Review Article

The release and catabolism of ferulic acid in plant cell wall by rumen microbes: A review

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1. Introduction

The global human population is projected to reach 9 to 10 billion by 2050, raising the hugely increased demand for foodstuffs and animal products (McNeill et al., 2013). Ruminant animals are important livestock to provide humans with quantity and quality of meat and milk, as well as leather and wool (Li, 2021). Plant cell walls are the most abundant renewable chemical energy on earth which amounts to $10^{11}$ tons synthesized annually (Topakas and Paul, 2007). About 70% of the metabolizable energy of feedstuffs is provided to ruminants by rumen microbial fermentation (Bergman, 1990). Due to the shortage of food, timber and fossil carbon, comprehensive utilization of plant cell walls has raised interest. Because of the presence of active and diverse microbial populations, the rumen functions as a large natural fermentation chamber to degrade nutrients from plant cell wall (Buana et al., 2008). Therefore, making good use of fiber-rich forage in the rumen can lead to considerable economic benefits. However, the complex structure of plant cell walls, mainly consisted of polysaccharides,
phenolic acids and protein, impedes the further utilization of these biomass (Hatfield et al., 2017).

Wang et al. (2012), in our previous laboratory study, collected 13 fibrous feeds including grass hay, alfalfa hay, grain bran, crop straw and/or stalks, and noted that both ferulic acid (FA) and p-coumaric acid (pCA) are the most two abundant phenolic acids, and the FA content much richer than pCA in grain brans comparison with hays crop straw and/or stalks. As shown in Fig. 1, FA is chemically named as 3-(4-hydroxy-3-methoxyphenyl) propenoic acid. Through the shikimic acid pathway, FA participates in the formation of plant cell walls (Seigler, 1998). Ferulate polysaccharides esters are the initiation and nucleation sites for lignification and are then incorporated into the lignin through peroxidase-H2O2-mediated formation of ether linkages between the FA molecules and phenolic monomers in the growing lignin polymer (Delmer and Stone, 1988; Jung and Allen, 1995; Ralph et al., 1995). As shown in Fig. 2, FA in plant cell walls form ether linkages with lignin through the hydroxyl groups in the aromatic ring and is ester-linked via its carboxylic acid group to the C(O)2 position of the arabinofuranosyl side group attached at the C(O)2 to the xylan chains (Barron et al., 2007; Wong et al., 2013). These ester- and ether-linked FA could be measured through mild and harsh alkaline hydrolysis, respectively (Wong, 2006). Lignin and arabinoxylans were connected by ferulate molecules through these linkages (Ralph et al., 1994). Ferulic acid dehydrodimers are ester-linked to plant cell wall polysaccharides and other cell wall components including proteins and lignin (McKinnon and Christensen, 2005; Pedersen et al., 2015). More recently, dehydrotriferulic acids and dehydrotetraferulic acids also have been isolated from plant cell walls (Bunzel et al., 2006). These cross-linkages limit the growth of cell walls, increase the mechanical strength and reduce the utilization of the plant (Iiyama et al., 2001; McKinnon and Christensen, 2005).

In this article, the effect of FA on fiber digestion, the release of bound FA and the possible metabolism pathways of FA in rumen were comprehensively reviewed and discussed.

2. Effect of ferulic acid on fiber digestibility in the rumen

2.1. The relationship between ferulic acid in plant cell wall and rumen digestibility

Forage cell walls are major source of nutritional energy in the rumen. However, less than 50% of these fractions are utilized by the ruminant hosts (Badhan et al., 2014). In an earlier study, ryegrass hay presented a highly positive correlation ($r = 0.98$) between cell wall digestibility to the ratio of FA to pCA (Hartley, 1972). Then, Casler (2001) highlighted that both lignin and phenolic acids were the main factors limiting the use of energy in rumen. In recent decades, in vitro rumen fiber digestion and gas production and in situ rumen degradation trials have been completed. Ester-linked FA (FAest) and ether-linked FA (FAeth) attracted attention to address their relationships with extent and rate of fermentation and/or digestion.

2.1.1. In vitro

As a rapid method for measuring gas production, the in vitro technique has been an important tool in evaluating ruminant feeds (Menke et al., 1979). Bermuda grass hays with higher FAest content presented higher digestibility of organic matter, neutral detergent fiber (NDF) and acid detergent fiber (ADF) (Jung and Allen, 1995; Mandebvu et al., 1999). A positive correlation between the FAest content on a NDF basis and 24 and 96-h in vitro dry matter digestibility (IVDMD) were observed in brown midrib corn silage ($r = 0.78$ for 24 h, $r = 0.60$ for 96 h, $P < 0.05$) and mature grasses ($r = 0.94$ for 24 h, $r = 0.60$ for 96 h, $P < 0.05$) (Raffrenato et al., 2017). The 48-h IVMDM ($r = 0.79$) and in vitro neutral detergent fiber digestibility (IVNDFD) ($r = 0.82$, $P < 0.05$) of meadow hay were positively correlated to the concentration of FAest (Rodrigues et al., 2007). Different breeds of perennial grasses exhibited different correlations between FAest and IVNDFD. Smooth bromegrass and cocksfoot had a positive correlation between FAest and 96-h IVNDFD while in reed canarygrass the relativity between FAest and 24-h IVNDFD was negative but not notable (Casler and Jung, 2006). In vitro digestion constants such as sharpness of the switching characteristic for the profile of the first phase ($r = 0.94$, $P < 0.01$) and asymptotic gas production of the second phase ($r = 0.89$, $P < 0.05$) were positively correlated with FAest (Rodrigues et al., 2007). However, a few negative correlations between FAest and IVMDM were reported. The FAest content on an ADF basis of mature grasses was negatively correlated to the 96-h IVMDM ($r = -0.75$, $P < 0.05$) (Raffrenato et al., 2017). Jung and Vogel (1992) found an occasional negative relationship between FAest and 48-h IVNDFD.

The concentration of FAeth of perennial grasses negatively related to the 24 and 96-h IVNDFD (Casler and Jung, 2006), suggesting that the content of ferulated cross-linkages were more pronounced for NDF digestion after a 96-h microbial incubation in comparison with the 24 h incubation (Casler and Jung, 2006). Through an in vitro study, a significant negative effect occurred between 24-h cell wall polysaccharide ($r = -0.71$, $P < 0.01$), arabinose ($r = -0.42$, $P < 0.01$), glucose ($r = -0.33$, $P < 0.05$) and uronic acid ($r = -0.32$, $P < 0.05$) degradation and FAeth in maize stem internodes and maize internodes (Jung et al., 1998; Jung and Buxton, 1994). A strong negative influence of FAeth on IVNDFD was found in smooth bromegrass, and this influence was independent of the lignin in fiber fraction (Casler and Jung, 1999). According to Raffrenato’s (2017) study the Klason lignin had more negative effect on the 24-h extent digestion of bm corn silage, whereas FAest and acid detergent lignin showed more negatively affected on controversial corn silages. However, Rodrigues et al. (2007) found a positive effect of FAeth fraction ($r = 0.93$, $P < 0.01$) on 48-h IVNDFD. 24 and 96-h IVMDM of BMR corn silage and immature grasses were positively correlated to FAeth on both NDF basis ($P < 0.05$) (Raffrenato et al., 2017).

2.1.2. In situ

The in situ technique was firstly used by Quin et al. (1941) to evaluate rumen degradability of feeds. Through an in situ study, Du and Yu (2011) revealed that FA in barley hull was highly and positively correlated to rumen indigestible dry matter (DM), NDF and ADF at either 12 or 24 h. Effective degradability of NDF...
(r = −0.98, P < 0.01), cellulose (r = −0.98, P < 0.05) and hemicellulose (r = −0.98, P < 0.05) of crop bran and husks inversely related to the content of FAeth (Cao et al., 2015). Rodrigues et al. (2007) found a high positive relationship between the potential degradation and FAeth (P < 0.05).

In most of the aforementioned studies, the concentration of FAest was positively correlated with the rumen fiber digestion. As mentioned, the deposition of FA during the primary cell wall development accompanies incorporation of other cell wall components (Rodrigues et al., 2007) and the ester-linked ferulic acids mainly exist in the primary cell wall which are more approachable for rumen microbes (Cao et al., 2016a). Thus, the content of FAest only affects the rate instead of the extent of cell wall digestion (Jung and Allen, 1995).

The FAeth was thought to be an indicator of cross-linkages between lignin and arabinoxylans and generally presented a negative effect on cell wall digestibility (Cao et al., 2015; Jung and Casler, 2006; Jung et al., 2011). Due to the lignin polymer, the ether linkage of FA was hard to access by microbes. These linkages could not be cleaved under anaerobic environments (Jung and Allen, 1995), and the negative effect of FAeth on cell-wall digestibility was considered to cause reduced cell wall digestion, but not a reduced digestion rate, in the rumen (Jung and Allen, 1995). Indigestible components of dietary fiber were associated with other food constituents, such as phenolic acid compounds, and this could be ascribed to the ability of polysaccharides to bind and trap phenolic compounds at several sites (Sauracalixto, 2011).

As noted in the above, with the correlation between feed digestion and the content of phenolic acids, the release of hydroxycinnamic acids from the animal fodder indirectly implicated an increase of feed digestibility. Cao et al. (2015) found that the in situ ruminal disappearance of FAest was positively correlated with disappearances of cellulose, hemicellulose and NDF.

The authors in this review summarize that the relationships between bound FA and forage degradation were affected by the plant species, breed, fractions and stage of maturity. Even though the effect on the rate and extent of fiber digestion are not the same, the properties of linkages play an inevitable role in forage digestion (Raffrenato et al., 2017). As stated in the above studies, it is still a somewhat controversial issue whether these ferulated linkages can be used as a predicator of forage digestibility in ruminants.

2.2. Reasons for the negative effect of ferulic acid on plant cell wall digestion in the rumen

2.2.1. Barrier of plant cell walls

The cross-linkages form an obstruction through substitution and steric hindrance for the accessing of hydrolytic enzymes to their polysaccharide substrate (Grabber et al., 1995; Várnai et al., 2014). Though a biomimetic model, Grabber et al. (2009) pointed
that the reduction of ferulate linkages increased the extent and the rate of cell wall enzymatic hydrolysis and noted that compared with lignin content, ferulate cross-linking had a more profound effect in determining the rate and extent of digestion of hemicellulose. Etherification protects FA from being decarboxylated during oxidative coupling which can impede the access of microbe and enzymes. Wong et al. (2019) noted that diferulates were responsible for the control of plant cell growth, and reduced cell wall digestibility as a biological protection against pathogenic attack. The hydrophobicity ability of phenolic compounds also impedes the access of enzyme to cell wall polysaccharides (Besle et al., 1994). Thus, feruloyl polysaccharides are critical entities in directing cell wall cross-linking and in limiting biodegradability by microorganisms (Ishii, 1997; Jung, 2003).

2.2.2. Toxic effects
Phenolic monomers inhibited digestibility of cellulose and xylan by influencing the attachment of the fibrolytic microorganisms to fiber particles (Hartley and Akin, 1989; Varel and Jung, 1986). The FA can inhibit the growth of microbes (such as bacteria, protozoa and fungi) (Zuhainis Saad et al., 2008; Zuhainis et al., 2007). At concentrations over 5 mmol/L, FA can suppress the growth of the cellulytic strain Ruminococcus albus, Ruminococcus flavefaciens, and Bacteroides succinogenes (Chesson et al., 1982). The growth rate of R. albus and IVDMĐ at 24 and 48 h was inhibited by FA at 10 mmol/L (Borneman et al., 1986). The ester-linked feruloyl showed the ability to inhibit the growth of ruminal bacteria R. flavefaciens FD1, Sekomonas ruminantium HD4, and Butyrivibrio fibrisolvens 49 (Akin et al., 1993). Dehydrodimers of FA inhibit the growth of microbes. Boutigny et al. (2010) found that the 8-5′-benzofuran dimer FA showed the same effect as inhibiting trichothecene biosynthesis as the monomer of FA. FA inhibits the digestibility of cellulose, not only producing the negative effect on rumen microbes, but also depressing enzyme activity. Free and bound phenolic-rich extracts from shaddock peels show a negative effect on α-amylase, β-glucosidase and angiotensin I-converting enzyme activity in a dose-dependent manner (Schmidt et al., 2014). The intestinal sucrases and maltases were inhibited by ferulic and isoferulic acid in a mixed type manner (Adisakwattana et al., 2009). The activities of cellulolytic enzymes (including carboxymethylcellulase, filterpaperase, xylanase and β-glucosidase) and the production of total volatile fatty acid (VFA) of Neocallimastix frontalis B9 were depressed by FA addition (Zuhainis Saad et al., 2008). However, some microbes show ability to detoxicate FA or even use FA as a single carbon source. Zymomonas mobilis ZM4 can detoxify phenolic aldehydes (Gu et al., 2015). Pirnyces sp. FNG5 (isolated from feces of wild nil gai) also showed tolerance to phenolic monomers and even had the ability to degrade them (Paul et al., 2003).

With these characteristics, the author in this review speculated that FA could inhibit rumen microbes and their enzymes and lead to low rumen digestibility. But the lowest standard for inhibiting the microbes in rumen still needs further research. It is necessary to take into consideration that the FA amounts consumed under a normal diet in culture fluid was 0.90 to 1.85 μg/75 mL. Even though the intake of FA depends on the type and amount of diet, the concentration of free and linked FA in rumen cannot reach the inhibitory level in former studies. Additionally, it is believed that the absorption of FA is quick within the rumen. Also, the released FA can be catabolized by microbes during rumen fermentation. There is still no identification of the toxic dose of FA for rumen microbes. Thus, whether the FA in diets could have toxic effect on rumen microbes and enzymes requires further research.

3. Release of bound ferulic acid in the rumen
To promote the existence of microbes, the rumen is a complex and efficient ecosystem that degrades plant biomass (Kothari et al., 2018). Through mechanical, chemical and enzymatic forces, bound FA are released by microbial action in ruminants (Chesson et al., 1999; Hegde et al., 2006). Three main microbial populations (protozoon, bacteria, fungi) help to degrade the structure of plant cell wall and release FA (Betts and Dart, 1988; Mathew and Abraham, 2006). Ester-linked FA can be extensively disrupted by phenolic acid esterases during the ruminal fermentation, while the ether bonds between FA and lignin cannot be broken in the rumen (Rodrigues et al., 2007). The breakdown of these linkages renders the cell wall more susceptible to enzymatic attack and increases cell wall degradability (Morris et al., 2017).

3.1. Mechanical competence of rumen microbes to release bound ferulic acids

3.1.1. Rumen protozoa
Rumen protozoa (10⁵ to 10⁶ cells/mL) constitute about 50% of the viable biomass in rumen and have long been reported to contribute to plant cell wall degradation (Sirohi et al., 2013). When protozoa are eliminated from rumen liquid, the breakdown of cellulose and hemicellulose is decreased (Williams and Coleman, 1997). Some protozoa could associate with plant cell walls and then penetrate deeply into the broken plant tissues and adhere via a special attachment organelle. Others show primary degradation abilities of plant cell tissues by ingesting small particles (Orpin and Letcher, 1978). Except for ingesting and attachment, enzymes in protozoa may also play an important role in the degradation of plant cell walls. Enzymes such as pectin esterase, amylase, cellulase and polygalacturonase have been found in rume protozoa (Béra-Mailllet et al., 2005; Devillard et al., 2003; Sirohi et al., 2013; Williams, 1979). However, the activity of feruloyl esterase (FAE) has not been detected in rumen protozoa. The degradation of plant tissues by protozoa help fungi and bacteria to approach cell wall more easily which lead to the further release of FA.

3.1.2. Fungi
Fungal (10³ to 10⁶ cells/mL) are the most efficient contributors to fiber degradation, even though they only make up 20% of the rumen biomass (Rezaein et al., 2004). Fungal parasites can penetrate and enter host cell walls. Thereafter, they differentiate specialized intracellular feeding structures, called haustoria, and invaginate the plants’ plasma membrane. Meanwhile, a series of highly active hydrolyase enzymes (such as cellulase, hemicellulose, esterases and other side chain enzyme) are secreted. The multi-component cellulase system produced by anaerobic fungi is the most important mechanism to degrade lignin and release FA. Rumen fungi shows chemotactic response to phenolic acids (such as ferulic, syringic and coumaric acid) then attacks lignin to release FA from plant cell walls (Wubah and Kim, 1996). Zoospores of fungi also prefer to colonize lignin-rich regions, and upon germination, solubilize these regions (Qi et al., 2011).
3.1.3. Bacteria

Due to their large biomass (10^{10} to 10^{11} cells/ml), bacteria play an important role in the release of FA. Rumen bacteria degrade fiber through the adhesion of their fibrolytic enzymes to their substrates (Cai et al., 2010). Cellulosic bacteria are divided into bacteria which adhere to plant fiber and those that do not. When bacteria degrade the plant cell wall, four steps are essential. First, the bacteria access the plant fragments. The second step is the initial non-specific adhesion at appropriate parts of plant debris. The third step is the specific adhesion on binding of the substrate to the surface of the bacteria. Then, adherent bacteria proliferate at specific sites in plant tissues. These mechanical steps of rumen microbes break plants into small fragments, and this step facilitates further enzyme attachment sites.

3.2. Enzymatic competence of rumen microbes to release ferulic acid

After attaching to plant fragments, microbes secrete a series of enzymes. Due to the ability to cleave ester-linkages between FA and the attached sugar, cinnamoyl esterases were regarded to be a "helper" enzyme which facilitate the access of cellulases to the main chain of plant cell wall (Benoit et al., 2008).

Still, rumen microbes lack the enzyme to degradation the ether bond in plant cell wall (Rodrigues et al., 2007).

3.2.1. F eruloyl esterases

Feruloyl esterases (EC 3.1.1.73, FAE) were first discovered from the culture filtrates of Streptomyces olivochromagens (Mackenzie et al., 1987). After then, more than 80 kinds of FAE have been discovered and characterized in fungi and bacteria (Oliveira et al., 2020). The FAE are key enzymes to hydrolyze the ester bond arabinofuranose fibers and release FAA, esterified diferulates and feruloyl oligosaccharides from agricultural biomass (Andreasen et al., 2001b; Cheng et al., 2012; Uraji et al., 2018). Expect secreted by microbes, FAE were also found in mammalian intestinal epithelial cells and of plant origin (Andreasen et al., 2001a; Kern et al., 2003; Oliveira et al., 2020).

Generally, based on the substrate utilization and amino acid sequences, FAE are classified into four types (Type A, B, C and D) (Crepin et al., 2004). Recently, new types of FAE have been identified (Uraji et al., 2018). In this system, FAE were divided into 12 subfamilies. All of these FAE possess a similar three-dimensional structure with a \( \beta \)-hydroxylase having a serine, histidine, and aspartic acid catalytic triad (Goldstone et al., 2010; Li et al., 2011).

Kühnel et al. (2012) summarized the activity of different types of FAE. Type A FAE prefer methyl ferulate, methyl \( p \)-coumarate and methyl sinapinate and can release 5,5'-diferulic acid. Until now, the production of Type A FAE was only observed in fungi (Mogodiniyi Kasmaei and Sundh, 2019). Type B FAE toward to hydroxycinnamonic acid ester with free hydroxyl substituents advance. Type C FAE can hydrolyze all hydroxycinnamic acid methyl esters. Type D esterases are unspecific esterases to hydrolyze all hydroxycinnamic acid methyl esters (Wong, 2006). When pretreated or co-incubated with endo-xylanases, Type A and type D are able to hydrolyze synthetic diferulate (Araf-FA-Araf-FA) while Type B and Type C FAE could not release free diferulates (Wong et al., 2019). A full range of FAE contribute to the high-efficiency fiber digestion by rumen microbes (Wong et al., 2019). Most A, B and C were found from aerobic fungi and worked in concert to hydrolyze s the ester linkages between polysaccharide main chain with phenolic acids (Li et al., 2011; Qi et al., 2011).

Because no less than 1% of microbes in rumen can be cultured, only a few of FAE produced by rumen microbes have been identified (Cheng et al., 2012). Presently, Aspergillus, Fusarium, Neocallimastix, Fusarium Orpinomycyes, Piromyces, Penicillum and Talaromycyes are reported to secrete FAE in the rumen or gastrointestinal tract (Benoit et al., 2008; Cao et al., 2013; Li, 2021; Paul et al., 2003). Compared with fungi, only a few bacteria are able to secrete FAE. Butyrivibrio, Prevotella, Clostridium, Cellulosilyticum, Butyrivibrio, Streptomycyes, Lactobacillus and Dickeya have been reported to produce FAE (Li et al., 2011; Stewart et al., 1988; Wang et al., 2005). More recently, Mogodiniyi Kasmaei and Sundh (2019) used whole-genome shotgun metagenomics and genome binning to explore novel prokaryotic FAE in cow, horse, sediment, and soil datasets and nominated Candidatus Rhodochlamydia genus as a novel FAE to produce taxonomic unit. In this study, four genomes: B. fibrisolvens, Butyrivibrio proteoclasticus, R. albus, and R. flavfaciens belonging to Clostridiales, were reported to produce FAE. Limited research has been conducted on the structure of FAE in ruminants. A promiscuous feruloyl esterase with a broad activity to release FA, coumaric acid, coumarin-3-carboxylic acid, and cinnamic acid was isolated from the rumen bacterium B. proteoclasticus (Goldstone et al., 2010). The structure of this FAE is identified in two different space groups, in both the apo-form, and the ligand bound form with FA located in the active site. The presence of three different conformations adopted by different molecules in the crystals shows the flexibility of the lid domain.

FAE are accessory enzymes which assist cellulose and hemicelulose to be more available to xylanolytic and pectinolytic enzymes (Dilokpimol et al., 2016; Gopalan et al., 2015). These enzymes break down the polysaccharides into low molecular weight fragments, which are more suitable as esterase substrate (Mathew and Abraham, 2004). Thus, the ability was enhanced with the addition of these cell wall degrading enzymes such as xylanase, cellulases, pectinases, hemicellulases and arabinofuranosidas (Mathew and Abraham, 2004; Shin et al., 2006). After pretreating wheat bran with xylanase, the diFA released by human faecal bacteria increased from 40% to 80% (Vardakou et al., 2007). Borneman et al. (1990) found that the activity of FAE may be facilitated by \( \beta \)-xylolysidase.

3.2.2. \( p \)-Coumaryl esterase

Compared with FAE, only a few studies have focus on \( p \)-coumaryl esterase (3.1.1.60, pCE). Trans-\( p \)-coumaryl esterase have been found in anaerobic rumen fungi (Borneman et al., 1990). Borneman et al. (1991) noted that \( p \)-coumaryl esterase secreted by Neocallimastix can release \( p \)-coumaryl groups from \( O-\{5-O-\{(\text{E})-p\text{-coumaryl}\}_3\}-\{3-O\}-D-xylopyranosyl- (1\rightarrow4)-D-xylopyranose. A feruloyl/\( p \)-coumaryl esterase purified from Penicillium pinophilum released 100% of the alkali-extractable FA from water-soluble wheat straw xylan (Castanares and Wood, 1992). This enzyme has a remarkably wide substrate specificity: hydrolyzing phenolic acids from model substrate and releasing acetate from \( p \)-nitrophenyl acetate and from an acetylated xylan. A recombinant purified enzyme hydrolyzing methyl MCPa and chlorogenic acid resulted in classification as a \( p \)-CE, with a distinct chlorogenic acid esterase side activity (Nieter et al., 2017). Both of FAE and \( p \)-CE can release FA and pCA from xylan polysaccharides, there exist differences in their specificity for hydrolysis of methyl ferulate (MFA) and MPCA, respectively (Nieter et al., 2017). Still, Aspergillus awamori, P. pinophilum, Neocallimastix and Rhizoctonia solani have been reported to secrete pCE (Castanares and Wood, 1992; Borneman et al. 1991; Nieter et al., 2017).

Lots of factors affect the activity of cinnamoyl esterases in ruminants. Yu et al. (2002) noted that FAE (produced by Aspergillus) could not release FA from oat hull ground through 1 mm screen but when using 250 nm screen, a small amount of FA was released. Thus, the substrate size affects the activity of FAE (Borneman et al., 1991; Yu et al., 2002). McKinnon and Christensen (2005) explained...
that the large substrate may restrict the access of FAE to feruloyl groups and lead to an undetectable release of FA. Wang et al. (2005) isolated a FAE from human intestinal bacterium Lactobacillus acidophilus and suggested that with the addition of FA, the concentration of FAE was increased, then reached a peak and declined. Thus, the concentration of FA affects the activity of FAE. Even under the same conditions, the FA released from barley spent grain, wheat bran and maize bran by the same FAE were different. The complex physical and steric factors of plant cell wall could affect the FAE to release FA (Bartolome et al., 1997). The activities of FAE are influenced by the substrate of forage and complex cell wall materials (Oliveira et al., 2020). Benoit et al. (2008) found that the expression of faeA and faeB (genes encoded FAE) were induced by FA and other aromatic compounds. The activity of FAE were stability under pH 8.0–9.0 and it was inhibited by Ca\(^2+\), Co\(^2+\), Mg\(^2+\), Zn\(^2+\), Mn\(^2+\), K\(^+\), Fe\(^2+\), Cu\(^2+\) (Cao et al., 2013; Yang et al., 2009).

In recent years, cinnamoyl esterases are widely used in agriculture waste utilization, food industries, pharmaceutical and biofuel industries. Making good use of FA leads to the comprehensive utilization of forage and favorable economic benefits.

4. Catabolism of ferulic acid in the rumen

After release from plant cell walls, FA and diferulic acids are absorbed in the rumen or further catabolized by microbes (Soberton et al., 2012). Microbes catabolize FA mainly from addition or deletion of side groups, production of other organic molecules and/or incorporation of carbon from other phenolic acids into microbial biomass, and polymerization (Martin and Haider, 1976; Singh et al., 2001). Using natural substrates through microbial fermentation to produce high-value products seems to be a commercial and environmentally-friendly renewable energy source (Wong, 2006). Some industries use microbes to convert FA to high value products such as vanillin.

The FA is catabolized by microbes through non oxidative decarboxylation (Mishra et al., 2014), β-oxidation (Deleri et al., 1995), demethylation (Grbić-Galić and Pat-Polasko, 1985), side chain reduction (Falconnier et al., 1994), coenzyme A independent deacetylation and direct decetylation (Plaggenborg et al., 2001). Theoretically, the rumen microbes are able to fully metabolize phenolic acids under anaerobic conditions. But, for the distribution of π electrons over its ring structure, the benzene nucleus becomes very stable (Besle et al., 2010). Thus, many microbes only hydrogenate the alkyl side chains but not transform further. The author summarized the possible pathways to catabolize FA in rumen as shown in Fig. 3.

4.1. Non-oxidative decarboxylation

Ferulic acid is catabolized to 4-hydroxy-3-methoxystyrene (4-vinyl guaiacol) through non-oxidative decarboxylation by phenolic acid decarboxylases (encoded by bipad) (Curiel et al., 2010). The decarboxylases are divided into ferulic acid decarboxylase (encoded by flad) and p-coumaric acid decarboxylases (encoded by pdc) (Hu et al., 2015; Rodriguez et al., 2010; Sheng et al., 2015; Wen et al., 2011). The non-oxidative decarboxylation of FA is a reversible reaction (Li et al., 2008; Hu et al., 2015) and has been found in both bacteria and fungi (Tunikul et al., 2018). The first step of decarboxylation is the deprotonation of the p-hydroxy group which ensures the electron flow through ferulate. The ortho-carbon atom of the carboxyl group of FA forms a nucleophilic center. Then a proton transfers from a general acid at the active site to nucleophilic C\(^2\) carbon, forming a quinone methide intermediate. The carboxyl of the quinoid intermediate starts a second electron flow, and then the C–C bond of the intermediate is cleaved and generates p-vinyl phenol and CO\(_2\). For the high price of 4-vinyl guaiacol (25–30 times more expensive than FA), the decarboxylation of FA is thought to be a commercial way to transfer FA into 4-vinyl guaiacol. In rumen, the 4-vinyl guaiacol can be further catabolized (Li et al., 2008; Mavinckve and Nazareth, 1986). Mathew and Abraham (2006) found that vinyl guaiacol was transformed to acetovanillone and ethyl guaiacol through biocatalytic routes. The position of the ring cleavage of protoacetacetic acid and catechol determines the final products of the pathway.

4.2. Demethoxylation

Haematococcus pluvialis demethoxylates FA at the meta position and forms into pCA which can be further oxidized into 3-hydroxybenzoic acid (Tripathi et al., 2002). Two different mechanisms of demethoxylation have been expounded. One degradation pathway was followed by the production of acetate from methoxyl groups. Another pathway is to degrade the acidic side-chain of FA without the formation of acetate (Bache and Pfennig, 1981; Grbić-Galić, 1986). Enterobacter cloacae O-demethylates FA into caffic acid as an intermediary or as an end product in both aerobic and anaerobic conditions (Micard et al., 2002).

4.3. Reduction

During catabolism, the reduction of FA to non-toxic compounds is always the first step (Jugal et al., 1981; Besle et al., 2010). The effect of the reductive anaerobic transformation is to dispose redox equivalents generated in oxidative reactions (Heider and Fuchs, 1997). Compared with demethylation and dihydroxylation, reduction is relatively rapid and faster (Chesson et al., 1999). The FA can be reduced into coniferyl aldehyde then transformed into coniferyl alcohol by white-rot fungus Pycnoporus cinnabarinus 1-937 (Falconnier et al., 1994). Reductases take part in this reduction pathway. Another kind of reduction happens in the double-bond of the side chain. Clostridium strains can reduce cinnamic acid, o-, m- and p-methoxycinnamic acid, caffic acid, FA to their corresponding 3-phenylpropionic acid derivatives. For example, pCA can be reduced to p-hydroxyhydrocinnamic acid (3- (4-hydroxyphenyl)) propionic acid (Chamkha et al., 2001), Wolinella succinogenes isolated from rumen reduced FA to dihydroferulic acid in the absence of hydrogen acceptors (Ohmiya et al., 1986; Poquet et al., 2008).

4.4. Dehydroxylation

The dehydroxylation of FA can reduce the double in the side chain (Grbić-Galić, 1986). Enterobacter and Escherichia transformed FA through O-demethylation, dehydroxylation, reduction and decarboxylation under strictly anaerobic conditions (Grbić-Galić, 1986). The dehydroxylation of FA occurs at C\(_4\) and has been detected in human feces (Duncan et al., 2016), Kern et al. (2003) summarized that diferulic acid can be metabolized by colonic bacteria and open the hydrofuran rings. Dehydroxylation at C\(_3\) is more rarely encountered (Chesson et al., 1999).

4.5. Deacetylation

The deacetylation of FA has been noticed in several strains such as Bacillus subtilis, Pseudomonas acidovorans and Streptomyces setonii (Plaggenborg et al., 2001; Toms and Wood, 1970). In the direct deacetylation, the hydroxylated dihydroferulic acid is formed as an intermediate. After C–C bond cleaved, acetate and vanillic acid are formed (Toms and Wood, 1970). The ferulic-acid-converting enzymes produced by P. acidovorans only can convert phenolic substrates with the hydroxy group in the para position; while in S. setonii, non-phenolic aromatic compounds also can be
A new coenzyme A-dependent, non-β-oxidation pathway and not direct deacetylation of FA was revealed in *Pseudomonas fluorescens* AN103, *Delftia acidovorans* and *Amycolatopsis* sp. strain HR167 (Overhage et al., 1999; Plaggenborg et al., 2001). The FA is activated by feruloyl-CoA synthetase (encoded by *fcs*) to feruloyl-CoA. Then the feruloyl-CoA is hydrated to 4-hydroxy-3-methoxyphenyl-β-hydroxypropionyl-CoA as a transient intermediate product by enoyl-CoA hydratase (encoded by *ech*) and subsequently cleaved to acetyl-CoA and vanillin (Plaggenborg et al., 2001).

Rumen microbes exist as a complex symbiotic network of a diverse population, and are affected by various conditions such as temperature, probiotic and antibiotic treatment (Bhatt et al., 2013). Different strains showed different pathways to catabolize FA with different end products (Chesson et al., 1982). The individual’s diet shows an effect on the type and the amount of phenolic substrates supplied to the intestinal bacteria, which may in turn cause fluctuations of these microbes in the gut (Hui et al., 2006). The anaerobic transformation is the main pathway to metabolize phenolic acids, but take longer than aerobic degradation (Besle et al., 2010). Theoretically, FA can be fully degraded in rumen, but the metabolism is limited by the low redox potential, the small populations of organisms able to metabolize them and their limited retention time. Cellulolytic bacteria could degrade phenolic acids but the total complete breakdown would require a ruminal retention time and large population of bacteria (Besle et al., 2010). Usually, the anaerobic bacteria catalyze specific substitution on aromatic ring through different strategies (Chamkha et al., 2001).

In the rumen, the reduction of side-chains, demethylation and dihydroxylation, are thought to be the main products of microbial action. But due to the mass of microbes in the rumen, the catabolization of FA is a complex process. According to Ohmiya’s (1986) study, the ability of anaerobic microbe to catabolize FA act as synergistic reaction with cellulolytic anaerobes. Ferulic acids released from plant cell walls were provided as substrates for microbes. Cellulolytic anaerobes could be inhibited by FA. The catabolism of FA is a detoxication pathway (Adeboye et al., 2015). Thus, the FA-modifying microbes help the cellulolytic anaerobes from the toxic environment of FA. Additionally, H₂ and formate produced during the fermentation of cellulose by *R. albus* can enhance the growth of *W. succinogenes* (Hungate and Stack, 1982; Stack and Hungate, 1984).
5. Recommendations for future work

In plant cell walls, FA forms ester and ether linkages between carbohydrates and lignin, which is a cross-linking agent. Due to the inhibition of microorganisms by FA and the limitation of ferulic acid-cross-linked complex cell walls, the existence of these linkages shows a negative effect on the digestibility of forage in ruminants. However, whether FA in diet level will inhibit the growth of rumen microbes and their enzymes still requires further research through in vitro trials. Bound FA in plant cell walls will influence the utilization of forage. The FA est in plant cell walls is generally positively correlated to the fiber degradation in rumen while FAeth mainly shows negative effects. However, relationships between FAest and FAeth in total-tract digestibility need further in vivo research. Breeding methods to reduce the cross linkages in plant cell walls are also ideal ways to increase the degradation of forages. FA undergoes several transformations when pass digestive tract. The authors wrote this review to draw attention to the release and catabolization of plant cell wall FA in rumen. After ingestion, FA is mainly released from plant cell walls by microbes in rumen. Both fungi and bacteria in rumen can release FA from plant cell walls through feruloyl esterases and p-coumaroyl esterases. The FAE hydrolyze the ester bonds between FA and sugar residues in plant cell wall polysaccharide. They cooperate with polysaccharide-degrading enzymes to improve microbe accessibility. Then, some of the released FA are absorbed in rumen, and others can be catabolized by microbes through reduction, demethylation, dihydroxylation or/and decarboxylation pathways. The product of metabolism may be further catabolized by microbes until the ring cleave. The catabolism of FA is affected by various factors. Thus, the isolation of rumen microbes may be essential for exploring the metabolism of FA in rumen.

Author contributions

Yan-Lu Wang: Conceptualization, Writing- Reviewing and Editing. Wei-Kang Wang: Writing - Original Draft. Qi-Chao Wu: Investigation. Hong-Jian Yang: Coordinator, supervision, critical manuscript review.

Declaration of competing interest

We declare that we have no financial and personal relationships with other people or organizations that can 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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