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Rumen function in goats, an example of adaptive capacity

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Research Reflection

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Abstract

The aim of this Research Reflection is to describe the basic rumen function of goats and its modification in response to environmental factors, as well as to discuss similarities and differences when compared to other ruminants. In so doing we shall reveal the adaptive capacity of goats to harsh environments. The basic rumen function in goats is similar to other species of ruminants, as stressed by the opportunity to apply the updates of feeding systems for ruminants to goats. The rumen epithelium acts as a protective barrier between the rumen and the host, but it can be damaged by toxic compounds or acidosis. The rumen also plays an important role in water balance, both for dehydration and rehydration. Recent studies show that the microbiota exhibits a high fractional stability due to functional redundancy and resilience, but this needs more investigation. The microbial community structure differs between goats and cows, which explains the difference in sensitivity to milk fat depression following intake of high lipid diets. Goats also differ from other ruminants by their enhanced ability to feed-sort, but as with cows they can suffer from acidosis. Nevertheless, goats can be considered to be very resistant to environmental factors such as water stress, salt stress or heat stress, and this is especially so in some endogenous breeds. They also are able to detoxify tannins, polyphenols and other secondary metabolites. Some new trials involving feeding behaviour, microbiota and omics or approaches by meta-analyses or modelling will improve our knowledge of rumen function in goats.

Introduction

Ruminants have developed a specific multiple-stomach system to use the biomass they select with browsing or grazing. Among them, goats are known to better survive harsh conditions than other ruminants (Silanikove, 1994), but also to take profit of highly nutritive diets. These specificities might be linked to the rumen, a complex organ where microbial fermentation has a major impact on the efficiency of feed utilisation. The aim of this short review is to describe the basic rumen function of goats and the modifications due to environmental factors in order to discuss if it differs from other ruminants or if goats are a good model for all species of ruminants in different environments.

Basic rumen function

Degradation of dietary constituents and ruminal metabolism

Goats are similar to other ruminants for the basic rumen function: biomass consumed by the animals is partly fermented in the rumen by the microbes and converted to microbial matter, volatile fatty acids (VFA), fermentation gases (methane and carbon dioxide) and ammonia, all together with the production of heat. The transit fractional rate responses to feeding level and proportion of concentrate are generally similar for cattle and small ruminants (Sauvant *et al.*, 2006). On the other hand, there are no publications where the efficiency of microbial growth in the rumen of goat has been compared, for the same diet, to that of other ruminants. Nevertheless, the global similarity between goat and cows has been used in the Feeding System for ruminants, like the recently updated INRA feeding system for ruminants (INRA, 2018), even if goats present some specific digestive features. The new concept of rumen protein balance (RPB) that represents the difference between crude protein (CP) intake and non-ammonia CP flowing out at the duodenum (i.e. undegraded feed CP + microbial CP + endogenous CP) can be applied to goats as to other ruminants (Giger-Reverdin and Sauvant, 2014). RPB is highly correlated with the ammonia level in the rumen, and then to the urinary N losses with no difference between goats and cattle (Sauvant *et al.*, 2018b). However, in contrast to cattle, there is no negative digestive interaction due to concentrate supply in goats (Sauvant *et al.*, 2018a). This is consistent with the fact that, for similar mixed diets, the rumen pH of goat is higher by about 0.4 point compared to cattle (Sauvant *et al.*, 2018c).

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For poor diets, despite the old results of Devendra (1978), the debate is still running regarding differences in digestive efficiency between goats and other ruminants, but the digestibility seems to be similar with good diets (Sales *et al.*, 2012).

Role of the ruminal epithelium

The ruminal epithelium acts as a barrier between the rumen and the host. It has two main functions: absorption of nutrients and protection against toxic products, as has been extensively reviewed recently (Baldwin and Connor, 2017). The rumen barrier function can be impaired when the animals suffer from an important drop of rumen pH (acidosis) as has been observed over many years in goats used as a model of ruminants (Das and Misra, 1992). Rumen epithelial tight junctions might be damaged with disruption of ruminal epithelial associated with a local inflammatory response (Liu *et al.*, 2013), electrophysiological properties are also modified with changes in net ion transfer and the ruminal epithelial permeability increases (Klevenhusen *et al.*, 2013).

Water storage and resistance to dehydration

The rumen plays an important role in water balance both at times of dehydration and rehydration, because it acts as a water reservoir containing a large volume of water (Jaber *et al.*, 2013). Some breeds that are well-adapted to harsh conditions such as the Black Bedouin goat might face a four day water deprivation with a loss of 40% body-weight. Since a large portion (50–70%) of the water lost during dehydration comes from the rumen, the animal is able to maintain a normal water balance in blood and body tissues to ensure a body water level compatible with life (Silanikove, 1994). During rapid rehydration, the rumen may store water for some hours to prevent haemolysis and osmotic shock to tissues. For example, Black Bedouin goats are able to drink water equivalent to 20–40% of their body mass in one episode every four days in the Sinai desert (Middle East), which is an extremely valuable trait in arid regions with few available feeds (Silanikove, 1994). There is a large difference in the capacity to cope with both dehydration and rehydration between animal species or breeds within species, such that European breeds like the Saanen goat are more sensitive than breeds indigenous to arid lands like Bedouin goats (Silanikove, 1994).

Microbiota

As in all ruminants, Bacteroidetes and Firmicutes are the dominant phyla in goats with low abundance of Fibrobacteres. The microbiota is usually dominated by Prevotella followed by Butyrivibrio and Ruminococcus, as well as unclassified *Lachnospiraceae*, *Ruminococcaceae*, *Bacteroidales*, and *Clostridiales*. Diversity within the archaea is much lower than for bacteria, with only a few methanogenic groups dominating the rumen microbiota (Methanosphaera, Methanobacteriaceae and/or Methanobrevibacter). The genera *Entodinium* and *Epidinium* are dominant for the protozoa. Even though the main micro-organisms are widespread in ruminants, the communities of the microbiota can be different according to the host species. For example, whatever the diets, goats have a higher relative abundance of unclassified *Veillonellaceae* and a lower relative abundance of *Fibrobacter* (Henderson *et al.*, 2015). Usually, diets fed to the ruminant are the major determinant of the bacteria structure (Henderson *et al.*, 2015). Even though diets affect the rumen microbiota structure, the microbiota usually exhibits a high functional stability due to functional redundancy and resilience. Nevertheless, diets rich in concentrate or supplemented with lipids can affect both the structure and function of the microbiota. In line with cows, high grain diets reshape the rumen microbial community by reducing its richness and diversity and changing the microbial composition in goats. Zhang *et al.* (2019) showed that 30 taxa were affected by the diet, there being 5 enriched taxa (*Selenomonas 1*, *Ruminococcus* and unclassified *Veillonellaceae)* in the high grain diet group and 25 enriched taxa in the hay diet group (*Butyrivibrio*, *Pseudobutyrivibrio, Fibrobacter* and several unclassified taxa such as unclassified *Christensenellaceae*, *Ruminococcaceae* and *Ruminococcaceae*) at the genera level. These changes in the composition of the microbiota were associated with modifications in the rumen metabolome with enhanced capacity to influence amino acid and nucleotide metabolisms. The linkages between rumen bacteria and metabolites are extremely complex (Zhang *et al.*, 2019).

The composition of the rumen microbiota is also altered by the dietary crude protein (CP) content. Min *et al.* (2019) observed that the proportions of proteolytic bacterial species tended to be higher in goats grazing sunn hemp (*Crotalaria juncea*, 17% CP) compared to bermudagrass (*Cynodon dactylon,* 10% CP). Similarly, the *Prevotella* and *Selenomonas* genera proportions were increased in cows fed alfalfa rather than a cornstalk-based diet (Zhang *et al.*, 2014).

Each adult animal harbours its own microbiota even when animals are bred and fed identically, suggesting that the host also has a significant impact on the composition of its microbiota. In dairy cows, Weimer *et al.* (2017) showed that the ruminal bacteria communities moved toward re-establishment of the pre-exchange communities within days to weeks at a similar diet, suggesting a high specificity and resilience of the rumen microbiota within its host. The animal might exert some influence over its rumen microbiota through its intake behaviour or its digesta passage rates such as the fractional turn-over rate of the solid particles. Because of the specificity of goats regarding their intake behaviour (intermediate feeder *vs.* grazer for cow) and their potential higher rumen turn-over rates compared to cows (Clauss *et al.*, 2006), specific studies in goats are needed. The influence of the host on ruminal functions is poorly documented except on the methanogenesis function. A better understanding of the microbial composition, the functional role of microbes in fermentation and how the host controls its own microbiota is essential to be able to manipulate the rumen microbiota.

Lipid metabolism and biohydrogenation

Dietary fatty acids (FA) in forage, cereals and oilseed are mainly C18-carbon polyunsaturated fatty acid (PUFA) especially linoleic (C18:2 9c,12c) and alpha linoleic (C18:3 9c,12c,15c) acids. Dietary unsaturated lipids undergo bacterial lipolysis and extensive biohydrogenation of released FA in the rumen resulting in the formation of saturated FA, and of a variety of positional or geometric (cis, trans) isomers of unsaturated FA (Lourenço *et al.*, 2010). *Butyrivibrio*-related bacteria isolated in the rumen were thought to be the main active population carrying out the biohydrogenation process. However, with the development of culture-independent high-throughput next-generation sequencing techniques, it was shown that uncultivated microbial species including *Prevotella, Lachnospiraceaeincertae* sedis, and unclassified *Bacteroidales, Clostridiales* and *Ruminococcaceae* might also be involved (Huws *et al.*, 2011). Knowledge is still limited on the microbial ecology of FA metabolism, especially in goats. The apparent biohydrogenation values of linoleic and linolenic acids ranged between 85 and 95% depending upon rumen

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conditions such as pH and microbial populations. Low ruminal pH observed with increasing amounts of concentrates can result in incomplete biohydrogenation leading to increased production of trans FA (Lourenço *et al*., 2010). A shift in the biohydrogenation pathways, from the 11t to the 10t pathways can also be observed with production of rumen biohydrogenation intermediates (C18:2 10t-12c; C18:1 10t…) with supposed antilipogenic effects on the mammary gland, inducing milk fat depression (MFD). However, interspecies differences in the rumen biohydrogenation process were poorly investigated except through indirect comparison of milk FA profiles. In line with interspecies differences in microbial population and composition (Henderson *et al*., 2015) and in rumen enzymes activities and DM degradation (Moon *et al*., 2010), it could not be ruled out that there might be differences in the biohydrogenation process between cows and goats. In a direct comparison of the ruminal lipid metabolism in dairy cows and goats, Toral *et al*. (2016) suggest that *Ruminococcaceae* may be linked to the saturation of C18:1 in the rumen of cows and *Pseudobutyrivibrio* in goats. Moreover, microorganisms are able to synthesise their own FA from carbohydrates or amino acids contributing up to 60% of the total FA outflows from the rumen leading to FA duodenal flows higher than FA intake in cows fed low fat diets (Schmidely *et al*., 2008). They also synthesise specific FA such as odd FA and methyl branched-chain FA (BCFA) of the iso and anteiso forms. As variation in the odd FA and BCFA profile leaving the rumen was expected to reflect changes in the relative abundance of specific bacterial populations in the rumen, these FA were thought to be useful as markers of rumen function and microbial synthesis (Fievez *et al*., 2012). But as dietary FA contents and treatments might affect the contribution of microbial FA to total FA outflows and also affect the odd-FA and BCFA bacterial content and outflows differently, these outflows as potential markers of changes in the relative abundance of rumen bacteria strains should be used with care (Berthelot *et al*., 2019).

Role of epigenetics and development of the rumen with age

Development of the digestive compartments begins at around the same prenatal stage in sheep and goats, but later than in cattle (Garcia *et al*., 2012). Microbial colonisation pattern and fermentation differs between young goats reared during the first month of life under different (natural *vs.* artificial) milk feeding systems (Abecia *et al*., 2014). However, the rumen epithelial immune development was not modified by distinct microbial colonisation patterns (Abecia *et al*., 2014). It must be stressed that some supplementation in early life could temporarily be of interest, as for example medium chain FA to decrease methane production, but might also have a negative effect on daily gain of kids and modify some rumen papillae characteristics (Debruyne *et al*., 2018).

Responses to environmental factors

Feeding behaviour and high concentrate diets

The rumen can be considered as a fermenter and the intake of feedstuffs as the supply of substrate for the fermenter. Thus, the pattern and the quality of intake play an important role on the fermentation occurring in the rumen (Desnoyers *et al*., 2011) Sheep and goats have quite similar feeding behaviour and graze selectively on heterogeneous resources in order to eat a diet of higher quality than offered (Baumont *et al*., 2000), however, goats eat more slowly than sheep because they tend to select their feeds more carefully (Morand-Fehr *et al*., 1991). The supply of concentrate might be up to 50% or more of the dry matter intake in some high producing herds, which can have the effect of inducing rumen acidosis. Eating and ruminating behaviours are key parameters to be considered in the occurrence of this disease in goats (Giger-Reverdin, 2018) as in cattle (Maekawa *et al*., 2002). When facing an acidogenic diet, goats develop different individual strategies. They can decrease their intake rate and duration and hence the dry matter eaten during the first eating bout (Serment and Giger-Reverdin, 2012). They can also sort against concentrates and search for fibre (Giger-Reverdin, 2018). Without concentrate, mean daily chewing time (962 ± 35 min/d) is close to the mean maximum of 1000 min/d generally observed in ruminants, but each supply of 100 g/day of concentrate decreases daily chewing duration by 23.3 ± 2.8 min/d as obtained from the bibliography data base 'Caprinut' (Sauvant and Giger Reverdin, 2018). This decrease in mastication causes a proportional reduction in salivary input to the rumen and buffer recycling, and thus increases the risk of rumen acidosis. With a total mixed ration (TMR), chewing duration decreases 57.6 ± 6.6 min/d for an increase of 10% concentrate. When compared to cattle the chewing time per g of dry matter intake (DMI) in goats is about 10 time higher (Sauvant *et al*., 2008). This difference could impact the flow of bicarbonate recycling/g of DMI and explain the higher value of rumen pH for similar diets, mentioned above.

Lipid supplementation

In most ruminant diets, fat represents less than 5% of total dry matter. However, fat can be added to the diet to improve its energetic value in dairy production. It is also often used to modify the FA profile of ruminant products (milk, meat) to improve their nutritional, organoleptic or technological properties. However, fat supplementation often decreases microbial growth, especially fibrolytic bacteria and protozoa, and rumen fibre digestibility. It also decreases the DMI of cows and goats except in goats in early lactation (Faverdin *et al*., 2018). As in cows, diets rich in lipid increase the level of trans FA in goats (Cremonesi *et al*., 2018). The biohydrogenation intermediates may vary according to the type of lipids. Those rich in C18:3 9c,12c,15c (linseed) favour biohydrogenation intermediates characteristic of C18:3 biohydrogenation (C18:3 9c,11t, 15c, C18:2 11t,15c, C18:1 15c, C18:1 15t) and those rich in C18:2 9c,12c produce intermediates more characteristic of C18:2 biohydrogenation (C18:1 6t–9t, C18:1 10t, C18:1 11t) (Cremonesi *et al*., 2018). In this study, despite different biohydrogenation pathways, *Butyrivibrio* and *Pseudobutyrivibrio* were not affected by the lipid supplementation. *Fibrobacteriaceae* and *Prevotellaceae* were the bacterial families showing the highest and significant correlation with FA involved in the biohydrogenation pathway of C18:3 and C18:2. When ruminal lipid metabolism was compared in dairy cows and goats with diets supplemented with starch and plant oil or fish oil, an interaction between diets and species was observed indicating that the responses of cows and goats to dietary treatments were different. With the plant or fish oil diets, goats exhibited greater increases in C18:1 trans FA in the rumen fluid compared to cows but the shift from C18:1 11t to 10t and the increase in C18:2 10t, 12c was greater in cows fed the starch and C18:2 oil-enriched diet. This suggests that the biohydrogenation pathways are more stable and robust in response to high starch diet with plant oils in goats (Toral *et al*., 2016). This is consistent with the higher sensitivity of cows to MFD. In line with these interactions, the bacterial populations affected by lipid

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supplemented diets differ between cows and goats, in agreement with species specific microbial community structures. *Ruminococcaceae*, *Lachnospiraceae* and *Succinivibrionaceae* were affected in cows whereas *Prevotella*, *Clostridium cluster IV* and *Veillonellaceae* were modified in goats (Toral *et al*., 2016).

Fate and detoxification of tannins, polyphenols and other secondary metabolites

A peculiarity of ruminants is the ability to avoid potentially toxic plant species in their diet and/or to be more resistant to secondary metabolites which represent potential toxic compounds, (for example, alkaloids, terpens and terpenoids, organic acids like oxalic acid and phytic acid, glucosinolates, cyanides, saponins and phenolic compounds like tannins and flavonoids). Due to its geographical distribution, a large proportion of the goat population is exposed to these situations, particularly in countries where climatic and soil conditions favour the development of plants which produce all the more secondary metabolites to defend themselves against heat or water stress. In these areas, small ruminants, including goats, appear particularly resistant to ingestion of large amounts of anti-nutritional compounds and even of toxic metabolites (Silanikove *et al*., 1996). They are also less sensitive to mycotoxins than monogastrics because of the rumen microbiota and the interactions inside the rumen with feed particles enabling the degradation, deactivation and hence detoxification of these metabolites (Gallo *et al*., 2015). Moreover, in the ruminants, there is a difference in detoxification capacity, one such example being the degradability of mycotoxins like aflatoxin B1 which is higher in goats than in steers (Upadhaya *et al*., 2009). Even so, this degradation of aflatoxin B1 in the rumen of the goat leads to the formation of aflatoxin M1 excreted in the milk like in other ruminant species (Battacone *et al*., 2009). This ability can be linked to a behavioural adaptation towards some secondary metabolites. It may lead to modifications of the dietary selection pattern (Duncan *et al*., 2000; Mkhize *et al*., 2018), but also to specific detoxification enzymatic batteries of secondary metabolites which can be realised at different places in ruminants but mainly in the epithelium of the rumen. In the case of rhodanese, a ubiquitous enzyme playing a central role in cyanide detoxification, the activity was highest in the epithelium of the rumen of goats (Nazifi *et al*., 2003).

Currently there is considerable research interest in the tannins and the benefits of agro-industrial by-products containing tannins (for example, chestnut husk, grape skin, winery residue) introduced into the diet of ruminants (Kondo *et al*., 2016). Tannins are part of the group of phenolic compounds and because of their multiple phenolic hydroxyl groups, one of their main properties is the ability to form complexes with proteins. Moreover, because of their varied natures (hydrolysable or condensed tannins), these metabolites can lead to beneficial or detrimental effects on the ruminant health and feed efficiency according to their concentration (Makkar, 2003). One of the interest aspects of dietary tannins is protection of proteins against ruminal degradation. This could become a handicap when the only sources of protein are provided by legumes rich in condensed tannins, reducing nitrogen availability to rumen microorganisms and inhibiting growth of the main ruminal bacteria. Nevertheless, McSweeney *et al.* (1999) could show that in sheep and goats fed a tannin-containing shrub legume *Calliandracalothyrsus,* some rumen bacteria isolated from goats had an ability to digest protein in the presence of condensed tannins, attesting to the specific digestion and resistance characteristics of the caprine species to secondary metabolites. The architecture of terpens (the presence of oxygen-containing ring structures) which are also important secondary metabolites has a strong influence on their rumen degradability (Malecky *et al*., 2009). These observations may prove useful to rationalise the use of essential oils and plant dry extracts which are increasingly incorporated as additives to the diet of other ruminant species to optimise ruminal fermentations (Calsamiglia *et al*., 2007).

Adaptation to salt or salt stress

Animals may intake large amounts of salt with either feedstuffs or drinking water. Quite often, both sources of salt are combined because water available for drinking is the same as that used by the plants to grow on salty soils. This can be of critical importance when the animals are grazing halophytes and when the saline water from underground wells is the only available drinking water (Ashour *et al*., 2016). According to the recent review of Attia-Ismail (2016), intake of salt might modify the rumen fermentative profile with an impact on the acid base equilibrium, especially on Na^+, K^+ and Cl^-, and thus on the osmotic pressure within the rumen. The animal drinks more water to balance this effect, which can decrease the adhesion of bacteria to feed particles in the rumen and increase the turnover rate of solid and liquid phases in the rumen. The consequence is a lower digestion in the rumen. Large differences in salinity tolerance between animal species or between breeds within species are observed, and it seems that sheep and goats are more tolerant to salt stress than cattle when adapted, and that goats have a slight tolerance advantage over sheep (Dunson, 1974; McGregor, 2004; Squires, 2016). Goats are able to cope without any detrimental effect on digestibility up to levels of 8326 mg TDS (total dissolved solutes) in water (Paiva *et al*., 2017) but, as in heifers, rumen function and cell wall digestibility decreases with an increase in TDS (Alves *et al*., 2017).

Heat stress

Heat stress is often associated with water deprivation or infrequent drinking in animals living in arid areas (Silanikove, 1992).Feed intake decreases during heat stress for several reasons. Thermoregulation operates to decrease heat production arising from rumen fermentation, and there is limited availability of water and of feeds, the majority of which have a poor nutritive value (Morand-Fehr and Doreau, 2000). Feeding pattern is also modified with an increase in night grazing. In these conditions, reduction of passage rate through the digestive tract might increase digestibility, but this benefit is overridden by the negative effects of heat stress and water deprivation (Silanikove, 1992). Rumen fermentation is modified by heat stress: rumen pH decreased at equivalent dry matter intake (Castro-Costa *et al*., 2015) and the rumen bacterial community changes in goats (Zhong *et al*., 2019). Indigenous goats adapted to harsh conditions are more capable of coping with heat stress than non-desert breeds (Silanikove, 1992). Moreover, goats have a poor insulation capacity in contrast to sheep, but have the advantage of dissipating heat by sweating (Silanikove, 1992).

Perspectives

This review exposes some areas in which knowledge is lacking and there is need for further research and new approaches.

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Feeding behaviour

Goats exhibit an important sorting behaviour compared to other ruminants, which impacts rumen function and the efficiency of microbial growth. More studies are needed to better separate the influence of feed sorting from the intrinsic species effect, and to find an explanation to the lack of digestive interaction due to the proportion of concentrate, or to the higher rumen pH compared to cattle for a similar diet.

Microbiota

Despite the wealth of information provided by modern omics techniques, little progress has been made in the understanding of the relationship between the structure and functions of rumen microbiota. The methodological effort needed to quantify the microbiota structural and metabolic characteristics is tedious enough to hinder the implementation of dedicated experiments. Moreover, the strong redundancy among the main functions in the ruminal ecosystem limits the potential number of unequivocal and specific relations between microbial species and functional abilities. However, two areas are worth exploring in this relationship; firstly, the consideration of the host phenotype for some important functions of the microbiota such as methanogenesis, and secondly, the consideration of smaller scales, close to the size of the plant tissues, that are potential ecological niches capable of harbouring specialised microbial communities.

Omics

As previously pointed out, the many interactions occurring between the different animal tissues and cells but also, at different levels, between the cell (genome) and exogenous events (environment) are hindrances to understanding the underlying mechanisms and the role of the host compared to that of the rumen microbiota. One of the ways to access all of the systemic and/or tissue-specific signatures is the approach *via* 'omics'. Indeed, these approaches are complementary in the search for interrelationships between genotypes and phenotypes (Shahzad and Loor, 2012). Metabolomics, in which advanced analytical chemistry techniques and multidimensional statistical analyses are applied to measure large numbers of small molecule metabolites in cells, tissues and biofluids (end products of these complex interactions), after being first exploited in biomedical research, is progressively used also in research and monitoring of livestock (Goldansaz *et al.*, 2017). Most of the time, it is the association between different complementary approaches which provides most information. For example, by combining metabolomics and proteomic studies, it is possible to get a better knowledge of the role of the rumen epithelium in goats adapted to grain-rich feeding compared to hay feeding (Guo *et al.*, 2019).The joint and simultaneous use of metabolomics and pyrosequencing studies in goats informs about the metabolic pathways preferentially involved in the response to high-grain diets (Zhang *et al.*, 2019), whilst the links between the ruminal bacterial community and metabolites represent a powerful tool in terms of prediction or monitoring of certain nutritional diseases such as acidosis (Mao *et al.*, 2016; Hua *et al.*, 2017). These approaches also make it possible to investigate more finely and specifically *via* co-culture the key role of microorganisms such as fungi and methanogens, but also the nature of the metabolites produced (Cheng *et al.*, 2013). Interrelationships between the different bacteria of the ruminal community in goat kids after birth and before weaning (Abecia *et al.*, 2018) can also be studied. These first studies using the 'omics' approaches in livestock (including small ruminants and goats), based on non-invasive sampling methodologies and analysing a high quantity of small molecules in different biological fluids and matrices to identify putative biomarkers, are probably only just the start of much more extensive research exploiting the opportunities offered by multi-omics studies (Goldansaz *et al.*, 2017).

Conclusion

This review points out that goats have globally similar rumen function when compared to other ruminants, even if there is a lack of detailed comparison between species in similar conditions. Knowledge needs to be improved in some areas, such as microbial efficiency and ecology or feeding behaviour. Moreover, some breeds of goats have developed specific characteristics to sustain them in harsh conditions, because they are able to cope with anti-nutritional or toxic compounds derived from secondary plant metabolites, and are quite tolerant to environmental stressors, which is a key point in the context of climate change.

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