How Live Yeasts Used as DFMs Can Improve Feed Efficiency in Ruminants: The Rumen Microbiota as a Crucial Target

F. Chaucheyras-Durand[1,2], A. Piron[1], E. Chevaux[1], A. Hall[3], A. Aguilar[3], R. Gill[3] and L. Dussert[1]

[1] Lallemand Animal Nutrition, Blagnac, France ; [2] INRA UR454 Microbiologie, Theix, France ; [3] Lallemand Animal Nutrition, Milwaukee, USA.

In order to answer to the increasing demand for safe and of good nutritional quality products of ruminant origin, and in the context of increasing feed costs and of sustainability concerns of agricultural systems, improving animal feed efficiency has become a critical need for cattle farmers.

Rumen function optimization appears to be a crucial target to improve animal efficiency. Indeed, this digestive compartment hosts a complex anaerobic microbiota responsible for degradation and fermentation of the main part of dietary components ingested by the animal. However, many factors can impair rumen function. In this context, direct fed microbials (DFMs), such as live yeasts are an important tool to improve feed efficiency and performance and at the same time to prevent health disorders (Chaucheyras-Durand et al., 2008; 2012). Yeasts benefit from a natural and well-accepted image by the consumer, as they are not involved in health disorders and do not have any detrimental impact on the environment. Recent multi-study analyses performed both in dairy and beef cattle have shown significant benefits with Saccharomyces cerevisiae I-1077 on yield and feed efficiency (Erasmus et al., 2009; De Ondarza et al., 2010). This paper addresses the last findings in terms of mechanisms of action of live yeasts on rumen microbiota, with a focus on pH stabilisation effect, improvement in plant cell wall degrading communities, and on consequences on rumen efficiency, animal productivity and health.

BENEFITS OF USING LIVE YEAST TO STABILIZE RUMEN PH

Intense microbial fermentation of feedstuffs in the reticulo-rumen leads to the production of VFAs and lactic acid, which may accumulate and decrease ruminal pH. Low rumen pH for prolonged periods definitely impairs feed intake, microbial metabolism, and nutrient degradation, and leads to acidosis, inflammation, laminitis, diarrhea and milk fat depression. High producing cattle fed diets rich in readily fermentable starch or sugars at high feed intake levels are particularly susceptible to acidosis and it is now recognized that subacute ruminal acidosis (SARA) affects from 10-40% of dairy cattle in a herd, resulting in large financial losses and major concern for animal welfare reasons (Kleen and Cannizzo, 2012). Feeding high levels of rumen fermentable starch also leads to a decreased fiber degradation. Sauvant (unpublished synthesis of literature data, cited by Nozière et al, 2010) established that an increase in 1% DM in the diet of rumen degradable starch reduces rumen pH (-0.1 unit) and NDF digestion (-3%).

The effect of a diet shift (from high forage to high concentrate) on the composition of the rumen microbiota has been extensively studied, over the last 10 years because of the development of culture-independent–techniques allowing to quantify microbial abundance and assess population dynamics. Tajima et al. (2001) have shown that a diet shift from high forage to high grain in steers was accompanied with profound changes in bacterial abundances, an increase in S.bovis and P.ruminicola 16S gene copy numbers and a decline in fibrolytic F.succinogenes population densities being measured. Using quantitative PCR, Mosoni et al. (2007) measured significant decrease in fibrolytic F. succinogenes, R. albus and R. flavefaciens abundance in sheep fed 50% concentrate, compared with a 100% hay diet. Indeed, fiber-degrading bacterial species are particularly sensitive to low pH. Cellulolytic bacteria cannot grow with a low intracellular pH, and an increase in pH gradient leads to an entry of undissociated VFA in the cells and an accumulation of dissociated anions in the intracellular compartment induces severe toxicity for the bacteria (Russell and Wilson, 1996).

Khafipour et al. (2009) analyzed the microbiome of rumen samples taken from 8 lactating dairy cows in which SARA had been induced with either grain or alfalfa pellets using molecular techniques.

The most predominant shift during SARA was a decline in Gram-negative Bacteroidetes organisms. Severe grain-induced SARA was dominated by S. bovis and E. coli, whereas mild grain-induced SARA was dominated by M. elsdenii and alfalfa pellet-induced SARA by P. albensis.

An increase in the percentage of rapidly degradable starch in the diet generally favors the development of protozoa as soon as the rumen pH is not below 5.5 (Martin et al., 2006). The genus Entodinium can represent up to 95% of the total ciliate community. When rumen pH is below 5.5, ciliate protozoa populations are decreased and defaunation can be observed transiently. As protozoa engulf starch granules and digest starch slower than lactate producing bacteria (Owens et al., 1998), their disappearance increases the risk for severe acidosis. Low rumen pH has also a strong impact on rumen fungi. Indeed, the production of zoospores by Caecomyces has been shown to be sharply decreased in vitro at pH 5.5. Zoospore numbers were below 10^3/ml or were not even detected in the rumen of animals fed with diets inducing low rumen pH (Grenet et al., 1989). The presence of large amounts of soluble sugars may induce saturation of the spore adhesion sites and reduce fungal colonisation (Fonty and Grenet, 1994).

Sauvant (2006) summarized studies conducted on different feedstuffs and established a strong relationship between rumen pH values induced in vitro by each feedstuff fermentation and its percentage of DM degradation, showing that the nature of the feedstuff impacts on its acidogenic potential. Indeed, rapidly degradable starch (as in barley, or wheat) will more strongly impact rumen pH than slow degradable starch (as in corn or sorghum). The particle length of forages can greatly affect rumen pH. Indeed, physically effective NDF (peNDF) represents the physical characteristics of fibre by accounting for particle length and NDF content, which promote chewing and the flow of salivary buffers to the rumen (Mertens, 1997). Yang and Beauchemin (2007) compared rumen pH response when short or long cut alfalfa silage was included in either high or low concentrate diets. They showed that increasing peNDF intake reduced ruminal acidosis; mean ruminal pH and the duration that pH remained below 5.8 were highly correlated to intake of long particles.

Rumen pH regulation is thus a key determinant in the maintenance of an optimal rumen function. Stabilisation of ruminal pH in the presence of live yeast has been often reported (Bach et al., 2007; Chaucheyras Durand et al., 2008; Desnoyers et al., 2009; Marden et al., 2008). In a meta-analysis, Desnoyers et al. (2009) concluded that yeast supplementation increased ($P<0.05$) rumen pH in vitro, but did not find any significant in vivo effect neither on pH, nor on VFA or lactate. However, the studies selected for the meta-analysis had used different strains of S. cerevisiae, or yeast culture which is defined to be mainly composed by dead cells and fermentation products. More than an increase in mean rumen pH, reductions in duration within a day under a certain pH threshold, as well as in area under the pH curve have been measured in the presence of live yeast using in-dwelling pH boluses (Bach et al., 2007; Thrune et al., 2008). A recent study (De Ondarza et al., 2012) compared sodium bicarbonate and live yeast supplementation in 2 pens of 60 cows on milk production and feed efficiency and rumen pH was monitored every 5 min during 5 weeks in 4 cows. Mean pH remained consistently higher ($P<0.001$) for the live yeast supplemented cows when compared to the bicarbonate cows (6.22 vs 6.03). In addition, live yeast supplemented cows spent less time below a pH threshold of 5.6 (141 vs 378 min, $P<0.001$).

MODES OF ACTION ON RUMEN MICROBIOTA AND LACTATE ACCUMULATION

Because lactate accumulation can be detrimental for rumen pH, effects of live yeasts have been studied on lactate-metabolizing bacteria. In vitro, S. cerevisiae I-1077 was able to outcompete S. bovis for the utilization of sugars; due to a higher affinity of the yeast cells for sugars, the decrease in fermentable substrate available for the bacterial growth consequently limited the amount of lactate produced (Chaucheyras et al., 1996). This effect was only observed with live yeast cells. Moreover, stimulation of growth and metabolism of lactate-utilizing bacteria, such as M. elsdenii or S. ruminantium was observed in vitro in the presence of live yeasts (Chaucheyras et al., 1996) through a supply of

different growth factors such as amino acids, vitamins, and organic acids, essential for the lactate-fermenting bacteria.The impact of live yeast S. cerevisiae I-1077 on ruminal lactate concentration has been confirmed in several in vivo studies. In sheep during their adaptation to a high-concentrate diet, ruminal lactate concentration was significantly lower in live yeast supplemented animals compared to control animals. Consequently, rumen pH was maintained at values compatible with an efficient rumen function, as shown by higher fibrolytic activities (Michalet-Doreau and Morand, 1997; Michalet-Doreau et al., 1997). In dairy cows, reductions in ruminal lactate concentrations have also been observed with yeast (Marsola et al., 2010).

These results demonstrate the interest to use live yeasts to limit rumen lactate accumulation. However, at earlier stages of rumen acidosis, lactate is only detected at low levels and the fermentation pattern is dominated by high total VFA concentrations (>150 mM) with a decrease in acetate and an increase in butyrate proportions inducing great variations of ruminal pH (Brossard et al., 2004). Moreover, as shown by Lettat et al. (2010), according to the composition of the diet, the fermentation pattern can be shifted to butyric orientated acidosis. Brossard et al. (2004; 2006) reported the pH stabilising effect of S. cerevisiae I-1077 in fistulated sheep fed a high-wheat diet under a butyric latent acidosis. Authors suggested that this strain could act by stimulating ciliate Entodiniomorphid protozoa. In addition, the main end-products of starch fermentation by protozoa are VFA rather than lactate, which may explain why these ciliates had a stabilizing effect in the rumen by delaying fermentation.

BENEFICIAL CONSEQUENCES OF LIVE YEAST ON RUMEN FERMENTATIONS, FEEDING BEHAVIOR, FEED EFFICIENCY, AND ANIMAL PRODUCTION

Bach et al. (2007) reported that the supplementation of live yeast increased average rumen pH and average maximum pH by 0.5 units, and average minimum pH by 0.3 units of loose-housed lactating cows. In this study, a significant change was observed in the eating behavior of the animals. Cows supplemented with live yeast had a shorter inter-meal interval (3.32 h) than unsupplemented cows (4.32 h). This change in feeding behaviour could help in rumen pH recovery, or the beneficial effect of live yeast on pH stabilisation could induce a change in eating behaviour.
In their multi-study analysis, De Ondarza et al. (2010) found that live yeast supplementation improved ($P < 0.0001$) milk yield by 1.15 kg/d (34.19 vs.33.04 kg/d for live yeast and control, respectively).

No effect on DMI was observed (De Ondarza et al., 2010). Live yeast seems to have an effect on intake pattern rather than on intake per se (Bach et al., 2007). As a result, feed efficiency is improved in the presence of live yeast (De Ondarza et al. 2010; Moallem et al., 2009). Milk composition is generally not or only slightly affected by yeast supplementation.

BENEFITS OF USING LIVE YEAST TO PROMOTE FIBER DIGESTION

Fiber digestion in the rumen is a key process in ruminant nutrition. A very large proportion of energy intake of ruminant comes in the form of structural complex polysaccharides, which are mainly present in the plant cell walls. Effective degradation is the result of microbial adhesion on plant tissue and production of active enzymatic equipments well adapted for plant cell wall polyholoside breakdown.

Many biotic and abiotic factors limit the efficacy of fiber degradation in the rumen which may be driven by changes in fiber colonisation efficacy. For example, the chemical composition of the plant material modulates the rate and extent of fiber digestion (Varga and Kolver, 1997). Digestibility of plant cell walls has long been known to be negatively associated with lignin concentration. This relationship between lignin and fiber digestibility is very strong for a same forage compared according to different maturity stages, but it is less clear when comparing different forages harvested at a similar maturity stage, so with similar lignin concentrations (Jung et al., 2011).

It is generally admitted that most of fiber degrading microorganisms are highly sensitive to oxygen because most of them lack detoxification enzymes necessary for removal of reactive oxygen. The

presence of dissolved oxygen in the rumen ecosystem has been demonstrated (Scott et al., 1983, Hillman et al., 1985) and oxygen regularly enters the rumen due to bloodstream exchange, feed and water uptake and mastication, which can be illustrated by a greater post-feeding redox potential in dairy cows (Marden et al., 2005; 2008). Newbold et al. (1996) measured the concentration of cellulolytic bacteria in Rusitec in which either normal or low O_2 concentrations had been maintained. Oxygen concentration significantly influenced cellulolytic bacteria, whose numbers were increased by almost 15-fold when low O_2 concentrations were applied in the fermentors. In gnotobiotically-reared lambs, the concentration of cellulolytic bacteria was strongly decreased after a surgical cannulation of the rumen; the authors suggested that the deterioration of physico-chemical conditions of the rumen biotope, i.e. the entry of oxygen during surgery, was responsible for this decrease (Chaucheyras-Durand and Fonty, 2001). Adhesion of cellulolytic bacteria to cellulose has been shown to be inhibited in the presence of oxygen in vitro (Roger et al. 1990), and in Neocallimastix frontalis, zoospore formation was found to be depressed in the presence of this gas (Fonty and Grenet, 1994).

Among biotic factors, the existence of a complex set of interactions between fibrolytic microbes and the other actors of feed digestion does impact fiber degradation. For example, synergistic cross feeding interactions have been described between cellulolytic and non cellulolytic species which lead to a global improvement of degradation mechanisms. Hydrogen transfer between fiber degrading organisms and hydrogen consuming methanogens is necessary for an optimal functioning of fiber degradation mechanisms. On the opposite, competition mechanisms have been described between cellulolytic bacterial species for adhesion on cellulose (Chen and Weimer, 2001; Mosoni et al., 1997). Finally, the physiology of the microorganisms plays also an essential role on overall fiber digestion. Indeed, there are great differences between species regarding their preference and affinity for substrates, their energy requirements, their capacity to resist to environmental stresses.

Thereby, to optimize fiber digestion, there is a need to minimize the indigestible fiber fraction, maximize rate of fiber digestion, and maintain a ruminal environment that promotes the population of fiber-digesting bacteria. The indigestible fiber in forages (iNDF) is related to lignin concentration, but also contains structural carbohydrates (cellulose and hemicellulose) which are ‘trapped’ with lignin. Whereas lignin, of which biochemical degradation process involves oxidative pathways, is considered not digested in the animal gastro-intestinal tract, the release of the carbohydrates bound to lignin would be interesting in terms of increasing feed value of the forage.

MODES OF ACTION ON RUMEN MICROBIOTA INVOLVED IN FIBER DIGESTION

In vitro, fungal zoospore germination and cellulose degradation were found to be increased in the presence of a strain of S. cerevisiae (Chaucheyras et al., 1995); the authors suggested that yeasts could enhance fungal colonisation of plant cell walls, which was confirmed recently (Chaucheyras-Durand et al., 2010). In vivo, using gnotoxenic lambs harbouring only three species of bacteria (F. succinogenes, R. albus, and R. flavefaciens) as sole cellulolytic organisms, cellulolytic bacteria became established earlier and remained at a high and stable level in lambs that received S. cerevisiae I-1077 (Chaucheyras-Durand and Fonty, 2001). Ciliate protozoa, which are not able to establish unless bacterial communities have previously colonized the rumen, appeared more rapidly in the rumen of conventional lambs in the presence of live yeasts (Chaucheyras-Durand and Fonty, 2002).This supports the hypothesis that live yeast supplementation accelerates maturation of the rumen microbial ecosystem. Fiber degradation processes would thereby be set up more efficiently in the early age of the animal, as shown by the increase in polysaccharidase and glycoside-hydrolase activities in the presence of yeast in the rumen of gnotoxenic lambs (Chaucheyras-Durand and Fonty, 2001).

Live yeast indirectly promote fiber degradation or fibrolytic microbial activities by stabilizing rumen pH in case of SARA. Greater polysaccharide-degrading activities of the solid-associated bacterial fraction in rumen-cannulated adult sheep fed a high-concentrate diet were measured in the presence of live yeasts (Jouany et al., 1998; Michalet-Doreau et al., 1997). In the latter study, the proportions of 16S rRNA of F. succinogenes, R. albus, and R. flavefaciens were increased in the rumen of sheep receiving

the yeast (Chaucheyras et al., 1997). A 2 to 4-fold increase in the number of 16S rRNA gene copies of R. albus and R. flavefaciens was also measured with real-time PCR in rumen contents of sheep receiving a high-concentrate diet and S. cerevisiae I-1077 (Mosoni et al., 2007).

Guedes et al. (2008) reported that S. cerevisiae I-1077 increased in situ NDF degradation (NDFd) of corn silage. In this study, cows were fed with grass silage-corn silage based diet and the rumen pH was not characteristic for SARA. However, it is noteworthy that a yeast effect was observed on pH and lactate concentration but the authors suggested that the yeast efficacy to increase NDFd was not only attributable to a pH stabilisation effect. Using the same technique, Chaucheyras Durand et al (2010; unpublished) have studied the effect of the same yeast strain on fiber degradation of different fibrous substrates and followed the kinetics of colonisation by fiber degrading bacteria and fungi using qPCR in rumen cannulated cows. In this study, the diet was composed of grass silage and hay and was not at risk regarding acidosis. Results showed that the supplementation of S. cerevisiae I-1077 could promote substrate colonisation by cellulolytic bacteria (F.succinogenes, R.flavefaciens, B.fibrisolvens) and fungi but that the degree of stimulation was depending on the nature of the substrate and on the microbial species. Indeed, feedstuffs with highest levels of ADL and thereby with less easily accessible digestible carbohydrates were better degraded in the presence of S. cerevisiae I-1077, suggesting a particularly marked impact on the microbial breakdown of lignin-polysaccharides linkeages. Rumen fungi could be particularly involved in this process, because apart from producing a very efficient set of cellulases and hemicellulases, they also possess esterase activities which contribute to the cleavage of ester bridges which link phenolic compounds of lignin to structural carbohydrates (Ljungdahl, 2008 ; Qi et al., 2011). Moreover, thanks to the development of a rhizoidal network, they weaken and disrupt plant tissue which enhances accessibility to digestible structures (Fonty et al., 1999). Further research aiming to better understand the respective roles of the fibrolytic communities on fiber degradation kinetics is needed, and in this aim high throughput gene expression quantification tools are under development in our team. The same strain of S.cerevisiae significantly improved NDF degradation of 40 corn silages samples incubated in sacco in rumen cannulated cows, with differences in the degree of improvement according to the degradability of the corn silage (Guedes et al., 2008). Indeed, S. cerevisiae I-1077 increased NDFd of the low digestible corn silages more strongly than that of the high digestible corn silages. These results suggest that S. cerevisiae I-1077 could help to reduce indigestible NDF by promoting the action of bacteria and fungi involved in the hydrolysis of lignin-polyholoside bonds.

In the study of Chaucheyras-Durand et al. (2010), a positive effect of a live yeast additive was demonstrated for the first time on Butyrivibrio fibrisolvens abundance on fibrous substrates. The hemicellulose fraction of forages consumed by ruminants consists mainly of xylan which is substituted with acetyl, arabinosyl, and glucuronyl residues. Xylan is also cross-linked via ferulic and p-coumaric acids which are esterified to the arabinose side chains. It is supposed that the ester linkages between these phenolic acids and polysaccharide provide a steric hindrance to the microbial fiber. Consequently, the promotion of B. fibrisolvens, that possesses ferulic and p-coumaric acid esterases which hydrolyse these ester linkages (McSweeney et al., 1998) would probably be of great interest.

One of the main factors implicated in the beneficial effect of live yeasts on fiber-degrading bacteria is probably the capacity of yeast cells to scavenge oxygen. Most of ruminal microorganisms are considered to be highly sensitive to oxygen, but this is particularly true for fiber-degrading organisms. Newbold et al. (1996) reported that respiratory-deficient mutants of S. cerevisiae were unable to stimulate bacterial numbers in rumen-simulating fermenters, whereas the wild-type parent strains, able to consume oxygen, did effectively stimulate bacterial activities. Other studies have reported that redox potential of lambs rumen fluid was lowered in the presence of live yeasts in lambs (Chaucheyras-Durand and Fonty, 2002), in sheep (Jouany et al., 1998; Mathieu et al., 1996), and in cows (Marden et al., 2008) suggesting that live yeast cells could create more favorable environmental conditions for growth and activities of the anaerobic cellulolytic microbiota. Due to the fact that live yeasts could release vitamins or other growth factors to closely associated bacterial cells (Jouany, 2006), yeast impact could also be mediated through the interplay between different bacterial species (i.e. non cellulolytic species) and not only a direct effect on oxygen consumption.

CONSEQUENCES ON FEED EFFICIENCY AND ANIMAL PRODUCTION

The beneficial effects on fiber digestion can be partly at the origin of the increase in dry matter intake often observed with yeast supplementation (Desnoyers et al., 2009; Jouany, 2006), but more generally a better fiber digestion is recognized to benefit the animal rumen health and its function by improvement of feed efficiency (Bitencourt et al. 2008). De Ondarza et al. (2010) concluded to an average milk yield increase ($P<0.001$) of 0.9 kg/d for the live yeast supplemented cows, in their multi-analysis representing over 1,600 cows; the effect was particularly strong in low yielding cows (<33kg FCM). Feed efficiency of the supplemented animals was improved which illustrates a better use of the diet. When targeting the cows fed diet above 30% NDF, feed efficiency was higher than the overall mean and the live yeast treated animals gained an extra 40g of FCM milk per kg DMI. The shorter intervals between meals ($P<0.05$) of live yeast fed cows recorded by Bach et al. (2007) strongly suggests the fact that the TMR digestibility was improved as the meal size and length were not affected by the treatment. The significant improvement of the rumen pH (6.05 vs 5.49, $P<0.01$) for the cows receiving the live yeast would also support a higher activity of the cellulolytic flora and thus explain the higher meal frequency.

PRACTICAL IMPLICATION : MODELLING THE EFFECT OF LIVE YEAST

Fiber digestibility is part of energy value of feed calculated in dairy models (CNCPS for example). As mentioned earlier, use of S. cerevisiae I-1077 will have an impact on fiber degradation directly through fibrolytic microflora enhancement but also undirectly through rumen pH stabilisation. Modelling this quantitative response on rumen pH and finally on fiber degradation (kd CHOB3 for CNCPS) will allow to get the expected feed efficiency and income over feed cost (IOFC) in the main dietary situations, providing guidelines to farmers and nutritionists.

CONCLUSIONS

Thanks to their beneficial impact on fiber microbial degradation and on promotion of an optimal rumen environment, live yeasts represent a valuable tool which allows maximising the forage portion of the diet and giving the possibility to farmers and nutritionists to increase milk revenue per kg feed or to optimise cost of feed with similar milk revenue They can be particularly useful in the transition cow, when decreased DMI is often observed in spite of high energy demand. In addition, current intensive farming practices require high levels of fermentable carbohydrates which put the animal at risk of developing metabolic disorders and in that sense live yeasts are particularly relevant during a feed transition (weaning, grazing, step up feeding programs) or during periods of stress (hot temperature, transportation).

REFERENCES

Bach, A., Iglesias, C., and M. Devant. 2007. Daily rumen pH pattern of loose-housed dairy cattle as affected by feeding pattern and live yeast supplementation. Anim. Feed Sci.Technol. 136: 156-163.

Bitencourt, L.L., Pereira, M.N., de Oliveira, B.M.L., Silva, J.R.M., Dias Júnior, G.S., Lopes, F., de Melo, R.C.M., and S. Siécola Júnior. 2008. Response of lactating cows to the supplementation with live yeast. J. Dairy Sci. 91(E-suppl1): 264.

Brossard, L., Martin, C, Chaucheyras-Durand, F., and B. Michalet-Doreau. 2004. Protozoa involved in butyric rather than lactic fermentative pattern during latent acidosis in sheep. Reprod. Nutr. Dev. 44: 195-206.

Brossard, L., Chaucheyras-Durand, F., Michalet-Doreau, B., and C. Martin. 2006. Dose effect of live yeasts on rumen microbial communities and fermentations during butyric latent acidosis in sheep: new type of interaction. Anim. Sci. 82: 1-8.

Chaucheyras, F., Fonty, G., Bertin, G., Salmon, J.M., and P. Gouet. 1996. Effects of a strain of Saccharomyces cerevisiae (Levucell SC), a microbial additive for ruminants, on lactate metabolism in vitro. Can. J. Microbiol. 42: 927-933.

Chaucheyras, F., Millet, L., Michalet-Doreau, B., Fonty, G., Bertin, G., and P. Gouet. 1997. Effect of the addition of Levucell SC on the rumen microflora of sheep during adaptation to high starch diets. Reprod. Nutr. Dev. EE 5 (suppl): 82.

Chaucheyras-Durand, F. Ameilbonne, A., Walker, N.D., Mosoni, P., and E. Forano. 2010. Effect of a live yeast, Saccharomyces cerevisiae I-1077 on in situ ruminal degradation of alfalfa hay and fibre-associated microorganisms. J. Anim. Sci.88(E-Suppl. 2): 145.

Chaucheyras-Durand, F., Chevaux, E., Martin, C. and E. Forano. 2012. Use of yeast probiotics in ruminants: effects and mechanisms of action on rumen pH, fibre degradation, and microbiota according to the diet. In: Rigobelo, E. (Ed.) Probiotics, InTech, Rikeja, Croatia, In press.

Chaucheyras-Durand, F. and G. Fonty. 2006. Effects and modes of action of live yeasts in the rumen. Biologia (Bratislava) 61(6): 741-750.

Chaucheyras-Durand, F. and G. Fonty 2001. Establishment of cellulolytic bacteria and development of fermentative activities in the rumen of gnotobiotically-reared lambs receiving the microbial additive Saccharomyces cerevisiae CNCM I-1077. Reprod. Nutr. Dev. 41: 57-68.

Chaucheyras-Durand, F. and G. Fonty 2002. Influence of a probiotic yeast (Saccharomyces cerevisiae CNCM I-1077) on microbial colonization and fermentation in the rumen of newborn lambs. Microb. Ecol. Health Dis.14: 30-36.

Chaucheyras-Durand, F., Walker, N.D., and A. Bach. 2008. Effects of active dry yeasts on the rumen microbial ecosystem: past, present and future. Anim. Feed Sci.Technol. 145: 5-26.

Chen, J., and P. Weimer 2001. Competition among three predominant ruminal cellulolytic bacteria in the absence or presence of non-cellulolytic bacteria. Microbiol. 147: 21-30.

De Ondarza, M.B., Sniffen, C.J., Dussert, L., Chevaux, E., Sullivan, J., and N.D. Walker. 2010. Case study: Multiple-Study analysis of the effect of live yeast on milk yield, milk component content and yield, and feed efficiency. Prof. Anim. Sci. 26: 661–666.

De Ondarza, M.B., Hall, T., Sullivan, J. and E. Chevaux 2012. Effect of live yeast supplementation on milk yield, milk components, and rumen pH in dairy cows. J. Dairy Sci. E-suppl. In press.

Desnoyers, M., Giger-Reverdin, S., Bertin, G., Duvaux-Ponter, C., and D. Sauvant. 2009. Meta-analysis of the influence of Saccharomyces cerevisiae supplementation on ruminal parameters and milk production of ruminants. J.Dairy Sci. 92: 1620-1632.

Erasmus, L.J., Coertze, R.F., Leviton, M.N., and E. Chevaux. 2009. A meta-analysis of the effect of monensin or live yeast or a combination thereof on performance of beef cattle. J. Anim. Sci. 87(E-Suppl. 2): 281.

Fonty, G, Chavarot, M, Lepetit, J, Canistro, J,and R. Favier. 1999. Mechanical resistance of wheat straw after incubation in cultures of ruminal cellulolytic microorganisms. Anim. Feed Sci. Technol. 80(3/4): 297-307.

Fonty, G., and E. Grenet. 1994. Effects of diet on the fungal population of the digestive tract of ruminants. In: Mountfort, D.O., Orpin C.G. (Eds.) Anaerobic fungi: biology, ecology and function. New York: Marcel Dekker; p 229-239.

Grenet, E., Breton, A., Barry, P., and G. Fonty 1989. Rumen anaerobic fungi and plant substrates colonization as affected by diet composition. Anim. Feed Sci. Technol. 26: 55-70.

Guedes, C.M., Gonçalves, D., Rodrigues, M.A.M., and A. Dias-da-Silva. 2008. Effect of yeast Saccharomyces cerevisiae on ruminal fermentation and fiber degradation of maize silage in cows. Anim. Feed Sci. Technol.145: 27-40.

Hillman, K., Lloyd, D., and A.G..Williams. 1985. Use of a portable quadrupole mass spectrometer for the measurement of dissolved gas concentrations in ovine rumen liquor in situ. Curr. Microbiol. 12: 335-340.

Jouany, J.P. 2006. Optimizing rumen functions in the close-up transition period and early lactation to drive dry matter intake and energy balance in cows. Anim. Reprod. Sci. 96: 250-264.

Jouany, J.P., Mathieu, F., Senaud, J. Bohatier, J., Bertin, G., and M. Mercier, 1998. The effect of Saccharomyces cerevisiae and Aspergillus oryzae on the digestion of the cell wall fraction of a mixed diet in defaunated and refaunated sheep rumen. Reprod. Nutr. Dev. 38: 401-416.

Jung, H.G., Mertens, D.R., and R.L. Phillips.2011. Effect of reduced ferulate-mediated lignin/arabinoxylan cross-linking in corn silage on feed intake, digestibility, and milk production. J.Dairy Sci. 94(10): 5124-5137.

Khafipour, E., Li, S., Plaizier, J.C., and D.O. Krause. 2009. Rumen microbiome composition determined using two nutritional models of subacute ruminal acidosis. Appl. Environ. Microbiol. 75(22): 7115-7124.

Kleen, J.L., and C. Cannizzo. 2012. Incidence, prevalence and impact of SARA in dairy herds. Anim. Feed Sci. Technol.172: 4-8.

Lettat, A., Nozière, P., Silberberg, M., Morgavi, D.P., Berger, C., and C. Martin C. 2010. Experimental feed induction of ruminal lactic, propionic, or butyric acidosis in sheep. J. Anim. Sci. 88(9): 3041-3046.

Ljungdahl, L.G. 2008. The cellulase/hemicellulase system of the anaerobic fungus Orpinomyces PC-2 and aspects of its applied use. Ann NY Acad. Sci. 1125: 308-321.

Mathieu, F., Jouany, J.P., Sénaud, J., Bohatier, J., Bertin, G., and M. Mercier. 1996. The effect of Saccharomyces cerevisiae and Aspergillus oryzae on fermentations in the rumen of faunated and defaunated sheep; protozoal and probiotic interactions. Reprod. Nutr. Dev. 36(3) 271-287.

McSweeney,C.S., Dulieu, A., and R. Bunch. 1998. Butyrivibrio spp. and other xylanolytic microorganisms from the rumen have cinnamoyl esterase activity. Anaerobe 4(1): 57-65.

Marden, J.P., Bayourthe, C., Enjalbert, F., and R. Moncoulon .2005. A new device for measuring kinetics of ruminal pH and redox potential in dairy cattle. J. Dairy Sci. 88(1): 277-281.

Marden, J.P., Julien, C., Monteils, V., Auclair, E., Moncoulon, R., and C. Bayourthe . 2008. How does live yeast differ from sodium bicarbonate to stabilize ruminal pH in high-yielding dairy cows? J. Dairy Sci. 91(9): 3528-3535.

Marsola, R.S., Favoreto, M.G., Silvestre, F.T., Shin, J.C., Walker, N., Adesogan, A., Staples, C.R., and J.E.P. Santos. 2010. Effect of feeding live yeast on performance of holstein dairy cows during summer. J. Dairy Sci. 93(E-Suppl1): 432.

Martin, C., Brossard, L., M. Doreau. 2006. Mécanismes d'apparition de l'acidose ruminale latente et conséquences physiopathologiques et zootechniques. INRA Prod. Anim. 19: 93-108.

Mertens, D.R. 1997. Creating a system for meeting the fiber requirements of dairy cows. J. Dairy Sci. 80(7): 1463-1481.

Michalet-Doreau, B., and D. Morand. 1997. Effect of yeast culture, Saccharomyces cerevisiae CNCM I-1077, on ruminal fermentation during adaptation to high-concentrate feeding. In: 4èmes Rencontres autour des Recherches sur les Ruminants, Paris. 4: 121.

Michalet-Doreau, B., Morand, D., and C. Martin. 1997. Effect of the microbial additive Levucell SC CNCM I-1077 on microbial activity in the rumen during the stepwise adaptation of sheep to high concentrate diet. Reprod. Nutr. Dev. supplEE5: 81.

Moallem, U., Lehrer, H., Livshitz, L., Zachut, M., and S. Yakoby. 2009. The effects of live yeast supplementation to dairy cows during the hot season on production, feed efficiency, and digestibility. J. Dairy Sci. 92: 343-351.

Mosoni, P., Fonty, G., and P. Gouet 1997. Competition between ruminal cellulolytic bacteria for adhesion to cellulose. Curr. Microbiol.35(1): 44-47.

Mosoni, P., Chaucheyras-Durand, F., Béra-Maillet, C. and E. Forano. 2007. Quantification by real-time PCR of cellulolytic bacteria in the rumen of sheep after supplementation of a forage diet with readily fermentable carbohydrates. Effect of a yeast additive. J. Appl. Microbiol. 103: 2676–2685.

Newbold, C.J. Wallace, R.J. and F.M. McIntosh. 1996. Mode of action of the yeast Saccharomyces cerevisiae as a feed additive for ruminants. Br. J.Nutr.76(2): 249-261.

Noziére, P., Ortigues-Marty I., Loncke C., and D. Sauvant. 2010. Carbohydrate quantitative digestion and absorption in ruminants: from feed starch and fiber to nutrients available for tissues. Animal 4: 1057–1074

Owens, F.N., Secrist, D.S., Hill, W.J., and D.R. Gill. 1998. Acidosis in cattle: a review. J. Anim. Sci. 76(1): 275-286.

Qi, M., Wang, P., Selinger, L.B., Yanke, L.J., Forster, R.J., and T.A. McAllister. 2011. Isolation and characterization of a ferulic acid esterase (Fae1A) from the rumen fungus Anaeromyces mucronatus. J. Appl. Microbiol. 110(5): 1341-1350.

Roger, V., Fonty, G., Komisarczuk-Bony, S. and P. Gouet 1990. Effects of physicochemical factors on the adhesion to cellulose Avicel of the rumen bacteria Ruminicoccus flavefaciens and Fibrobacter succinogenes subsp. succinogenes. Appl. Environ. Microbiol. 56: 3081-3087.

Russell, J.B., and D.B. Wilson. 1996. Why are ruminal cellulolytic bacteria unable to digest cellulose at low pH? J. Dairy Sci. 79: 1503-1509.

Sauvant, D. 2006. Le contrôle de l'acidose ruminale latente. INRA Prod. Anim. 19(2): 69-78.

Scott, R.I., Yarlett, N., Hillman, K., Williams, T.N., Williams, A.G., and D. Lloyd. 1983. The presence of oxygen in rumen liquor and its effects on methanogenesis. J. Appl. Bacteriol. 55: 143-149.

Tajima, K., Aminov, R.I., Nagamine, T., Matsui, H., Nakamura, M., and Y. Benno. 2001. Diet-dependent shifts in the bacterial population of the rumen revealed with real-time PCR. Appl. Environ. Microbiol. .67: 2766-2674.

Thrune, M., Bach, A., Ruiz-Moreno, M., Stern, M.D., and J.G. Linn. 2008. Effects of Saccharomyces cerevisiae on ruminal pH and microbial fermentation in lactating dairy cows. J. Dairy Sci. 90(Suppl. 1): 172.

Varga, G.A., and E.S. Kolver. 1997. Microbial and animal limitations to fiber digestion and utilization. J. Nutr. 127(5 Suppl): 819S-823S.

Yang, W.Z., and K.A. Beauchemin. 2007. Altering physically effective fiber intake through forage proportion and particle length: digestion and milk production. J. Dairy Sci. 90(7): 3410-3421.