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1 **Rumen function in goats, an example of adaptive capacity**

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30 **Abstract:**

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

49 **Key-words:** digestive tract, ruminant, environmental conditions, microbiota, omics

50 **Introduction**

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

59 **Basic rumen function**

60 *Degradation of dietary constituents and ruminal metabolism*

61 Goats are similar to other ruminants for the basic rumen function: biomass consumed by the
62 animals is partly fermented in the rumen by the microbes and converted to microbial matter,
63 volatile fatty acids (VFA), fermentation gases (methane and carbon dioxide) and ammonia, all
64 together with the production of heat. The transit fractional rate responses to feeding level and
65 proportion of concentrate are generally similar for cattle and small ruminants (Sauvant *et al.*,
66 2006). On the other hand, there are no publications where the efficiency of microbial growth
67 in the rumen of goat has been compared, for the same diet, to that of other ruminants.
68 Nevertheless, the global similarity between goat and cows has been used in the Feeding System
69 for ruminants, like the recently updated INRA feeding system for ruminants (INRA, 2018),
70 even if goats present some specific digestive features. The new concept of rumen protein
71 balance (RPB) that represents the difference between crude protein (CP) intake and non-
72 ammonia CP flowing out at the duodenum (i.e. undegraded feed CP + microbial CP +
73 endogenous CP) can be applied to goats as to other ruminants (Giger-Reverdin & Sauvant,
74 2014). RPB is highly correlated with the ammonia level in the rumen, and then to the urinary
75 N losses with no difference between goats and cattle (Sauvant *et al.*, 2018b). However, in
76 contrast to cattle, there is no negative digestive interaction due to concentrate supply in goats
77 (Sauvant *et al.*, 2018a). This is consistent with the fact that, for similar mixed diets, the rumen
78 pH of goat is higher by about 0.4 point compared to cattle (Sauvant *et al.*, 2018c). For poor
79 diets, despite the old results of Devendra (1978), the debate is still running regarding
80 differences in digestive efficiency between goats and other ruminants, but the digestibility
81 seems to be similar with good diets (Sales *et al.*, 2012).

82

83 *Role of the ruminal epithelium*

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

93

94 *Water storage and resistance to dehydration*

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

109

110 *Microbiota*

111 As in all ruminants, Bacteroidetes and Firmicutes are the dominant phyla in goats with low
112 abundance of Fibrobacteres. The microbiota is usually dominated by Prevotella followed by
113 Butyrivibrio and Ruminococcus, as well as unclassified *Lachnospiraceae*, *Ruminococcaceae*,
114 *Bacteroidales*, and *Clostridiales*. Diversity within the archaea is much lower than for bacteria,
115 with only a few methanogenic groups dominating the rumen microbiota (Methanosphaerae,
116 Methanobacteriaceae and/or Methanobrevibacter). The genera *Entodinium* and *Epidinium* are
117 dominant for the protozoa. Even though the main micro-organisms are widespread in
118 ruminants, the communities of the microbiota can be different according to the host species.
119 For example, whatever the diets, goats have a higher relative abundance of unclassified
120 *Veillonellaceae* and a lower relative abundance of *Fibrobacter* (Henderson *et al.*, 2015).
121 Usually, diets fed to the ruminant are the major determinant of the bacteria structure
122 (Henderson *et al.*, 2015). Even though diets affect the rumen microbiota structure, the
123 microbiota usually exhibits a high functional stability due to functional redundancy and
124 resilience. Nevertheless, diets rich in concentrate or supplemented with lipids can affect both
125 the structure and function of the microbiota. In line with cows, high grain diets reshape the
126 rumen microbial community by reducing its richness and diversity and changing the microbial

127 composition in goats. Zhang *et al.* (2019) showed that 30 taxa were affected by the diet, there
128 being 5 enriched taxa (*Selenomonas 1*, *Ruminococcus* and unclassified *Veillonellaceae*) in the
129 high grain diet group and 25 enriched taxa in the hay diet group (*Butyrivibrio*,
130 *Pseudobutyrvibrio*, *Fibrobacter* and several unclassified taxa such as unclassified
131 *Christensenellaceae*, *Ruminococcaceae* and *Ruminococcaceae*) at the genera level. These
132 changes in the composition of the microbiota were associated with modifications in the rumen
133 metabolome with enhanced capacity to influence amino acid and nucleotide metabolisms. The
134 linkages between rumen bacteria and metabolites are extremely complex (Zhang *et al.*, 2019).
135 The composition of the rumen microbiota is also altered by the dietary crude protein (CP)
136 content. Min *et al.* (2019) observed that the proportions of proteolytic bacterial species tended
137 to be higher in goats grazing sunn hemp (*Crotalaria juncea*, 17 % CP) compared to
138 bermudagrass (*Cynodondactylon*, 10 % CP). Similarly, the *Prevotella* and *Selenomonas*
139 genera proportions were increased in cows fed alfalfa rather than a cornstalk-based diet
140 (Zhang *et al.*, 2014).

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

155

156 *Lipid metabolism and biohydrogenation*

157 Dietary fatty acids (FA) in forage, cereals and oilseed are mainly C18-carbon polyunsaturated
158 fatty acid (PUFA) especially linoleic (C18:2 9c,12c) and alpha linoleic (C18:3 9c,12c,15c)
159 acids. Dietary unsaturated lipids undergo bacterial lipolysis and extensive biohydrogenation
160 of released FA in the rumen resulting in the formation of saturated FA, and of a variety of

161 positional or geometric (cis, trans) isomers of unsaturated FA (Lourenço *et al.*, 2010).
162 *Butyrivibrio*-related bacteria isolated in the rumen were thought to be the main active
163 population carrying out the biohydrogenation process. However, with the development of
164 culture-independent high-throughput next-generation sequencing techniques, it was shown
165 that uncultivated microbial species including *Prevotella*, *Lachnospiraceae incertae sedis*, and
166 unclassified *Bacteroidales*, *Clostridiales* and *Ruminococcaceae* might also be involved (Huws
167 *et al.*, 2011). Knowledge is still limited on the microbial ecology of FA metabolism,
168 especially in goats. The apparent biohydrogenation values of linoleic and linolenic acids
169 ranged between 85 and 95% depending upon rumen conditions such as pH and microbial
170 populations. Low ruminal pH observed with increasing amounts of concentrates can result in
171 incomplete biohydrogenation leading to increased production of trans FA (Lourenço *et al.*,
172 2010). A shift in the biohydrogenation pathways, from the 11t to the 10t pathways can also be
173 observed with production of rumen biohydrogenation intermediates (C18:2 10t-12c; C18:1
174 10t...) with supposed antilipogenic effects on the mammary gland, inducing milk fat
175 depression (MFD). However, interspecies differences in the rumen biohydrogenation process
176 were poorly investigated except through indirect comparison of milk FA profiles. In line with
177 interspecies differences in microbial population and composition (Henderson *et al.*, 2015) and
178 in rumen enzymes activities and DM degradation (Moon *et al.*, 2010), it could not be ruled
179 out that there might be differences in the biohydrogenation process between cows and goats.
180 In a direct comparison of the ruminal lipid metabolism in dairy cows and goats, Toral *et al.*
181 (2016) suggest that *Ruminococcaceae* may be linked to the saturation of C18:1 in the rumen
182 of cows and *Pseudobutyrvibrio* in goats. Moreover, microorganisms are able to synthesize
183 their own FA from carbohydrates or amino acids contributing up to 60 % of the total FA
184 outflows from the rumen leading to FA duodenal flows higher than FA intake in cows fed low
185 fat diets (Schmidely *et al.*, 2008). They also synthesize specific FA such as odd FA and
186 methyl branched-chain FA (BCFA) of the iso and anteiso forms. As variation in the odd FA
187 and BCFA profile leaving the rumen was expected to reflect changes in the relative
188 abundance of specific bacterial populations in the rumen, these FA were thought to be useful
189 as markers of rumen function and microbial synthesis (Fievez *et al.*, 2012). But as dietary FA
190 contents and treatments might affect the contribution of microbial FA to total FA outflows
191 and also affect the odd-FA and BCFA bacterial content and outflows differently, these
192 outflows as potential markers of changes in the relative abundance of rumen bacteria strains
193 should be used with care (Berthelot *et al.*, 2019).

194

195 *Role of epigenetics and development of the rumen with age*

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

205

206 **Responses to environmental factors**

207 *Feeding behaviour and high concentrate diets*

208 The rumen can be considered as a fermenter and the intake of feedstuffs as the supply of
209 substrate for the fermenter. Thus, the pattern and the quality of intake play an important role
210 on the fermentation occurring in the rumen (Desnoyers *et al.*, 2011) Sheep and goats have
211 quite similar feeding behaviour and graze selectively on heterogeneous resources in order to
212 eat a diet of higher quality than offered (Baumont *et al.*, 2000), however, goats eat more
213 slowly than sheep because they tend to select their feeds more carefully (Morand-Fehr *et al.*,
214 1991). The supply of concentrate might be up to 50% or more of the dry matter intake in some
215 high producing herds, which can have the effect of inducing rumen acidosis. Eating and
216 ruminating behaviours are key parameters to be considered in the occurrence of this disease in
217 goats (Giger-Reverdin, 2018) as in cattle (Maekawa *et al.*, 2002). When facing an acidogenic
218 diet, goats develop different individual strategies. They can decrease their intake rate and
219 duration and hence the dry matter eaten during the first eating bout (Serment & Giger-
220 Reverdin, 2012). They can also sort against concentrates and search for fibre (Giger-Reverdin,
221 2018). Without concentrate, mean daily chewing time (962 ± 35 min/d) is close to the mean
222 maximum of 1000 min/d generally observed in ruminants, but each supply of 100g/day of
223 concentrate decreases daily chewing duration by 23.3 ± 2.8 min/d as obtained from the
224 bibliography data base “Caprinut” (Sauvant & Giger Reverdin, 2018). This decrease in
225 mastication causes a proportional reduction in salivary input to the rumen and buffer
226 recycling, and thus increases the risk of rumen acidosis. With a total mixed ration (TMR),
227 chewing duration decreases 57.6 ± 6.6 min/d for an increase of 10 % concentrate. When
228 compared to cattle the chewing time per g of dry matter intake (DMI) in goats is about 10

229 time higher (Sauvant *et al.*, 2008). This difference could impact the flow of bicarbonate
230 recycling/g of DMI and explain the higher value of rumen pH for similar diets, mentioned
231 above.

232

233 *Lipid supplementation*

234 In most ruminant diets, fat represents less than 5% of total dry matter. However, fat can be
235 added to the diet to improve its energetic value in dairy production. It is also often used to
236 modify the FA profile of ruminant products (milk, meat) to improve their nutritional,
237 organoleptic or technological properties. However, fat supplementation often decreases
238 microbial growth, especially fibrolytic bacteria and protozoa, and rumen fiber digestibility. It
239 also decreases the DMI of cows and goats except in goats in early lactation (Faverdin *et al.*,
240 2018). As in cows, diets rich in lipid increase the level of trans FA in goats (Cremonesi *et al.*,
241 2018). The biohydrogenation intermediates may vary according to the type of lipids. Those
242 rich in C18:3 9c,12c,15c (linseed) favor biohydrogenation intermediates characteristic of
243 C18:3 biohydrogenation (C18:3 9c,11t, 15c, C18:2 11t,15c, C18:1 15c, C18:1 15t) and those
244 rich in C18:2 9c,12c produce intermediates more characteristic of C18:2 biohydrogenation
245 (C18:1 6t-9t, C18:1 10t, C18:1 11t) (Cremonesi *et al.*, 2018). In this study, despite different
246 biohydrogenation pathways, *Butyrivibrio* and *Pseudobutyrvibrio* were not affected by the
247 lipid supplementation. *Fibrobacteriaceae* and *Prevotellaceae* were the bacterial families
248 showing the highest and significant correlation with FA involved in the biohydrogenation
249 pathway of C18:3 and C18:2. When ruminal lipid metabolism was compared in dairy cows
250 and goats with diets supplemented with starch and plant oil or fish oil, an interaction between
251 diets and species was observed indicating that the responses of cows and goats to dietary
252 treatments were different. With the plant or fish oil diets, goats exhibited greater increases in
253 C18:1 trans FA in the rumen fluid compared to cows but the shift from C18:1 11t to 10t and
254 the increase in C18:2 10t, 12c was greater in cows fed the starch and C18:2 oil-enriched diet.
255 This suggests that the biohydrogenation pathways are more stable and robust in response to
256 high starch diet with plant oils in goats (Toral *et al.*, 2016). This is consistent with the higher
257 sensitivity of cows to MFD. In line with these interactions, the bacterial populations affected
258 by lipid supplemented diets differ between cows and goats, in agreement with species specific
259 microbial community structures. *Ruminococcaceae*, *Lachnospiraceae* and
260 *Succinivibrionaceae* were affected in cows whereas *Prevotella*, *Clostridium cluster IV* and
261 *Veillonellaceae* were modified in goats (Toral *et al.*, 2016).

262

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

287 Currently there is considerable research interest in the tannins and the benefits of agro-
288 industrial by-products containing tannins (for example, chestnut husk, grape skin, winery
289 residue) introduced into the diet of ruminants (Kondo *et al.*, 2016). Tannins are part of the
290 group of phenolic compounds and because of their multiple phenolic hydroxyl groups, one of
291 their main properties is the ability to form complexes with proteins. Moreover, because of
292 their varied natures (hydrolysable or condensed tannins), these metabolites can lead to
293 beneficial or detrimental effects on the ruminant health and feed efficiency according to their
294 concentration (Makkar, 2003). One of the interest aspects of dietary tannins is protection of
295 proteins against ruminal degradation. This could become a handicap when the only sources of
296 protein are provided by legumes rich in condensed tannins, reducing nitrogen availability to

297 rumen microorganisms and inhibiting growth of the main ruminal bacteria. Nevertheless,
298 McSweeney *et al.* (1999) could show that in sheep and goats fed a tannin-containing shrub
299 legume *Calliandracalothyrsus*, some rumen bacteria isolated from goats had an ability to
300 digest protein in the presence of condensed tannins, attesting to the specific digestion and
301 resistance characteristics of the caprine species to secondary metabolites. The architecture of
302 terpens (the presence of oxygen-containing ring structures) which are also important
303 secondary metabolites has a strong influence on their rumen degradability (Malecky *et al.*,
304 2009). These observations may prove useful to rationalize the use of essential oils and plant
305 dry extracts which are increasingly incorporated as additives to the diet of other ruminant
306 species to optimize ruminal fermentations (Calsamiglia *et al.*, 2007).

307

308 *Adaptation to salt or salt stress*

309 Animals may intake large amounts of salt with either feedstuffs or drinking water. Quite
310 often, both sources of salt are combined because water available for drinking is the same as
311 that used by the plants to grow on salty soils. This can be of critical importance when the
312 animals are grazing halophytes and when the saline water from underground wells is the only
313 available drinking water (Ashour *et al.*, 2016). According to the recent review of Attia-Ismail
314 (2016), intake of salt might modify the rumen fermentative profile with an impact on the acid
315 base equilibrium, especially on Na⁺, K⁺ and Cl⁻, and thus on the osmotic pressure within the
316 rumen. The animal drinks more water to balance this effect, which can decrease the adhesion
317 of bacteria to feed particles in the rumen and increase the turnover rate of solid and liquid
318 phases in the rumen. The consequence is a lower digestion in the rumen. Large differences in
319 salinity tolerance between animal species or between breeds within species are observed, and
320 it seems that sheep and goats are more tolerant to salt stress than cattle when adapted, and that
321 goats have a slight tolerance advantage over sheep (Dunson, 1974, McGregor, 2004, Squires,
322 2016). Goats are able to cope without any detrimental effect on digestibility up to levels of
323 8326 mg TDS (total dissolved solutes) in water (Paiva *et al.*, 2017) but, as in heifers, rumen
324 function and cell wall digestibility decreases with an increase in TDS (Alves *et al.*, 2017).

325

326 *Heat stress*

327 Heat stress is often associated with water deprivation or infrequent drinking in animals living
328 in arid areas (Silanikove, 1992). Feed intake decreases during heat stress for several reasons.
329 Thermoregulation operates to decrease heat production arising from rumen fermentation, and
330 there is limited availability of water and of feeds, the majority of which have a poor nutritive

331 value (Morand-Fehr & Doreau, 2000). Feeding pattern is also modified with an increase in
332 night grazing. In these conditions, reduction of passage rate through the digestive tract might
333 increase digestibility, but this benefit is overridden by the negative effects of heat stress and
334 water deprivation (Silanikove, 1992). Rumen fermentation is modified by heat stress: rumen
335 pH decreased at equivalent dry matter intake (Castro-Costa *et al.*, 2015) and the rumen
336 bacterial community changes in goats (Zhong *et al.*, 2019). Indigenous goats adapted to harsh
337 conditions are more capable of coping with heat stress than non-desert breeds (Silanikove,
338 1992). Moreover, goats have a poor insulation capacity in contrast to sheep, but have the
339 advantage of dissipating heat by sweating (Silanikove, 1992).

340 **Perspectives**

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

343

344 *Feeding behaviour*

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

350

351 *Microbiota*

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

363

364 *Omics*

365 As previously pointed out, the many interactions occurring between the different animal
366 tissues and cells but also, at different levels, between the cell (genome) and exogenous events
367 (environment) are hindrances to understanding the underlying mechanisms and the role of the
368 host compared to that of the rumen microbiota. One of the ways to access all of the systemic
369 and/or tissue-specific signatures is the approach *via* “omics”. Indeed, these approaches are
370 complementary in the search for interrelationships between genotypes and phenotypes
371 (Shahzad & Loor, 2012). Metabolomics, in which advanced analytical chemistry techniques
372 and multidimensional statistical analyses are applied to measure large numbers of small
373 molecule metabolites in cells, tissues and biofluids (end products of these complex
374 interactions), after being first exploited in biomedical research, is progressively used also in
375 research and monitoring of livestock (Goldansaz *et al.*, 2017). Most of the time, it is the
376 association between different complementary approaches which provides most information.
377 For example, by combining metabolomics and proteomic studies, it is possible to get a better
378 knowledge of the role of the rumen epithelium in goats adapted to grain-rich feeding
379 compared to hay feeding (Guo *et al.*, 2019). The joint and simultaneous use of metabolomics
380 and pyrosequencing studies in goats informs about the metabolic pathways preferentially
381 involved in the response to high-grain diets (Zhang *et al.*, 2019), whilst the links between the
382 ruminal bacterial community and metabolites represent a powerful tool in terms of prediction
383 or monitoring of certain nutritional diseases such as acidosis (Mao *et al.*, 2016, Hua *et al.*,
384 2017). These approaches also make it possible to investigate more finely and specifically *via*
385 co-culture the key role of microorganisms such as fungi and methanogens, but also the nature
386 of the metabolites produced (Cheng *et al.*, 2013). Interrelationships between the different
387 bacteria of the ruminal community in goat kids after birth and before weaning (Abecia *et al.*,
388 2018) can also be studied. These first studies using the “omics” approaches in livestock
389 (including small ruminants and goats), based on non-invasive sampling methodologies and
390 analysing a high quantity of small molecules in different biological fluids and matrices to
391 identify putative biomarkers, are probably only just the start of much more extensive research
392 exploiting the opportunities offered by multi-omics studies (Goldansaz *et al.*, 2017).

393 **Conclusion**

394 This review points out that goats have globally similar rumen function when compared to
395 other ruminants, even if there is a lack of detailed comparison between species in similar
396 conditions. Knowledge needs to be improved in some areas, such as microbial efficiency and

397 ecology or feeding behaviour. Moreover, some breeds of goats have developed specific
398 characteristics to sustain them in harsh conditions, because they are able to cope with anti-
399 nutritional or toxic compounds derived from secondary plant metabolites, and are quite
400 tolerant to environmental stressors, which is a key point in the context of climate change.

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