



Review Article

Influence of yeast on rumen fermentation, growth performance and quality of products in ruminants: A review

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ABSTRACT

This review aims to give an overview of the efficacy of yeast supplementation on growth performance, rumen pH, rumen microbiota, and their relationship to meat and milk quality in ruminants. The practice of feeding high grain diets to ruminants in an effort to increase growth rate and weight gain usually results in excess deposition of saturated fatty acids in animal products and increased incidence of rumen acidosis. The supplementation of yeast at the right dose and viability level could counteract the acidotic effects of these high grain diets in the rumen and positively modify the fatty acid composition of animal products. Yeast exerts its actions by competing with lactate-producing (*Streptococcus bovis* and *Lactobacillus*) bacteria for available sugar and encouraging the growth of lactate-utilising bacteria (*Megasphaera elsdenii*). *M. elsdenii* is known to convert lactate into butyrate and propionate leading to a decrease in the accumulation of lactate thereby resulting in higher rumen pH. Interestingly, this creates a conducive environment for the proliferation of vaccenic acid-producing bacteria (*Butyrivibrio fibrisolvens*) and ciliate protozoa, both of which have been reported to increase the ruminal concentration of *trans*-11 and *cis*-9, *trans*-11-conjugated linoleic acid (CLA) at a pH range between 5.6 and 6.3. The addition of yeast into the diet of ruminants has also been reported to positively modify rumen biohydrogenation pathway to synthesise more of the beneficial biohydrogenation intermediates (*trans*-11 and *cis*-9, *trans*-11). This implies that more dietary sources of linoleic acid, linolenic acid, and oleic acid along with beneficial biohydrogenation intermediates (*cis*-9, *trans*-11-CLA, and *trans*-11) would escape complete biohydrogenation in the rumen to be absorbed into milk and meat. However, further studies are required to substantiate our claim. Therefore, techniques like transcriptomics should be employed to identify the mRNA transcript expression levels of genes like stearoyl-CoA desaturase, fatty acid synthase, and elongase of very long chain fatty acids 6 in the muscle. Different strains of yeast need to be tested at different doses and viability levels on the fatty acid profile of animal products as well as its vaccenic acid and rumenic acid composition.

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1. Introduction

Associated with the rapid growth in human population is the corresponding increase in the demand for livestock products in developing countries which may double by the year 2030 (FAO, 2015). This has led to an increased intensification of livestock production worldwide which necessitates the use of a high-grain diet in order to boost animal production (Lara et al., 2018). However, the use of a high grain diet to improve the performance of livestock predisposes the animals to increased fat deposition and

metabolic disorders like acidosis in ruminants. As such, the use of feed additives that will improve rumen health when feeding high grain diets is necessary (Nozière et al., 2014).

Consumers in developed countries are beginning to reject meat with a high composition of saturated fatty acid which is linked to cardiovascular diseases and cancer. This has challenged animal nutritionists to find ways to modify the fatty acid content of meat to increase its acceptability (Wood et al., 2004; Webb and O'Neill, 2008; Chikwanha et al., 2018).

Probiotics, though not fully explored, have the capacity to modify the gut microbial ecology and that may have an effect on lipid metabolism which might, in turn, affect the quality of animal products. A definite mode of action for probiotics is yet to be demarcated, but a variety of pathways have been hypothesized. Probiotics have the ability to modify microbial populations in the rumen or hindgut, change its fermentation pattern, increase the flow of nutrients to the small intestine and enhance feed digestibility (Krehbiel et al., 2003). Other authors reported that the addition of probiotics to livestock diets may decrease the concentration of serum cholesterol through direct assimilation of the cholesterol molecules by the microbes (Nami et al., 2019). Therefore, the supplementation of probiotics could enhance livestock performance through the maintenance of healthy rumen, enhancing the breakdown of fibrous feeds in the rumen by improving the uptake of nutrients, thereby resulting in an increased yield of livestock products (Arowolo and He, 2018).

Yeast is a commonly used probiotic in ruminant nutrition and has been proven to be effective in restoring gut microbial balance, especially during digestive disorders (McAllister et al., 2011). It is widely used in ruminant production to improve feed efficiency, and prevent rumen acidosis through its fermentation activities, by competing with other microbes within the rumen (Fonty and Chaucheyras-Durand, 2006). Although several authors have been investigating the efficacy of including yeast into the diets of ruminants for decades, there are still a lot of research gaps that need to be filled. Many of the published literature on yeast have reported inconsistent results and its mechanism of action is not entirely understood. With the current global crusade against the use of antibiotics in livestock feeds, the use of yeast in improving rumen fermentation and growth performance has received renewed attention. However, the efficacy of yeast in improving meat and milk quality, especially their fatty acid profiles and conjugated linoleic acid (CLA) composition, have been neglected. Since yeast is capable of altering the rumen fermentation, it could affect the rumen biohydrogenation which could in turn influence the fatty acid deposited into animal products. Therefore, this review aims to give an overview of the efficacy of yeast supplementation on growth performance, rumen pH, rumen microbiota, and their relationship to meat and milk quality in ruminants.

2. Influence of dietary yeast supplementation on rumen fermentation

2.1. Effects on rumen microbial composition

Yeast is known to play a vital role in the maintenance of a healthy rumen environment through its association with lactate-utilising bacteria and it supports the proliferation of other useful microorganisms in the rumen (Newbold 1996; Yang et al., 2004). It is able to stabilise the rumen pH through fermentation activities that suppress the activities of a lactate-producing microbe and encourages the proliferation of lactate-utilising bacteria resulting in less accumulation of lactic acid in the rumen (Lesmeister et al., 2004; Guedes et al., 2008). The common lactate-utilising bacteria in the rumen of grain-fed cattle are *Megasphaera elsdenii*

(Chaucheyras-Durand et al., 2008). The increase in the population of this bacteria has been found to be effective in decreasing the accumulation of lactate in a rumen culture (Kung and Hession, 1995) and reducing the incidence of ruminal acidosis in cattle (Robinson et al., 1992). Interestingly, yeast has been reported to stimulate the growth of this important lactate-utilising bacteria. A study conducted by Pinloche et al. (2013) observed that yeast supplementation increased the population of *M. elsdenii* in the rumen of cows on a high-grain diet. Similarly, yeast was found to be effective in increasing the proportion of *M. elsdenii* in the rumen of cows having sub-acute rumen acidosis (SARA) (Malekkhahi et al., 2016). This can be ascribed to the ability of yeast to provide nutrients that stimulate the proliferation of the bacteria (Chaucheyras et al., 1996). In another study conducted by Ogunade et al. (2019), the inclusion of yeast into the diet of steers caused an increase in the population of carbohydrate digesting bacteria (*Ruminococcus albus*, *R. champanellensis*, *R. bromii*, and *R. obeum*) and lactate-utilising bacteria (*M. elsdenii*, *Desulfovibrio desulfuricans*, and *Desulfovibrio vulgaris*). The rumen microbial composition of ruminants fed yeast has been summarized in Table 1.

On the other hand, Zhu et al. (2017) reported a reduced proportion of lactate-utilising bacteria (*M. elsdenii* and *Selenomonas ruminantium*) whereas the population of fungi and some cellulose digesting bacteria (*R. albus*, *R. flavefaciens*, and *Fibrobacter succinogenes*) were observed to increase after yeast supplementation in dairy cows fed low-quality forage. Furthermore, the authors recorded a decreased population of lactic acid-producing bacteria (*Streptococcus bovis*). This could be due to reduced availability of fermentable sugar caused by low-quality forage. Generally, yeast is known to suppress the proliferation of lactate-producing bacteria, however, Fomenky et al. (2017) observed an increase in the total population of *Lactobacilli* in the rumen of weaned calves supplemented with yeast. This might be due to the age of the animals as the rumen is still developing.

The ability of yeast to stimulate the growth of fibre digesting bacteria is well established. Several authors (Wiedmeier et al., 1987; Harrison et al., 1988; Williams 1989; Mao et al., 2013) investigated the effects of yeast on rumen microbiota and reported an increase in the population of cellulolytic bacteria (*F. succinogenes* and *R. flavefaciens*). This can be attributed to yeast's ability to provide nutrients that encourage the growth of cellulolytic bacteria such as *F. succinogenes*, *R. albus*, and *R. flavefaciens* (Chaucheyras-Durand et al., 2008). Chiquette et al. (2012), however, reported a decrease in the population of *F. succinogenes* in the rumen during the SARA challenge. In another study, Bach et al. (2019) observed that the inclusion of yeast to the diets of pregnant cows increased the population of *Bacteroidales*, *Lachnospiraceae*, and *Flexilinea* in the rumen 14 d before calving. All these bacteria are fibre-digesting because *Flexilinea* was reported to degrade all kinds of carbohydrates (Sun et al., 2016), and *Bacteroidales* and *Lachnospiraceae* specialise in the fermentation of cellulose (Henderson et al., 2015) and pectin (Cotta and Forster, 2006) respectively. In a recent study (Ogunade et al., 2019), the 16S rRNA gene sequencing and "liquid chromatography-mass spectrometry-based metabolomics" were used to classify rumen microbes at specie level following yeast supplementation in beef steers and the results showed that yeast increased the population of some rare species of cellulose-digesting bacteria (*Rhodopseudomonas palustris* and *Sorangium cellulosum*). These studies confirm the efficacy of yeast in supporting the growth of several species of fibre digesting bacteria.

On the other hand, Bayat et al. (2015) reported no significant effect of live yeast on the population of *F. succinogenes*, *R. flavefaciens*, *Methanogenic archaea*, total bacteria, protozoa, and fungi in the rumen of cows fed silage-based diets. In a study conducted by Xiao et al. (2016), the addition of yeast culture into the

Table 1
Summary of the rumen microbial composition of ruminants fed yeast.

Item	Diet	Dose of yeast	Response	Source
Weaner lambs	High concentrate diet	1 mL live yeast culture (1.5×10^9 to 2.0×10^9 CFU/mL) per kilogram live weight	Increased ciliate protozoa; increased feed intake and growth rate; increased entodinomorphs population	Tripathi and Karim (2011)
Calves	Milk replacer, starter feed, and hay	Yeast at 7.5×10^8 CFU/L before weaning and 3×10^9 CFU/kg after weaning	Increased total <i>Lactobacilli</i> population around weaning period	Fomenky et al. (2017)
Holstein bull calves	Milk and starter grains (no forage)	0.5% and 1% of yeast fermentation product on an as-fed basis in starter diets and milk	Increased <i>Butyrivibrio</i> and decreased <i>Prevotella</i> composition of the rumen fluid	Xiao et al. (2016)
Dry Holstein cows	F:C was 70:30	Yeast at 3.3 g/kg of diet per d (1×10^{10} CFU/d)	Increased the relative abundance of <i>Bacteroidales</i> , <i>Lachnospiraceae</i> , and <i>Flexilinea</i>	Bach et al. (2019)
Rumen-fistulated Holstein dairy cows	F:C was 40:60	A yeast culture at 10 g/cow per d (20×10^9 CFU/cow per d)	Increased the population of <i>Fibrobacter succinogenes</i> during adaptation; an increased population of <i>Megasphaera elsdenii</i> during SARA	Malekhhahi et al. (2016)
Finnish Ayrshire cows	F:C was 50:50	Live yeast at 0.5 g/cow per d (10^{10} CFU/cow per d)	No effects on animal performance and rumen fermentation	Bayat et al. (2015)
Qinchuan cattle	F:C was 55:45	1 and 2 g live yeast or 20 g yeast cell wall polysaccharides/cow per d	Higher digestibility of ADF and NDF; increased the population of <i>F. succinogenes</i> S85, <i>Ruminococcus albus</i> 7 and <i>R. flavefaciens</i> FD-1; decreased the percentage of <i>Streptococcus bovis</i> JB1	Peng et al. (2020)
Holstein steers	F:C was 50:50	Live yeast at 15 g/d	Increased the population of <i>R. albus</i> , <i>R. champanellensis</i> , <i>R. bromii</i> , <i>R. obeum</i> , <i>M. elsdenii</i> , <i>Desulfovibrio desulfuricans</i> , and <i>D. vulgaris</i>	Ogunade et al. (2019)

F:C = forage:concentrate ratio; SARA = sub-acute rumen acidosis.

diets of Holstein calves improved the percentage of *Butyrivibrio* and reduced the relative proportion of *Prevotella* in the rumen. These results revealed the efficacy of the yeast in affecting the composition of rumen microbiota. The viability of the yeast has been shown to influence how the rumen microbes respond to it. Jiang et al. (2017b) compared the effects of live yeast and dead yeast on the rumen microbiota of cows and the results obtained revealed that live yeast increased the population of cellulose-digesting bacteria, whereas the dead yeast did not affect the population of cellulolytic bacteria.

In one of the few studies that investigated the efficacy of yeast on gene expression, Ogunade et al. (2019) reported an increase in the expression of genes associated with oxidative phosphorylation (ubiquinol-cytochrome c reductase cytochrome b subunit and cytochrome c oxidase subunit) which suggests the ability of yeast to scavenge oxygen within the rumen. The efficacy of yeast in removing oxygen within the rumen has earlier been reported by Rose (1987). This is very important for maintaining a healthy rumen ecosystem because the majority of the rumen microbiota are anaerobic in nature (Loesche, 1969). This could be the reason as to why yeast is able to support the growth of several species of rumen microbes.

2.2. Rumen volatile fatty acid composition

Yeast supplementation could alter the rumen microbial population, making the environment more conducive for fibre digesting bacteria, thereby causing a change in the type and proportions of individual volatile fatty acids (VFA) produced in the rumen. In a study conducted by Xiao et al. (2016), the addition of yeast to the diet of cows was effective in increasing the concentration of butyrate in the rumen. Similarly, Zhu et al. (2017) observed an increased concentration of butyrate in addition to acetate, propionate, and total VFA concentration following yeast supplementation in dairy cows. Furthermore, increased ruminal butyrate concentrations in calves (Laarman et al., 2012) and a higher proportion of propionate in the rumen of matured cattle (Harrison et al., 1988; Hinman et al., 1998; Dias et al., 2018) have been reported after yeast supplementation. This could be attributed to the ability of yeast to

stimulate the growth of *M. elsdenii* (Chaucheyras et al., 1996; Pinloche et al., 2013; Malekhhahi et al., 2016) which has been reported to degrade lactate into propionate and butyrate (Chen et al., 2019). However, this depends on the culture pH and concentration of lactate due to their role in the regulation of genes associated with lactate metabolism. Interestingly, pH was found to be more effective than lactate concentration in influencing lactate-utilisation by *M. elsdenii*. Consequently, the increase in rumen pH will positively affect lactate utilisation by the bacteria during rumen acidosis (Chen et al., 2019). This suggests that increasing the rumen pH during rumen acidosis will result in higher degradation of lactate to propionate and butyrate by *M. elsdenii* which will help reduce the accumulation of lactate in the rumen. Since propionate is the main source of glucose supply to the ruminant animal and a major substrate for gluconeogenesis (Dijkstra et al., 2012), it will be rapidly absorbed by the rumen papillae to be used as an energy source. Butyrate is also utilized for energy production as well as rumen papillae and epithelial development (Laarman et al., 2012). In another study, Al Ibrahim et al. (2010) observed a higher proportion of ruminal acetate following yeast supplementation in dairy cows. In the same way, other studies on calves (Hučko et al., 2009) and dairy cows (Malekhhahi et al., 2016) reported an increased concentration of acetate in addition to a higher ratio of acetate to propionate after feeding yeast-based diets. The increased acetate concentration observed in these studies could be due to the positive influence of yeast on the growth of *D. desulfuricans* and *D. vulgaris* (Ogunade et al., 2019) both of which have been reported to convert lactate into acetate (Vita et al., 2015).

In another study, Opsi et al. (2012) tested the effects of yeast viability on VFA production in-vitro and observed that live yeast decreased acetate concentration but increased valerate proportions, and inactive yeast increased acetate proportions and decreased propionate concentrations.

2.3. Rumen pH

Livestock producers generally use high grain diets to encourage rapid growth which comes with serious consequences to gut health. A study conducted by Commun et al. (2009) confirmed that

feeding high levels of concentrate diets to lambs resulted in lower pH and rumen acidosis. Rumen acidosis can be either acute or sub-acute. Clinical acute acidosis is the increased concentration of lactate in the rumen which leads to a decrease in rumen pH below 5.0, and sub-clinical ruminal acidosis is characterized by a pH range between 5.0 and 5.8 for a period longer than 3 h in a day (Beauchemin et al., 2000; AlZahal et al., 2007). Sub-clinical ruminal acidosis is usually caused by a high concentration of VFA rather than the accumulation of lactate (Beauchemin et al., 2003). This does not imply that lactic acid is not produced during sub-clinical ruminal acidosis, but it is usually utilized by micro-organisms faster than it is synthesized (Yang et al., 2004). Yeast is capable of either competing with *S. bovis* and *Lactobacillus* for fermentable carbohydrates or encouraging the growth of lactate-utilising bacteria which results in the low accumulation of lactate and consequently, a higher pH (Nisbet and Martin, 1990; Chaucheyras et al., 1996; Chaucheyras-Durand and Fonty 2001, 2006; Bach et al., 2007). This is because yeast is capable of utilising the available sugar within the rumen to deprive *S. bovis* of having access to enough glucose for its metabolic activity. Yeast has also been reported to stimulate the growth of lactate utilising bacteria (*M. elsdenii*) (Chaucheyras et al., 1996). Several studies have investigated the effects of yeast on rumen pH, however the response has been inconsistent. A study conducted by Dias et al. (2018) observed a higher ruminal pH in the rumen of yeast-fed cows. Similarly, yeast has been reported to decrease lactic acid

concentration (Erasmus et al., 1992) and increase the ruminal pH (Bach et al., 2007; Thrune et al., 2009) in dairy cows. In a meta-analysis of several published studies, yeast was reported to increase rumen pH (Desnoyers et al., 2009). In another study, Chademana and Offer (1990) investigated the efficacy of yeast on sheep and observed a non-significant increase in rumen pH. Contrary to the above studies, some authors (Harrison et al., 1988; Edwards et al., 1990) reported lower rumen pH in cattle supplemented with yeast. The viability of the yeast has been shown to affect its fermentation mechanism, which in turn affects the response of an animal to yeast treatment. In a study conducted by Lynch and Martin (2002), the addition of live yeast increased the culture pH, and dead yeast resulted in a decreased pH during in-vitro incubation. Similarly, Opsi et al. (2012) observed that inactivated yeast had no effects on ruminal pH, but live yeast decreased ruminal pH during an in-vitro digestibility of feed. Many other authors (Erasmus et al., 1992; Putnam et al., 1997; Miller-Webster et al., 2002; Yang et al., 2004; Xiao et al., 2016) did not observe any change in rumen pH of animals treated with yeast. The variability in the efficacy of yeast reported in the studies above could be due to the differences in basal diets given to animals, viable cell numbers in yeast, the dosage of yeast supplemented, the type of forage fed and feeding strategy (Cole et al., 1992; Piva et al., 1993; Cabrera et al., 2000; Kawas et al., 2007). The effects of yeast on rumen pH and VFA obtained from various sources are summarized in Table 2.

Table 2
Effects of *Saccharomyces cerevisiae* on rumen pH and volatile fatty acids.

Item	Diet	Dose of yeast	Response	Mean pH of treatment groups	Source
Santa Ines lambs	F:C was 40:60	Inactive dry yeast at 4.87%, 9.73%, and 14.60% of diets	No effects on pH	5.83	Rufino et al. (2013)
Dry Holstein cows	F:C was 60:40	Live dried yeast 3.0 g/cow per d	Increased ruminal pH	6.26	Křížová et al. (2011)
Primiparous Holstein cows	Low starch (F:C was 50:50); high starch (F:C was 40:60)	Inactivated dry yeast at 15 g/cow per d	Increased ruminal pH	Low starch, 6.36; high starch, 6.08	Dias et al. (2018)
Malpura lambs	High starch diet (no forage)	Yeast at 9.0×10^7 CFU/kg body weight	No effects on pH	6.59	Bhatt et al. (2018)
Holstein bull calves	Milk and starter grains (no forage)	0.5% and 1% of yeast fermentation product on an as-fed basis in starter diet and milk	Increased butyrate concentration; no effect on pH	5.69	Xiao et al. (2016)
Feedlot cattle	High grain	10 g of <i>E. faecium</i> + <i>S. cerevisiae</i> /steer per d (6×10^8 CFU/g)	No effects on pH	5.85	Yang et al. (2004)
Multiparous Holstein cows	F:C was 60:40	0.5 g of active dry yeast/cow per d (10^{10} CFU/d)	Increase in ruminal pH; increased butyrate concentration	6.53	Thrune et al. (2009)
Holstein cows	F:C was 40:60	60, 120 or 180 g of yeast fermentation product/cow per d	No effects on pH	6.34	Zhu et al. (2017)
Lactating Holstein cows	High concentrate	10 g of yeast culture/cow per d	No effects on pH; decreased lactic acid concentration	6.0	Erasmus et al. (1992)
Charolais bulls	High concentrate	5 g of live yeast/bull or (1×10^{10} CFU/bull per d)	No effects on pH; increased acetate and butyrate concentrations; increased acetate:propionate ratio	5.89	Magrin et al. (2018)
Finnish Ayrshire cows	F:C was 50:50	0.5 g of live yeast/cow per d (10^{10} CFU/d)	No effects on pH	6.65	Bayat et al. (2015)
In vitro fermentation (Rumen fluid collected rumen-fistulated Assaf sheep)	High forage and high concentrate	5×10^9 CFU inactivated and 10^9 CFU live yeast/L of medium	Live yeast decreased ruminal pH; inactivated yeast did not affect pH	High forage, 6.64; high concentrate, 6.7	Opsi et al. (2012)

F:C = forage:concentrate ratio.

3. Growth performance and quality of ruminant products following yeast treatment

3.1. Growth performance

Yeast is believed to improve the performance of ruminants by encouraging the growth of fibre digesting microbes. This is important when concentrate based diets are fed to ruminants (Dias et al., 2018). In addition, active yeast has the potential to stimulate the proliferation of cellulolytic bacteria and lactate-utilising bacteria resulting in increased feed intake, reduced frequency of diarrhoea, increased animal performance, and improved stability of the rumen in young ruminants at weaning (Chaucheyras et al., 1995). Galvao et al. (2005) reported improved weight gain and reduced cases of diarrhoea in calves supplemented with yeast. Similarly, the supplementation of yeast was effective in promoting increased feed intake, growth rate and rumen development in calves (Adams et al., 2008) meanwhile causing a higher weight gain in bulls on a high grain diet (Geng et al., 2016). Furthermore, improved feed intake and weight gain were recorded in ruminants fed yeast-based diets (Lesmeister et al., 2004; Tripathi and Karim, 2011; Domínguez-Vara et al., 2009). On the contrary, Sales (2011) conducted a meta-analysis and the results revealed that active dry yeast did not have any effect on growth and feed conversion ratio of sheep. Similarly, several authors (Kawas et al., 2007; Titi et al., 2008; Bayat et al., 2015) reported that the inclusion of yeast into diets of livestock (lambs, kids, and cows) did not have any effect on the growth performance of the animals.

Interestingly, the effects of the dose and strain of yeast on the performance of buffalo calves were investigated and the results revealed that the addition of a high dose of yeast (3×10^9 CFU/kg dry matter) and mixed strains had a higher effect on growth rate than the low dose (1×10^9 CFU/kg dry matter) and single strain (Malik and Bandla, 2010). In a related study, the inclusion of a higher dose of yeast (2%/kg DM) improved feed intake, weight gain, and feed efficiency of calves, whereas the inclusion of a lower dose (1% dry yeast/kg DM) has no effect on the performance of the calves (Lesmeister et al., 2004). Although the strain and dose of yeast were found to affect the performance of calves, the proximate composition of the basal diet, particularly crude protein, also has a role to play. The efficacy of yeast on a low protein diet and high protein diet were investigated in sheep and the results obtained revealed that yeast supplementation improved the weight gain of sheep that were fed low protein diets, but had no effect on the weight of animals fed high protein diets (Bonilla et al., 1992). Factors such as strain, dose, frequency, and duration of supplementation may affect the response of livestock to probiotics (Buntyn et al., 2016; Slattery et al., 2016).

3.2. Potential of yeast in improving the quality of meat and milk in ruminants

3.2.1. Effects of yeast on meat fat deposition and fatty acid profile

Limited studies have been carried out on the effects of yeast supplementation on meat quality probably due to the lack of a clear understanding of the connection between the two; however, the results obtained were promising (Table 3). The inclusion of yeast

Table 3
Meat quality parameters of ruminants supplemented with yeast.

Item	Diet	Dose of yeast	Response	Source
Santa Ines lambs	F:C was 40:60	4.87%, 9.73%, and 14.60% inactive dry yeast of diets	The subcutaneous fat thickness decreased; meat crude protein and ash increased	Rufino et al. (2013)
Lambs	F:C was 60:40	300 µg yeast-Cr/kg of diet	Decreased serum total cholesterol and serum triglyceride levels	Zhou et al. (2013)
Awassi lambs and Shami goat kids	High concentrate diet	12.6 g yeast/kg of diet	No effects on growth performance of both lambs and goat kids; increased fat content in the carcass	Titi et al. (2008)
Kamieniec rams	Forage and concentrate	50 g yeast/kg of diet	Increased composition of C14:1, C18:2, C22:6, C18:2 (cis-9 trans-11) in meat; increased vitamin A content of meat; increased intramuscular fat	Milewski et al. (2012)
Rambouillet lambs	Forage and concentrate	0.25 and 0.35 mg Cr-yeast or 0.3 mg Se-yeast per day	Decreased fat in the carcass; increased average daily weight gain and final body weight	Domínguez-Vara et al. (2009)
Male Pelibuey lambs	High grain diet	0.12% yeast culture of diets	No effects on growth performance; no effects on marbling score and external fat score	Kawas et al. (2007)
Rambouillet ram lambs	Concentrates	0.3 mg Cr enriched yeast/kg dry matter	Increase backfat thickness; higher meat pH; no effects on the fatty acid profile of meat	Rodríguez-Gaxiola et al. (2020)
Lambs	Forage and concentrate	Yeast culture drenched at 1 mL/kg live weight	No effects on carcass characteristics	Bhatt et al. (2018)
Kamieniecka lambs	Hay silage and concentrate	50 g/kg concentrate per day	Higher protein content and lower cooking loss; improved water-holding capacity of meat; higher composition of cis-9, trans-11 CLA, C14:1, C18:2 and C22:6 fatty acids in the intramuscular fat	Milewski and Zaleska (2011)
Limousin-Nelore and Simmental-Nelore heifers	Corn silage and corn	Yeast at 16.35% of diets	An increased concentration of polyunsaturated fatty acid in the Longissimus muscle; a lower level of cholesterol in the Longissimus muscle; lower n6:n3 ratio in the muscle	Silva et al. (2002)
Crossbred young bulls (Zebu × European)	F:C was 44:56	15 g of yeast per animal per day	Increased linolenic acid concentration in the meat; increased n6:n3 ratio in meat	Maggioni et al. (2009)
Small-tailed Han lambs	Pelleted total mixed rations	0.8 and 2.3 g of yeast/kg dietary dry matter	An increased concentration of linoleic acid concentration in the muscle; a decreased conversion of linoleic acid to stearic acid	Liu et al. (2019)
Iranian Zandi lambs	Forage and concentrate	3 and 4.5 g of yeast per lamb per day	Increased meat fat; no effects on meat fatty acid composition	Raghebian et al. (2007)
Simmental × Luxi F1 crossbred bulls	Forage and concentrate	0.8 g dry yeast/bull per day and 50 g yeast culture/bull per day	No effects on intramuscular fat content or cholesterol content; decreased backfat thickness; an increased concentration of free fatty acids in the blood	Geng et al. (2016)

F:C = forage:concentrate ratio.

into the diet of ruminants can alter the activities of rumen microbiota through the maintenance of rumen pH in animals fed high starch diets (McAllister et al., 2011). A study by Milewski et al. (2012) revealed an increase in the proportion of *cis*-9, *trans*-11 CLA, and vitamin A content of mutton after yeast supplementation in sheep. Similarly, Milewski and Zaleska (2011) reported a higher composition of *cis*-9, *trans*-11-CLA, C14:1, C18:2, and C22:6 fatty acids in the intramuscular fat of lambs supplemented with yeast. To corroborate these findings, Liu et al. (2019) investigated the efficacy of yeast on modifying the fatty acid profile in lambs and the results obtained revealed that yeast supplementation caused an increase in the concentration of linoleic acid in the muscle by reducing its conversion to stearic acid. In another study conducted by Silva et al. (2002), the supplementation of yeast in heifers resulted in an increased concentration of polyunsaturated fatty acid and a decreased level of cholesterol in the longissimus muscle. The authors also observed a decrease in the ratio of n6:n3 fatty acids in the meat which is an indication of improved meat quality. Conversely, Maggioni et al. (2009) reported an increase in the ratio of n6:n3 fatty acids in the meat of bulls supplemented with yeast, which suggests a negative effect on meat quality. However, an increased concentration of linolenic acid was recorded by the authors. Raghebian et al. (2007) added yeast to the diets of lambs but the fatty acid profile of the meat remained unaffected. In a similar study, Rodríguez-Gaxiola et al. (2020) supplemented chromium enriched yeast to lambs but reported no effects on the fatty acid profile of the meat.

Other reported effects of yeast that could be linked to meat quality include the reduction of serum cholesterol and carcass fat deposition. In lambs, chromium-yeast supplementation has been effective in decreasing the level of blood cholesterol and carcass fat deposition (Zhou et al., 2013), and inactive dry yeast was found to reduce the subcutaneous fat thickness and increase the crude protein percentage of the meat (Rufino et al., 2013). Furthermore, the addition of yeast to the diets of bulls did not affect the level of intramuscular fat or cholesterol composition; however, there was a significant reduction in backfat thickness and an increase in the concentration of free fatty acids in the blood (Geng et al., 2016). Contrary to the previous studies, other authors observed a higher amount of carcass fat (Raghebian et al., 2007; Titi et al., 2008) and increased backfat thickness (Rodríguez-Gaxiola et al., 2020) following yeast supplementation in lambs. The exact reason for the conflicting response remained unclear but the proposed mechanism through which yeast influenced the fatty acid profile of meat is via the manipulation of rumen biohydrogenation (details in section 3.2.3).

3.2.2. Effects on milk quality and yield

Yeast has been used to improve milk production and quality in ruminants for more than 50 years. However, there is still a dearth of published literature on the efficacy of yeast in modifying the milk fatty acid profile and its conjugated isomers. The majority of the available literature highlights its effects on milk yield and milk fat yield as shown in Table 4.

Several studies investigated the effects of including yeast to the diets of lactating Holstein cows and the results obtained showed an improved milk yield, a higher concentration of milk fat (Alshaikh et al., 2002; Rezaeian, 2003; Ramsing et al., 2009; Ayad et al., 2013; Jiang et al., 2017a; Dias et al., 2018; Nasiri et al., 2019; Elaref et al., 2020) and increased milk protein (Alshaikh et al., 2002; Jiang et al., 2017a). The increase in milk fat yield could be attributed to the yeast's ability to stimulate acetate production in the rumen (Hučko et al., 2009; Al Ibrahim et al., 2010; Malek Khahi et al., 2016) which is a precursor of milk fat. The increased proliferation of cellulolytic bacteria following yeast supplementation (Wiedmeier

et al., 1987; Harrison et al., 1988; Williams 1989; Mao et al., 2013) could also explain the higher milk yield and milk fat yield. This suggests that yeast supplementation could be useful in preventing milk fat depression in lactating cows. In another study, Elaref et al. (2020) added yeast to the diets of ewes and reported an increased milk yield, improved milk fat, increased milk protein, and solids rather than fats. Contrary to the above studies, some authors reported no effect of yeast treatment on milk yield and milk fat in lactating Holstein cows (Ambriz-Vilchis et al., 2017; Al-Mallah, 2018; Ferreira, 2019). Similarly, the milk yield, milk fat, and milk protein of buffalo cows were not affected by yeast supplementation (Ramírez et al., 2007). Typical of animal experiments, contrasting findings are bound to arise probably due to variations in the stage of lactation of the cows and/or the dose, viability, or strains of yeast used.

There are very few studies that investigated the milk fatty acid profile of ruminants. In one of the studies on goats, Sulistyowati et al. (2013) reported an increased concentration of long-chain fatty acids and medium-chain fatty acids in the milk after yeast supplementation and the proportion of short-chain fatty acids and unsaturated fatty acids were observed to decrease. A reduced ratio of n6:n3 fatty acids was also recorded which indicates an improved milk quality. In another study, the inclusion of yeast into the diets of cows increased the composition of linolenic acid (18:3) and the concentration of some essential amino acids in milk (Yalçın et al., 2011). The improvement in the ratio of n6:n3 and linolenic acid composition in the first and second studies respectively could be attributed to the efficacy of yeast in modulating the biohydrogenation of unsaturated fatty acids in the rumen, which lead to its increased deposition in the milk. In contrast to the above studies, Bayat et al. (2015) supplemented live yeast at a dose of 0.5 g/d to dairy cows and reported no effects on the fatty acid profile of milk. The authors also observed no effects on milk yield, milk fat, protein, and lactose. Similarly, Longuski et al. (2009) did not observe any effect on milk fatty acid and its CLA composition after yeast supplementation in lactating cows.

3.2.3. Role of yeast in modulating rumen biohydrogenation to improve meat and milk quality

Ruminal biohydrogenation involves the transformation of linoleic acid into *cis*-9, *trans*-11 CLA (rumenic acid) followed by its hydrogenation to produce *trans*-11 (vaccenic acid) and subsequent conversion into stearic acid (Harfoot and Hazlewood 1997; Kim et al., 2000). Several species of bacteria are involved in the biohydrogenation of linoleic and linolenic acids in the rumen. These bacteria can be divided into groups A and B depending on the products synthesized from their fermentation activities. The bacteria in group A are responsible for converting linoleic and linolenic fatty acids into *trans*-11 (vaccenic acid), whereas group B specialises in the production of stearic acid (18:0). Examples of rumen bacteria belonging to group A include some strains of *Butyrivibrio fibrisolvens*, and those in group B consist of 2 strains of *Fusocillus* (Harfoot and Hazlewood, 1997). Yeast has the ability to influence the biohydrogenation pathway in the rumen by encouraging the growth of these bacteria involved in the process. It can also maintain the rumen pH at an appropriate condition to promote or inhibit some steps in the biohydrogenation of unsaturated fatty acids (Julien et al., 2010). Although a decrease in the biohydrogenation of dietary unsaturated fatty acids is beneficial, because higher concentrations of PUFA can be absorbed and deposited into animal products, a change in the biohydrogenation pathway to produce higher amounts of *trans*-11 and *cis*-9, *trans*-11 is more advantageous (Fig. 1). Julien et al. (2010) reported a decrease in the concentration of stearic acid together with an increased concentration of *trans*-11 C18:1 following yeast supplementation in Holstein

Table 4
Influence of yeast supplementation on milk composition and yield.

Item	Lactation stage	Diet	Dose of yeast	Response	Source
Holstein cows	96 ± 14 DIM	Dry ground corn grain	56 g/cow per day	No effects on rumen pH; no effect on milk protein, lactose, and solid non-fat; no effect on individual fatty acid isomers in milk fat; increased yield of milk fat	Longuski et al. (2009)
Holstein cows	284 ± 18 DIM	Concentrate and corn silage	5.7 × 10 ⁷ CFU/d (live yeast at a low level), 6.0 × 10 ⁸ CFU/d (live yeast at a high level) and 6.0 × 10 ⁸ CFU/d (killed yeast at a high level)	Only the low level of live yeast increased milk yield, milk fat and milk protein	Jiang et al. (2017a)
Holstein cows	Trial 1, 104 ± 12 DIM; trial 2, 97 ± 4.3 DIM; trial 3, 139 ± 4.5 DIM	Grass silage and concentrate	0.8 g/cow per day (1 × 10 ¹⁰ CFU/cow per day) and 4.0 g/cow per day (6 × 10 ¹⁰ CFU/cow per day)	No effects on milk yield, butterfat, milk protein, or lactose	Ambriz-Vilchis et al. (2017)
Sohagi ewes	Last 2 months of pregnancy	Concentrate and forage	5 or 10 g of yeast per ewe per day	Increased milk yield, milk fat, protein and solids non-fats	Elaref et al. (2020)
Holstein cows	116 ± 9 DIM	Concentrates and corn silage	15 g selenium-enriched yeast per day	Increased selenium concentration; no effects on milk production	Faccenda et al. (2020)
Ayrshire dairy cows	53 ± 7 DIM	Concentrate	0.5 g live yeast per day	No effects on milk fat, protein, and lactose; no effects on proportions of the major fatty acids in milk	Bayat et al. (2015)
Holstein cows	118 to 134 DIM	Concentrate pellets	15 and 50 g yeast culture/cow per day	Increased milk yield; increased milk fat; increased concentrations of protein, lactose, total solids and solids non-fat	Alshaikh et al. (2002)
Holstein cows	21 d prepartum to 21 d postpartum	Concentrates	57 and 227 g yeast per day	Increased milk yield; increased milk fat yield; no effects on milk protein yield, milk protein percentage, milk fat percentage	Ramsing et al. (2009)
Holstein cows	14 d prepartum to 45 d postpartum	Forage and concentrates	20 g yeast per day	Increased milk production; improved milk fat	Ayad et al. (2013)
Water buffalo cows	84 ± 13 DIM	<i>Brachiaria humidicola</i> pasture only	100 g yeast grown/cow per day on a media of yellow corn	No effects on milk yield; no effects on milk fat and milk protein	Ramírez et al. (2007)
Holstein Friesian cows	Mid-lactation	Concentrate	2.5 g yeast/cow per day	Increased milk yield; no effects on milk composition	Maamouri et al. (2014)
Holstein cows	20 ± 2 wk of lactation	Forage and concentrate	10 g yeast/cow per day	Increased milk yield; increased yield of milk fat	Rezaeian (2003)
Holstein cows	130 ± 16 DIM	Forage and concentrate	5.4 × 10 ¹¹ CFU yeast per day	No effects on milk fat yield, milk yield, milk protein concentration; no effects on milk protein yield, milk lactose concentration, and milk lactose yield	Ferreira (2019)
Holstein cows	21 d prepartum to 60 d postpartum	Forage and concentrate	4 g yeast/cow per day	Increased milk total solid; increased concentrations of milk fat; increased milk yield	Nasiri et al. (2019)
Holstein cows	95 ± 12 DIM	Forage and concentrate	35 g yeast/cow per day	No effects on milk yield, fat corrected milk, milk fat; no effects on milk protein and lactose	Al- Mallah (2018)
Holstein cows	176 ± 18 DIM	Forage and concentrate	15 g inactivated dry yeast/cow per day	Increased milk yield; increased milk fat; increased lactose concentration	Dias et al. (2018)
Holstein cows	90 ± 35 DIM		50 g yeast/cow per day	An increased concentration of 18:3 (n-3) in milk fat; increased milk yield; increased levels of methionine, tryptophan, tyrosine, phenylalanine, and taurine in the milk	Yalçın et al. (2011)
Ettawa crossed breed goats	Late lactation (4.6 ± 0.55 months postpartum)	Forage and concentrate	0.5% or 5 g yeast/goat per day	An increased concentration of long-chain fatty acids and medium-chain fatty acids in the milk; decreased concentration of short-chain fatty acids and unsaturated fatty acids in the milk; decreased n6:n3 ratio in the milk	Sulistyowati et al. (2013)

DIM = days in milk.

cows. The authors ascribed this to the ability of yeast to stimulate the growth of *B. fibrisolvens* which are the main bacteria responsible for the biohydrogenation process in the rumen (Kepler et al.,

1966; Harfoot and Hazlewood, 1988; Martin and Jenkins, 2002). The efficacy of yeast in increasing the ruminal population of *B. fibrisolvens* as speculated earlier was confirmed in a study on

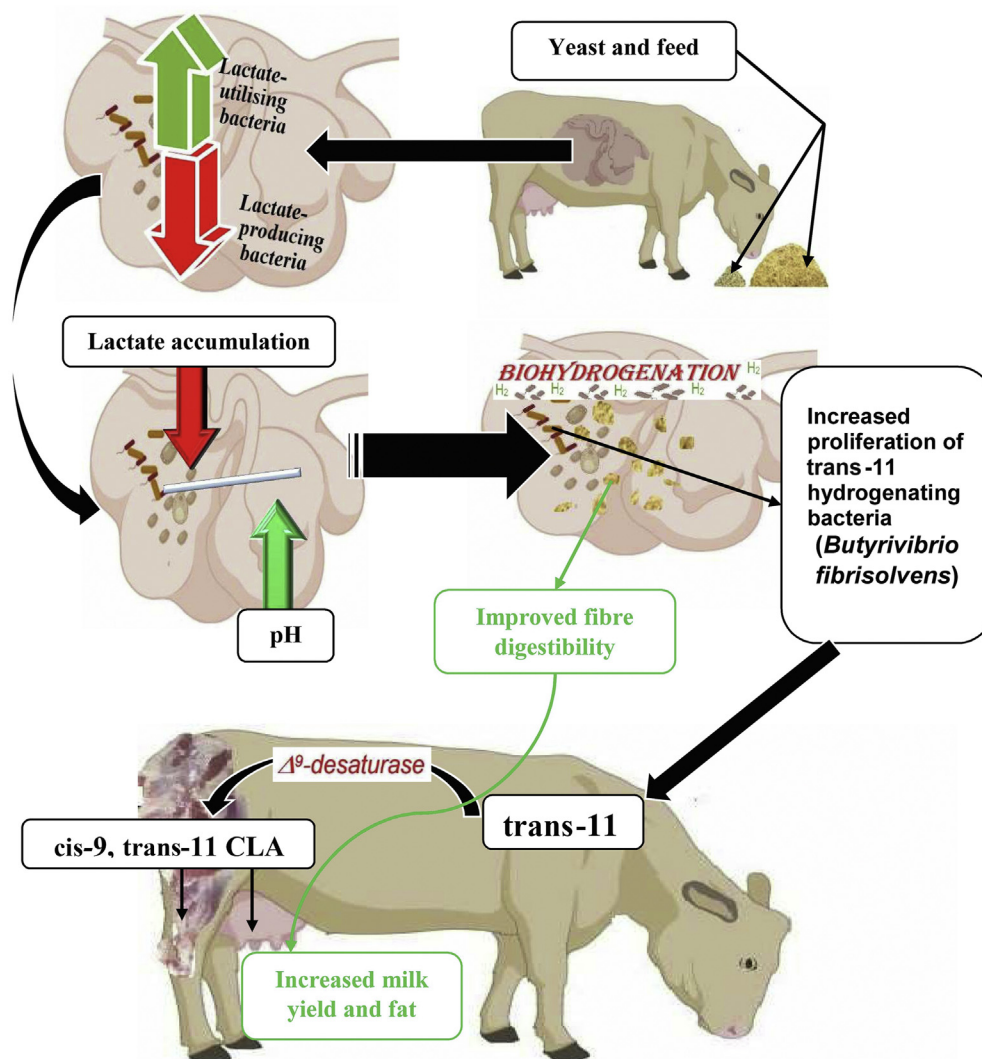


Fig. 1. Major effects of yeast supplementation on rumen fermentation and quality of products in ruminants. CLA = conjugated linoleic acid.

Holstein calves conducted by Xiao et al. (2016). An increase in the ruminal production of *trans*-11 C18:1 implies that a higher amount of *cis*-9, *trans*-11 CLA will be deposited into milk and meat due to the conversion of *trans*-11 to *cis*-9, *trans*-11 CLA in the tissue by the enzyme Δ^9 -desaturase (Bauman et al., 2000, 2003).

Rumen pH is another important factor affecting ruminal biohydrogenation (Sun et al., 2017). In a study conducted by Troegeler et al. (2006), the inclusion of yeast increased the rumen pH above 6.0 which lead to a reduction in the concentration of stearic acid in the rumen fluid. The authors also reported an increased proportion of linoleic acid and oleic acid which they attributed to a reduction in the biohydrogenation of unsaturated fatty acids in the rumen. To further support this, Lee (2013) studied the effect of pH on rumen biohydrogenation and reported a decreased biohydrogenation of linoleic, linolenic, and oleic acid at a culture pH of 5.5, and a higher biohydrogenation of the PUFA was seen at a pH of 6.5. This could be due to the inhibitory effects of low pH on the growth and activities of some biohydrogenating bacteria (*Anaerovibrio lipolytica* and *B. fibrisolvens*) at a rumen pH below 5.6 (Fuentes et al., 2009). In a related study, Choi et al. (2005) investigated the effects of pH on biohydrogenation and the results obtained revealed that the concentration of *cis*-9, *trans*-11 CLA was found to increase when the culture pH rises above 5.6. However, the authors recorded a higher

quantity of *trans*-10, *cis*-12 CLA at pH 5.6 to 6.3 before *cis*-9, *trans*-11 CLA predominated in the culture. Fuentes et al. (2009) confirmed the synthesis of *trans*-10 C18:1 and *trans*-10 *cis*-12 CLA at a rumen pH of 5.6. Similarly, Sun et al. (2017) reported an increase in the production of *trans*-10, *cis*-12 CLA under a low pH condition. This is possible because different enzymes and pathways are involved in the formation of both *trans*-10, *cis*-12 CLA and *cis*-9, *trans*-11 CLA (Wallace et al., 2007). This suggests that the bacteria responsible for the synthesis of the biohydrogenation intermediate *trans*-10, *cis*-12 CLA thrives well in low pH conditions which could explain why low rumen pH causes milk fat depression. Therefore, a pH range between 5.6 and 6.3 is suggested for increased synthesis of *trans*-11 (vaccenic acid) and *cis*-9, *trans*-11 in the rumen. This means that the composition of CLA in the meat and milk of ruminant animals can be increased through dietary modification (Bauman et al., 2000), which in turn alters the rumen pH to effect a change in the population of microbes involved in ruminal biohydrogenation (Harfoot and Hazlewood, 1997; Bauman et al., 2000).

The ability of yeast to stimulate the growth of ciliate protozoa (Tripathi and Karim, 2011) could also contribute to improving meat and milk quality in ruminants. Ciliate protozoa are known to integrate *cis*-9, *trans*-11 CLA, and *trans*-11, 18:1 into their cells. The fatty acids within the cells of these protozoa eventually become

available for absorption in the small intestine after the microbes get degraded during acidic digestion in the abomasum (Francisco et al., 2019). Ciliate protozoa are also important in the maintenance of rumen pH by competing with amylolytic bacteria in the assimilation of starch particles within the rumen when high grain diets are fed (Mendoza et al., 1993). However, pH is very critical to the survival of ciliate protozoa and they are usually killed when subjected to rumen pH lower than 5.5 for more than 15 h in a day (Franzolin and Dehority, 1996). This further corroborates the earlier findings which suggest that a rumen pH range between 5.6 and 6.3 is ideal for an increased flow of CLA and other PUFAs out of the rumen to be absorbed in the small intestine.

4. Areas of future research

There is a wide research gap in the area of meat and milk quality improvement and yeast has the potential to alter the composition of rumen fatty acid profile and possibly the fatty acid profile of animal products like milk and meat. Very few studies investigate the effects of yeast on the fatty acid profile and its conjugated isomers in animal products. Different strains of yeast need to be tested at different doses and viability levels on the fatty acid profile of animal products as well as its vaccenic acid and rumenic acid composition. This will enable researchers to comprehend the mechanism of the action of yeast and ascertain the ideal strain and dose to obtain a positive effect. Transcriptomics should be employed to identify the mRNA transcript expression levels of genes like stearoyl-CoA desaturase, fatty acid synthase, and elongase of very long chain fatty acids 6 due to their association with intramuscular fat and fatty acid composition in the muscle.

5. Conclusion

Yeast supplementation has been reported to increase feed intake and growth rate in young ruminants as well as improve milk production and milk fat in dairy cows. This could be due to the ability of yeast to stimulate fibre digestion and stabilise the rumen pH. The supplementation of yeast at the right dose and viability level in a concentrate diet could counteract the acidotic effects of high concentrate diets in the rumen by competing with lactate-producing (*S. bovis* and *Lactobacillus*) bacteria for available sugar and providing nutrients to encourage the growth of lactate-utilising bacteria (*M. elsdenii*). *M. elsdenii* is known to convert lactate into butyrate and propionate leading to a decrease in the accumulation of lactate. This causes an increase in rumen pH to support the proliferation of some beneficial bacteria like *B. fibrisolvans*. This group of bacteria (*B. fibrisolvans*) is responsible for the biohydrogenation of linoleic acid to produce *trans*-11 (a precursor of *cis*-9, *trans*-11) and *cis*-9, *trans*-11. Moreover, ciliate protozoa also decrease the production of stearic acid in the rumen by incorporating *trans*-11, *cis*-9, and *trans*-11 into their cells to protect them from being reduced to stearic acid. Interestingly, both thrive well at rumen pH above 5.6. The addition of yeast into the diet of ruminants has been reported to alter the rumen biohydrogenation pathway to synthesise more of the beneficial biohydrogenation intermediates (*trans*-11 and *cis*-9, *trans*-11). This implies that more dietary sources of linoleic acid, linolenic acid, and oleic acid along with beneficial biohydrogenation intermediates (*cis*-9, *trans*-11-CLA, and *trans*-11) would escape complete biohydrogenation in the rumen to be absorbed into milk and meat. However, several factors such as the dosage of yeast, the viability of yeast, age of the animal, specie, and breed of animal, physiological status of animal, duration of yeast treatment, diet composition, and environment may affect the response of an animal to yeast supplementation.

Conflict of interest

We declare that we have no financial or personal relationships with other people or organizations that might inappropriately influence our work, and there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the content of this paper.

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