further compromise the already depressed feed intake in those animals arising from higher temperatures in that region. This scenario is likely to be further exacerbated by the predicted global warming occasioned by climate change, unless mitigating measures in dietary manipulation and other management practices such as sheltering the animals from extreme heat and watering them regularly are put in place. However, the magnitude may not be as high as predicted given that herbivores may modify their foraging and rumination behaviour so that these potential heat producing activities are shifted to times of the day, especially at night when ambient temperatures are likely to be lower.

From the foregoing, it is apparent that voluntary intake of high fibre forage in ruminant herbivores can be constrained by impediments associated with inefficient processes at both enteric microbial fermentation level as well as at the tissue metabolism level resulting in high heat increment. Therefore, any attempt to address the intake constraint in ruminants subsisting entirely on high fibre-low protein basal roughage must of necessity be aimed at surmounting digestion and metabolism impediments at these two levels (i.e. at the rumen and at also tissue metabolism levels). This inevitably requires a deeper understanding of the intricate inter-relationship between the functioning of various compartments and their effect on voluntary intake in ruminants as illustrated earlier in this paper (see Figure 1). While the impediments related to rumen digestion may be somehow addressed by incorporating rumen degradable nutrients such as N and S, the use of bypass supplements, particularly preformed protein, in ruminants subsisting on high fibre-low protein roughage may assist in surmounting those at the tissue metabolism level.

The role of bypass nutrients in enhancing metabolism at the tissue level

By-pass protein

Various by-pass nutrients such as protein, carbohydrate and even modified fats that are wholly or partially protected from rumen degradation are likely to benefit ruminant herbivores subsisting on high fibre basal diets (Devendra 1991). Among these, a deficit in dietary protein is more serious than supplies of energy from cereals and strategies in its supply need to be put in place to ensure growth in productivity from these animals (Devendra 2010b). Indeed in many cases, inadequate animal nutrition is the major cause of low animal productivity, especially the ASALs areas (Mnene et al 2004). Generally the low animal productivity has been associated with poor immune response system and therefore resulting in very poor health and body condition of the animals a situation that can be significantly alleviated by adequate supply of dietary protein (Leng 2005). This is mainly because such supplements normally escape wasteful ruminal digestion while delivering key limiting nutrients such as amino acids, glucose and essential fatty acids directly to the body tissues efficiently. Some preformed protein supplements such as cotton seed cake that are partially degraded in the rumen do also have an added advantage compared to non-protein nitrogen (NPN) sources such as urea. This is due to the fact that they not only improve rumen microbial fermentation through enhanced supply of NH_3-N to rumen microbes, but also stimulate a higher tissue metabolism by supplying amino acid N from the intestinal digestion of the undegradable dietary protein fraction. As a result numerous on-farm trials were conducted in the 1990's and the results were very positive in terms of responses in both milk yield from dairy and average daily gain in beef cattle (Sansoucy 1995).

Bypass carbohydrates

There are also reports that when rumen NH_3-N is not limiting, the supplementation with bypass carbohydrate postruminally may have some beneficial effects in boosting the level of glucogenic substrates in the body tissues (Migwi 2006; Migwi et al 2011a,b). This is likely to lead to more efficient acetate metabolism in the body tissues and thus stimulating higher intake of fibrous forage in ruminants (Migwi 2006; Migwi et al 2011a,b). However, the practical application of this supplementation strategy at the farm level, especially in low-input ruminant production systems is open to question, though compared to protein sources carbohydrate supplements, particularly cereal by-product starch are generally more readily available and therefore cheaper.

Carbohydrate supplementation in the form of higher grain/forage ratio also has been reported as being fairly effective in reducing CH_4 gas production and therefore reducing the feed energy lost as methane to only 2-3 % (Johnson et al 1996). This suggests carbohydrates can be used to improve efficiency of forage utilisation with an added benefit of reducing greenhouse gas emission. However, in developing countries where production systems are essentially low input and the high demand for cereal grain to feed the increasing human population, the use of carbohydrate supplementation may be hampered by cost considerations unless cereal based by-products such as bran that are more cheaply available are utilised (Devendra 1991; 2010b). Even in some Western countries such as North America, the continued availability of cereal grain for ruminant livestock feeding is already facing a major challenge due to the emerging competition from biofuel production, especially ethanol (Preston 2009). In most cases the price offered for cereal grain destined for biofuel production is way beyond what would be considered to be economical for animal feed. The issue of cost notwithstanding, when roughage diets are supplemented with readily digestible carbohydrates caution must be exercised due to the possible occurrence of negative associative effect that may depress fibre digestion in the rumen and therefore reduce intake of basal forage, unless strategies are put in place to by-pass rumen fermentation. Furthermore, even where such strategies are used, the benefits of by-passing the rumen fermentation must be weighed against the limited capacity of the ruminant's small intestines to efficiently digest and absorb the by-passed carbohydrates. This is crucial given that there are reports dating back to 1970's and 80's suggesting that sucrase (invertase) activity in the small intestines of ruminants is generally low (Ørskov et al 1972), thus making it difficult for ruminants to effectively digest and/or absorb large quantities of readily fermentable carbohydrates in the small intestines (Ørskov et al 1971, 1972; DeGregorio et al 1982; Siciliano-

Jones and Murphy 1989a, 1989b). Moreover, another major hurdle is that the development of a practical and commercially viable technological package that effectively by-passes the rather inefficient rumen fermentation in favour of the more efficient intestinal digestion of carbohydrates is yet to become a reality, which is in contrast to the case in protein.

The net result of these dietary manipulations is a more efficient utilization of absorbed digestion products, especially the conservation of surplus acetogenic substrates (mainly acetate) as fat for later use during periods of feed scarcity, rather than being wastefully oxidised through the what is normally referred to as the"futile" or "substrate cycle" with the unwanted effect of high heat increment (MacRae and Lobley, 1982; MacRae et al 1985; Crabtree et al 1987, 1990). An efficient metabolism of acetate is likely to lead to lower heat increment in the animal's body and may stimulate higher intake of forage with the attendant benefits of improved animal productivity. This is likely to be of major benefit to ruminant livestock producers in the tropics where adoption of coping strategies to the predicted changes in climate is now more urgent than ever before. Furthermore, this can be achieved while simultaneously reducing CH_4 gas emission from ruminants and therefore contribute to a sustainable livestock production in a changing climate in the medium and long term.

Conclusion

- There is an urgent need to optimise efficiency in the use of high fibre forage in ruminants, especially under low input production systems that characterize most of the livestock production in the tropics. This can be done through a multi-pronged approach that enhances efficiency in enteric microbial fermentation in the rumen to increase absorption of VFA energy. This can be achieved while simultaneously ensuring high microbial protein absorption in the small intestines. A multipronged approach that combines physical and chemical treatment of high fibre forage with strategic supplementation of limiting rumen degradable and by-pass nutrients, especially those that are locally available is proposed. The net result is a duo benefit of an efficient enteric fermentation in the rumen and metabolism of absorbed nutrients at the tissue level which reduces wastage of feed gross energy as heat increment and methane gas emission. This has the potential benefit of increasing the adaptive capacity of vulnerable livestock producers in the agro-pastoral and pastoral areas in the tropics in coping with the ravages of predicted changes in climate while simultaneously contributing to a reduction in greenhouse gas emission.

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