

## Symposium on 'Food supply and quality in a climate-changed world'

### Session 2

## Plant-based strategies towards minimising 'livestock's long shadow'

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Ruminant farming is an important component of the human food chain. Ruminants can use offtake from land unsuitable for cereal crop cultivation via interaction with the diverse microbial population in their rumens. The rumen is a continuous flow fermenter for the digestion of ligno-cellulose, with microbial protein and fermentation end-products incorporated by the animal directly or during post-ruminal digestion. However, ruminal fermentation is inefficient in capturing the nutrient resource presented, resulting in environmental pollution and generation of greenhouse gases. Methane is generated as a consequence of ruminal fermentation and poor retention of ingested forage nitrogen causes nitrogenous pollution of water and land and contributes to the generation of nitrous oxide. One possible cause is the imbalanced provision of dietary substrates to the rumen micro-organisms. Deamination of amino acids by ammonia-producing bacteria liberates ammonia which can be assimilated by the rumen bacteria and used for microbial protein synthesis. However, when carbohydrate is limiting, microbial growth is slow, meaning low demand for ammonia for microbial protein synthesis and excretion of the excess. Protein utilisation can therefore be improved by increasing the availability of readily fermentable sugars in forage or by making protein unavailable for proteolysis through complexing with plant secondary products. Alternatively, realisation that grazing cattle ingest living cells has led to the discovery that plant cells undergo endogenous, stress-mediated protein degradation due to the exposure to rumen conditions. This presents the opportunity to decrease the environmental impact of livestock farming by using decreased proteolysis as a selection tool for the development of improved pasture grass varieties.

**Ruminant: Protein: Nitrogen: Methane: Grass: Clover: Forage**

Making assessments of the impact and value of livestock farming is complex. The rearing of domestic livestock is important in food production, although there are conflicts between the use of land for production of animal feed as opposed to producing grain for human consumption<sup>(1)</sup>. The livestock sector is economically valuable. Livestock contributes 1.4% of global gross domestic product providing employment for 20% of the global population in both developed and developing countries<sup>(1)</sup>. Livestock products can provide an important addition to diet especially in the developing world, providing key vitamins and nutrients. Indeed, the consumption of meat has been linked to both physical and mental development in children<sup>(2)</sup>, but in the developed world over-consumption of meat has been

linked to development of serious health problems<sup>(3)</sup>. Current projections estimate that the global demand for meat and milk will have doubled by 2050 compared with that at the onset of the 21st century<sup>(4)</sup>. This is being driven by demographic changes, (the emergence of a larger, but older population) and economic growth<sup>(1)</sup>. Increased demand for livestock products comes mostly from developing countries as affluence increases, and these same countries also show population increases, with the global population predicted to reach 8.9 billion in 2050, 90% of whom will reside in less developed regions<sup>(5)</sup>.

Meeting the increased demand for livestock products will not be easy. Livestock currently occupies 30% of global (ice free) land area<sup>(1)</sup> with production systems

**Abbreviation:** PPO, polyphenol oxidase.

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varying in scale from the extensive (rangelands) to the intensive (the feedlot system). Land take for livestock production has increased several-fold over recent centuries, but currently competes with land needed for housing, growth of crops for human consumption and increasingly, the growth of bioenergy/biomass crops. This limits the ability to meet the increased demand for animal products by increasing production through the further expansion of grazing lands<sup>(6)</sup>. Intimately coupled with this are the effects that livestock has on the local and global environment. Lands used for livestock farming are man-made ecosystems which contribute to carbon and nitrogen cycles as well as providing habitats. However, deforestation in order to allow access to new rangelands leads to the loss of biodiversity. At a global scale, recent estimates suggest that livestock are responsible for 9% of the anthropogenic CO<sub>2</sub> emissions (including the effects of deforestation) and 37% of the anthropogenic methane (which has 23 times the warming potential of CO<sub>2</sub>), the latter mostly being due to ruminal fermentation which on its own accounts for 30.5% of anthropogenic methane production<sup>(1)</sup>. Livestock farming is also a major consumer of water resources, and a major polluter. Animal wastes contribute about 30% of the N and P in water courses<sup>(1)</sup>, and the use of both organic and inorganic fertilisers in feed production contributing to the emission of NO<sub>x</sub>, N<sub>2</sub>O and ammonia<sup>(7,8)</sup>. Livestock contribute 65% of anthropogenic N<sub>2</sub>O, with 35% of this linked specifically to the abundance and handling of manure-N<sup>(1)</sup>. Although N<sub>2</sub>O is of relatively minor abundance in the atmosphere, it has 296 times the warming potential of CO<sub>2</sub>, and persists for a considerable length of time (>100 years). Locally, N deposition in urine and manures favours proliferation of grasses at the expense of dicotyledonous species, thereby decreasing the biodiversity of the pasture ecosystem. More remotely, N compounds entering the water courses cause eutrophication and nitrate poisoning of aquatic life as well as the loss of biodiversity<sup>(8,9)</sup>.

It is clear that action is needed to facilitate an increased consumption of livestock products in a way which minimises the local and global environmental impact of livestock farming. As with many complex problems, there may not be one overall solution, and not all solutions are practical in all situations, but improvements come as a result of combined actions. The concept of 'stabilisation wedges'<sup>(10)</sup> has been proposed to illustrate how the combined contribution of various strategies can be effective in achieving targets for the reduction of greenhouse gases set under the Kyoto Protocol. A similar concept can be applied to identify numerous targets that individually appear to be inconsequential, but which together would be effective in mitigating the effects of livestock production. Some of these strategies are effective at a policy level, for example, enforcing limitations of N emission to watercourses<sup>(11)</sup> through penalties for non-compliance. There is also the possibility of increasing intensive agriculture to minimise damage to ecosystem services which arises for instance by deforestation to increase grazing. The FAO suggest that the removal of subsidies and realistic pricing would be effective in restricting demand, with knock-on effects on production needs<sup>(1)</sup>. Improvements to the impact of livestock

and arable agriculture can also be made by reducing inputs. Other options identified by the UN include an increased uptake of precision agriculture techniques, such as satellite imaging to inform on the need for fertiliser application, decreasing transport (and hence use of fossil fuels) through an increased awareness of the 'food-miles' concept and minimising the use of pesticides by developing crops with increased nutrient use efficiencies and increased pest/pathogen tolerance<sup>(1)</sup>.

Something that would undoubtedly make a huge contribution to decreased environmental impact is increasing the efficiency with which livestock utilise their feed, and great potential benefits could be gained from the ruminant sector in particular. Although the capacity to perform pre-gastric fermentation enables ruminants to utilise forage species unsuitable for other animals, their environmental impact is disproportionate. Due to the size of the 'global herd' (estimated to be 3.45 billion cattle, buffalo, sheep and goats in 2007<sup>(4)</sup>), relatively modest improvements in performance could result in significant effects in terms of lowering the generation of undesirable emissions. Later, it is discussed how recent advances in understanding the functioning of the rumen have shown that improving rumen function is a realistic target for future improvements given the potential for exploitation of plant-based solutions to mitigate ruminal-based inefficiencies.

### Ruminants as a source of environmental pollutants

Ruminant production is beset by two major problems resulting from inefficiencies in ruminal fermentation: nitrogen and methane emission. It has been estimated that globally ruminal fermentation produces 86 million tonnes of methane a year<sup>(1)</sup>. Anaerobic decomposition of manure from ruminants is estimated to release a further 8.5 million tonnes of methane a year<sup>(1)</sup>. Methane is produced by methanogenic archaea during the final stages of the anaerobic fermentation of plant biomass in the rumen, a process which involves the integrated activities of a variety of different microbial taxa<sup>(12,13)</sup>. Plant carbohydrates including starch, cell-wall polymers and water-soluble carbohydrate are hydrolysed to simple sugars and undergo microbial fermentation via pyruvate, resulting in the production of volatile fatty acids (principally acetate, propionate and butyrate), CO<sub>2</sub> and hydrogen as end-products. The latter two products are the primary substrates for ruminal methanogenic archaea. Although methane generation is considered to be an undesirable process, resulting in ruminal-based inefficiencies in the use of plant biomass, it provides an important hydrogen sink for the rumen ecosystem. The accumulation of hydrogen produced during microbial fermentation can be toxic to certain ruminal micro-organisms unless it is removed<sup>(14)</sup>. Methane production can be calculated from the stoichiometry of the main volatile fatty acids formed during fermentation; acetate and butyrate production results in methane production as they are hydrogen-producing reactions, while propionate formation is a hydrogen-consuming reaction resulting in lowered methane production<sup>(13)</sup>. Animal-based approaches to methane production are

discussed in Scollan *et al.*<sup>(3)</sup>, but plant-based approaches are also appropriate as the ruminant diet has been shown to alter the molar proportions of volatile fatty acids, and consequently can reduce ruminal methane production and methane emission<sup>(13–17)</sup>. Initially, efforts focused on dietary changes involved either adjustment of a major dietary component(s) or the use of supplements to manipulate ruminal fermentation patterns (and subsequently volatile fatty acids production) through the perturbation of microbial populations which contribute to and/or produce ruminal methane. These methods include the application of yeast (*Saccharomyces cerevisiae*), *Aspergillus oryzae* extracts, ionophores (i.e. monensin), organic acids (i.e. fumarate, malate), defaunation and using starch-enriched concentrate feeding systems<sup>(16)</sup>. The potential of plant extracts containing essential oils to manipulate rumen function in order to improve nutrient use efficiency and environmental burden has been demonstrated<sup>(16,18)</sup> and the provision of linseed fatty acid as a dietary supplement can also depress ruminal methanogenesis<sup>(19)</sup>. Future advances could involve the identification of other plants' secondary and primary products which can advantageously perturb rumen function. For example, at the whole forage level, an *in vitro* fermentation study has shown that perennial ryegrass cultivars differing in nutrient composition (for example, water-soluble carbohydrate) could be exploited to mitigate enteric methane emission in a pasture-based production system<sup>(20)</sup>.

Ruminants are also responsible for the direct deposition of N in urine and faeces as urea and ammonia. While in low input systems this does fulfil a role in supplying organic fertiliser, the resource is poorly captured. Soil micro-organisms catalyse conversion to nitrites (by *Nitrosomonas* spp.) and then to nitrates (by *Nitrobacter* spp.). Where nitrate run-off from land enters water sources, it is extremely toxic to aquatic life, and to infants if it enters the source of drinking water supply<sup>(7)</sup>. Although poorly understood, the deposition of N onto land contributes to the soil-borne capacity for N<sub>2</sub>O generation by supplying substrate, in addition to the direct emission of N<sub>2</sub>O in manure<sup>(7)</sup>. A solution to this problem would simply be to decrease stocking density, but this does not address the need to maintain production. A forage-specific effect on the production of atmospheric pollutants has been identified, with the application of slurries from sheep fed kale silage resulting in more N<sub>2</sub>O production than after application of slurry from sheep fed lucerne or ryegrass silage<sup>(21)</sup>. Interestingly, although leguminous crops fix N (so do not require additional N fertiliser) leguminous pastures can also give rise to N leaching, thus permitting N<sub>2</sub>O production<sup>(7)</sup>. Realistic targets for environmental improvement include an increased use of precision agricultural techniques for fertiliser application and increasing N use efficiency (the ability of plants to take up and sequester N) of crop plants<sup>(7)</sup>. A further opportunity is to exploit the natural presence of N-fixing endophytic bacteria on the roots of non-leguminous crop plants, including grasses<sup>(22–24)</sup>, the success of which will enable decreased requirement to add N fertilisers to land for forage production. These bacteria are apparently able to colonise (at low level compared with numbers present in the soil) not just

the root surface, but also the apoplastic spaces (possibly xylem elements) to overcome oxygen toxicity of the nitrogenase enzyme<sup>(23,24)</sup>. The potential of this has been demonstrated by yield improvements in wheat inoculated with *Azospirillum*<sup>(25)</sup>, although this may be mediated by hormonal effects rather than by the modest increase in N fixation<sup>(26)</sup>. An alternative strategy to address N pollution is to move to a more intensive livestock production system which removes waste to a point source<sup>(1)</sup>, but does not fully address the problem of minimising N waste in the first place.

The rumen is a complex ecosystem which essentially functions in the conversion of plant material to microbial protein, driven by the fermentation of plant biomass by a community of bacteria, anaerobic fungi, ciliate protozoa and methanogenic archaea<sup>(27)</sup>. The diversity of these microbial taxa is only now becoming truly acknowledged, due to the application of cultivation-independent techniques<sup>(28–32)</sup>. However, it is with this complex microbial population that the source of ruminal inefficiencies in feed use lies. Forage supplies the nutrients required for microbial proliferation. However, it is believed that there is an imbalance in the relative delivery of protein and carbohydrate which favours the abundance of protein breakdown products during a period of cellulolysis<sup>(33,34)</sup>. The hyper-ammonia-producing bacteria are key contributors to an excessive production of ammonia in the rumen. Hyper-ammonia-producing bacteria can derive energy from amino acids by deamination with a consequential generation of ammonia, which can be assimilated by the rumen bacteria and used for microbial protein synthesis. However, when carbohydrate is limiting, microbial growth rates are slow meaning that an excess of ammonia is produced relative to what can be re-assimilated by the microbial population to generate microbial protein. The excess ammonia cannot be used by the animal, and enters the blood stream for processing into urea before it is removed in the form of excreta. This extremely poor nutrient use efficiency underlies the low retention of dietary N by ruminants, which is in the order of just 20–30%<sup>(33,35)</sup>. Therefore an important target is to find a strategy that can improve N use efficiency in ruminant production systems.

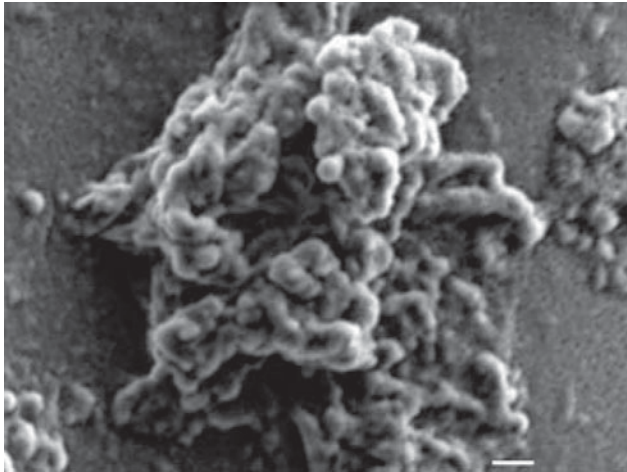
### Plant-based solutions

It is undisputed, and supported by an abundance of literature, that different forage species have different intrinsic qualities in terms of digestibility. Some of these qualities are easily understood, such as increasing protein content of the crop and transfer into ruminant product, albeit with associated N outputs. However, the mechanisms of action of other plant components are less understood. Many plant species contain a diverse collection of secondary products including condensed cyanogenic glycosides, glucosinolates, alkaloids, tannins, phenolics and saponins<sup>(36,37)</sup>. Although originally believed to be undesirable by-products of primary metabolism, the roles of these secondary products are now thought to be mainly defensive (excluding interactions with the specialist feeders), for example, to

prevent attack by insect herbivores<sup>(36–38)</sup>. Indeed, many of these chemicals can be induced by developmental stage, damage, pathogenesis and environment<sup>(36,38,39)</sup>. Furthermore, the presence of secondary metabolites in forage also has implications for large herbivores via the perturbation of rumen function. One example is the non-protein amino acid mimosine which is found in the tropical legume *Leucaena leucocephala*. Although mimosine is toxic, it has been found that ruminants can graze *Leucaena* following an adaptive change in the rumen microflora favouring proliferation of *Synergistes jonesii* which facilitates detoxification of the mimosine derivative<sup>(40–42)</sup>. In terms of potential beneficial effects on ruminant digestion, two groups of compounds have attracted most attention; the condensed tannins (proanthocyanidins) and phenolics. Commonly used tanniferous forage species include the trefoils (*Lotus* species), sainfoin (*Onobrychis viciifolia*) and chicory (*Cichorium intybus*). Tannins have been shown to have a beneficial effect on ruminant production and parasite load when included in ruminant diets, typically at less than 6% DM<sup>(43,44)</sup>. However, tannins can also have negative effects on feed utilisation by decreasing digestibility and microbial growth in the rumen, especially when dietary protein is low<sup>(45)</sup>. It is thought that the inclusion of tannins in feed improves nutrient use efficiency in the rumen by complexing with protein making it unavailable for degradation, thus increasing the pool of 'bypass protein' which is degraded post-ruinally in the abomasum<sup>(46)</sup>. An alternative explanation is that the protein protective effect is mediated via the formation of tannin-protease complexes<sup>(47)</sup>, thereby limiting degradative potential<sup>(48,49)</sup>. Despite the complexity of the biosynthetic pathways involved in tannin synthesis, molecular approaches have shown that it is possible to alter the tannin content of forage<sup>(50–52)</sup>. Much remains to be understood about the fundamentals of the regulation of tannin biosynthesis *in planta*, especially regulation by *myb* and *myc* genes<sup>(53)</sup>. Some plant species, including the forage and model legume *Medicago sativa*, contain saponins. Saponins are amphipathic glycosides which can also complex with protein and, although the results are variable, forage saponins have been linked with decreased methane production (reviewed in Niederhorn and Baumont<sup>(45)</sup>). Likewise, some plant species (e.g. *Trifolium pratense*, red clover) contain the enzyme polyphenol oxidase (PPO) which catalyses the oxidative complexing of plant phenolics with cellular proteins<sup>(54)</sup>, thus decreasing the availability of forage protein for degradation<sup>(55,56)</sup>. Genetic control of PPO is complex, involving at least six genes<sup>(57)</sup> and mutants with lower than normal PPO activities have been identified in red clover<sup>(58)</sup>. The protein protective benefits of PPO-containing forage is largely exploited in silage, where there is an adequate window in time for this oxygen-dependent enzyme to be catalytically active<sup>(55,58)</sup>. However it is estimated that mastication by grazing cattle takes approximately 3 min (at approximately 55–60 chews per bolus and a chew rate of 15–18 per minute<sup>(59)</sup>); so given that PPO is active within 5 min post-damage there is the potential for exploitation of this trait in the protection of protein before the down bolus is swallowed into the anaerobic rumen environment<sup>(58)</sup>.

Recent research has indicated that plants can affect nutrient use efficiency in more subtle ways than merely on a compositional basis (reviewed in Kingston-Smith *et al.*<sup>(60)</sup>). In a grazing situation, the ruminant ingests living plant material, which invokes endogenous stress responses upon exposure to the primary environmental stresses of the rumen: anoxia, elevated temperature and invasion by micro-organisms. These conditions are found in the field, for example during flooding, in high summer and during attack by pathogenic micro-organisms (e.g. mildew, rust etc). As plants cannot move away from adverse conditions they have evolved mechanisms to enable them to withstand periods of environmental stress, but these efforts are of limited duration in the rumen as the plant cells will eventually die<sup>(61)</sup>. However, how the plant cells die and how they use their endogenous constituents to prevent death has an impact on nutrient availability for the ruminal micro-organisms. For instance, it has been demonstrated that exposing forage species to the ruminal conditions of heat and anoxia in the absence of a microbial inoculum is sufficient to promote rapid degradation of plant protein by the plant's own proteases<sup>(61–63)</sup>. Stress-induced proteolysis in plants is a phenomenon that has been widely reported for biotic and abiotic stresses<sup>(64–67)</sup>. Finding a way to inhibit this stress-induced proteolysis would therefore produce immediate benefits in terms of decreasing the relative availability of protein breakdown products in recently ingested forage<sup>(68)</sup>. This is not a trivial concern, because proteolysis is highly regulated at transcriptional and post-translational levels. In addition, plant cells are highly compartmented which means that proteases could be present at relatively low abundance on a whole cell basis, but could be present at high concentrations within an organelle. Hence, low abundance proteases may have an apparently disproportionately large effect if co-localised with their protein substrate prior to or as a result of stress-induced activation. For example, the majority of protease activity is in vacuoles<sup>(69)</sup>, which can account for up to 70 % of the cell volume in mesophyll cells, but about 70 % of the soluble protein of the plant cell is located in the chloroplasts, accounting for about 25 % of the mesophyll cell volume<sup>(70)</sup>. To date, there is little evidence that forage variety improvement comes about on the basis of selection for total protease activity in the standing crop<sup>(71,72)</sup>. Research is required to identify control points in proteolysis as the plant cells die, and how amenable these are for manipulation for forage improvement.

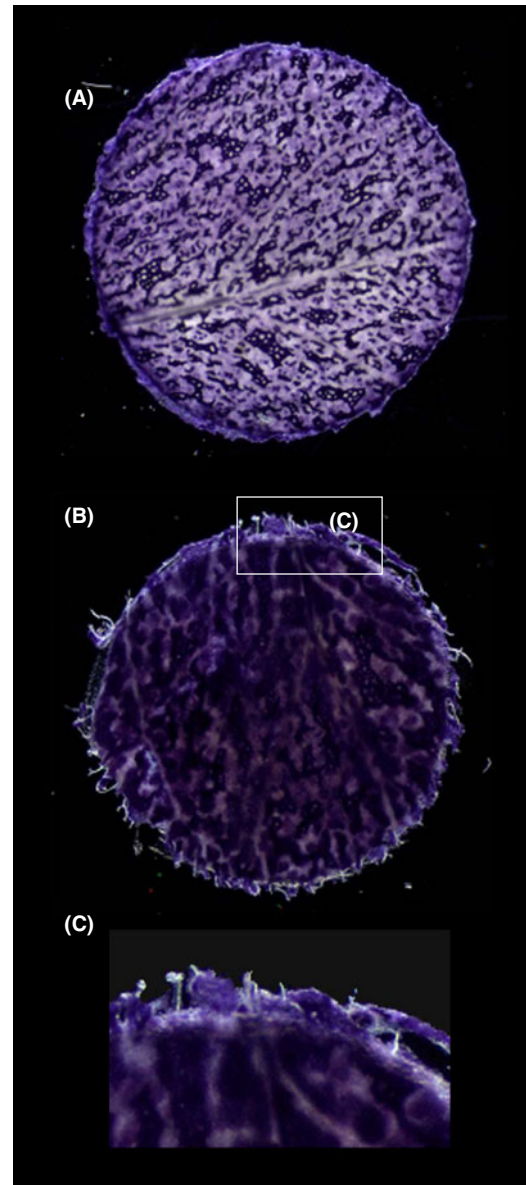
It is clear that to fully understand rumen function consideration must be paid to all components of the ecosystem and how they interact, particularly the plant-microbe 'interactome'. Microbial colonisation of newly ingested plant material by a complex microbial community is a prerequisite for ruminal degradation of plant biomass<sup>(73–75)</sup>. The dynamics of this process are poorly understood, although recent work has demonstrated that this process is similar to other microbial colonisation events in nature in that the biofilm phenotype prevails<sup>(76)</sup>. Biofilms are defined as attached microbes which are enveloped in exopolymeric substances<sup>(77)</sup>. This 'slimy matrix' encases the colonising microbes, offering them protection from predation and concentrating their plant degradative enzymes (Fig. 1).



**Fig. 1.** Scanning electron microscopy image of a biofilm community on a perennial ryegrass leaf following 2 h of incubation under ruminal conditions. Scale: 1  $\mu$ m.

The initial attachment of ruminal bacteria and anaerobic fungi to plant material occurs within minutes of its ingestion<sup>(75,78,79)</sup>. Ciliate protozoa also rapidly colonise ingested plant material<sup>(80)</sup>, although it is currently unclear whether this reflects attachment *per se*. Following initial colonisation events, the production of extracellular polymeric substances by the colonising bacteria ensues. The production of exopolymeric substances is quick and reaches its maxima early on in the colonisation process, although the exact timing of this is dependent on the plant material. For example, under ruminal conditions exopolymeric substances production on perennial ryegrass leaf and stem material is maximal after 1 h and 4 h of incubation respectively<sup>(76)</sup>. This observation is not really surprising considering the heterogeneity of the plant as a microbial substrate<sup>(81)</sup>.

As well as spatial differences associated with differences in plant structure, the organisation of plant metabolites within these structures also has an impact on the ability of microbes to utilise plant nutrients. The mosaic distribution of condensed tannin containing plant cells within *Lotus corniculatus* leaf tissue, for example, results in the preferential microbial degradation of non-tanniferous areas of leaf tissue (Fig. 2). As well as the structural heterogeneity of plant material, it appears that the nature of the plant may also influence the timing of the changes in the population composition of colonising microbes. Differences in the populations of rumen bacteria colonising *Lotus corniculatus* over time have been reported, with a change in the population composition evident after 8 h of ruminal incubation<sup>(17)</sup>. In contrast, with perennial ryegrass the temporal difference in the colonising bacterial population composition occurred after just 2 h of ruminal incubation<sup>(76)</sup>. The mechanism underlying this temporal change in the bacterial populations colonising fresh plant material is currently unclear; however, this appears to be correlated with a decrease in exopolymeric substances quantity, and as such quorum sensing may play a role. With due consideration of how plants and microbes interact in the rumen, it will be possible to understand the mechanistic basis for many of



**Fig. 2.** Rumen microbial degradation of *Lotus corniculatus*. Leaf discs (5 mm) of *L. corniculatus* were anaerobically incubated in 10% (v/v) rumen fluid at 39°C for 24 h prior to being stained for the presence of condensed tannins (purple) with 4-dimethylaminocinnamaldehyde. Representative light microscopy images of leaf discs before (A) and after 24 h of incubation (B) show the preferential degradation of non-tanniferous areas of the leaf tissue (C).

the feed-specific effects identified by decades of research. Not only will this be of academic interest, but it will also allow a refinement of screening parameters, plus provide the potential for enhanced throughput by utilisation of molecular markers, to derive improved forage more rapidly.

#### Opportunities for selective breeding for impact mitigation

Selective breeding of forage has enabled significant improvements in livestock productivity to be made.

Considerable progress has been made with respect to the yield, persistency and tolerance to abiotic and biotic stresses of the grasses and clovers used in temperate agriculture. In recent years, considerations of quality and of reducing deleterious environmental impacts associated with livestock production have been emphasised alongside these agronomic traits. Recently, improved grass varieties containing elevated contents of water soluble carbohydrates (sucrose, glucose, fructose and fructan) with an approximate average annual water soluble carbohydrate content of 24% (e.g. AberDart) have proved commercially successful. In research trials, feeding ruminants with grasses containing increased carbohydrate have resulted in significant improvements in the incorporation of N into milk and meat when used as grazed and conserved feed<sup>(82)</sup>. This effect could be due to a more favourable provision of protein breakdown products and readily fermentable carbohydrate than in control grass varieties with lower carbohydrate content. Of course, an improved retention of N inputs means decreased N outputs to the benefit of the local and wider environment. Future opportunities for improvement could arise from capitalising on the observations of species-specific differences in endogenous rates of induced proteolysis<sup>(68,83)</sup>.

The results described above, together with efforts to understand the rumen interactome in terms of the microbial competition and the ecological niches required by methanogens, in addition to how their proliferation can be minimised, enable the identification of key traits required for the development of the next generation of improved forages<sup>(17)</sup>. The ability to incorporate new selection criteria in plant breeding programmes is greatly facilitated by the integration of molecular marker-based approaches into germplasm development, together with genomics and modelling<sup>(84)</sup>. In grasses and white clover, interspecific hybridisation and introgression of genes from related species has an important role to play. Modern breeding programmes will increasingly be based on high throughput phenotyping techniques operating in parallel with next generation sequencing to ensure that enhanced understanding of gene function can be rapidly incorporated into variety development.

### Conclusions

Agricultural advances in mechanisation, fertiliser application and genetic improvement of both crop and livestock have led to increased production potentials, but have done little to address the adverse effects of demand for ruminant-derived products; with such a significant environmental impact, there is a correspondingly large potential for improvement. There is a real opportunity to use improved forages to increase nutrient use efficiencies by ruminants, thereby producing a double benefit of not only decreasing environmental footprint, but also simultaneously increasing productivity. Furthermore, there is the opportunity to deliver additional benefits through the development of multifunctional pastures that not only support biodiversity and ecosystem services but also attract income, for example, through tourism. The ultimate goal is

to realise better incorporation of inputs into product to feed a growing population, but with decreased generation of undesirable by-products. Over the last century, selective breeding of forage has led to significant improvements in the quality of raw materials given to livestock, from what could be considered to be the original improved pasture grass, the variety named S23, to current high sugar grass varieties and mixtures. In the future, strategic breeding can continue to provide pasture forages with less environmental impact. Admittedly, on a global scale much of the land used for grazing is unimproved, and here a genetic improvement of livestock is likely to have the greatest impact, but the utilisation of improved forages where possible has the potential to make a real contribution to minimising the impact of livestock farming. By treating the rumen as an ecosystem and exploiting the interactions between plant and micro-organisms, realistic mitigation strategies can be developed and, most crucially, applied to deliver real benefits.

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