Whole-plant corn silage improves rumen fermentation and growth performance of beef cattle by altering rumen microbiota

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Abstract
In recent years, whole-plant corn silage has been widely used in China. Roughage is an important source of nutrition for ruminants and has an important effect on rumen microbiota, which plays an important role in animal growth performance and feed digestion. To better understand the effects of different silages on rumen microbiota, the effects of whole-plant corn silage or corn straw silage on growth performance, rumen fermentation products, and rumen microbiota of Simmental hybrid cattle were studied. Sixty healthy Simmental hybrid cattle were randomly divided into 2 groups with 6 replicates in each group and 5 cattle in each replicate. They were fed with whole-plant corn silage (WS) diet and corn straw silage (CS) diet respectively. Compared with corn straw silage, whole-plant corn silage significantly increased daily gain and decreased the feed intake-to-weight gain ratio (F/G) of beef cattle. Whole-plant corn silage also decreased the acetic acid in the rumen and the acetate-to-propionate ratio (A/P) compared with corn straw silage. On the genus level, the relative abundance of Prevotella was significantly increased while the relative abundance of Succinivibrionaceae_UCG-002 was decreased in cattle fed whole-plant corn silage compared with those fed corn straw silage. Prevotella was positively correlated with acetic acid and A/P. Succinivibrionaceae_UCG-002 was positively correlated with propionic acid and butyric acid, and negatively correlated with pH. Feeding whole-plant corn silage improved amino acid metabolism, nucleotide metabolism, and carbohydrate metabolism. Correlation analysis between rumen microbiota and metabolic pathways showed that Succinivibrionaceae_UCG-002 was negatively correlated with glycan biosynthesis and metabolism, metabolism of co-factors and vitamins, nucleotide metabolism, and translation while Prevotellaceae_UCG-003 was positively correlated with amino acid metabolism, carbohydrate metabolism, energy metabolism, genetic information processing, lipid metabolism, membrane transport, metabolism of cofactors and vitamins, nucleotide metabolism, replication and repair, and translation. Ruminococcus_2 was positively correlated with amino acid metabolism and carbohydrate metabolism. Feeding whole-plant corn silage can improve the growth performance and rumen fermentation of beef cattle by altering rumen microbiota and regulating the metabolism of amino acids, carbohydrates, and nucleotides.

Key points
• Feeding whole-plant corn silage could decrease the F/G of beef cattle
• Feeding whole-plant corn silage improves rumen fermentation in beef cattle
• Growth performance of beef cattle is related to rumen microbiota and metabolism

Keywords Roughage · Whole-plant corn silage · Beef cattle · Rumen fermentation · Microbiota

Introduction
Roughage plays an important role in ruminant feeding. For a long time, corn straw has been used as an important source of roughage for ruminants, especially in beef cattle production. Corn straw is rich in carbohydrates, which can be used for fermentation of silage, but its serious lignification leads to low digestibility, and low nutritional value, making it difficult to meet the requirement of ruminant production with corn straw alone. Whole-plant corn silage is a high-quality source of roughage; it contains a considerable amount of corn kernels and is usually used to replace the concentrated part of the diet, playing a nutritional role similar to that of concentrated feed (Moloney and Drennan 2013). Production practice shows that whole-plant corn silage possesses rich nutrition and high feeding value that
effectively meets the production requirements of the ruminants (Hameleers 1998; O’Mara et al. 1998). Zaralis et al. (2014) showed that the daily gain of beef cattle fed with whole-plant corn silage alone was higher than that of cattle fed whole-plant corn silage and forage silage. Meanwhile, whole-plant corn silage can effectively increase milk yield, improve milk quality, reduce breeding costs, and increase economic benefits (Hameleers 1998).

Improving animal growth performance by manipulating rumen microbiota and ruminant metabolism through diet has gained increasing attention in recent years. The rumen is a digestive organ unique to ruminants and plays an important role in the whole digestive process (Anantasook et al. 2013). Ruminants employ microbiota in the rumen to ferment and degrade nutrients such as cellulose and hemicellulose in roughage to form volatile fatty acids (VFAs), such as acetic acid, propionic acid, and butyric acid (Luo et al. 2001). VFAs are the main source of energy for ruminants, providing 70% of the energy needed by the body (Bergman 1990). VFAs produced by rumen fermentation are partially absorbed by the rumen epithelial cells, partially neutralized by saliva, and partially absorbed by the small intestine along with the chyme. Absorption and utilization of VFAs play an important role in the life activities of ruminants. Kolver and de Veth (2002) showed that the increasing proportion of concentrate in the diet could increase the concentration of VFAs, thus improving the growth performance of ruminants.

Rumen microbiota is a relatively stable but continuously dynamic community. It is reported that the composition and distribution of rumen microbiota are affected by diet, season, host health, environmental temperature, humidity, and other factors (Russell and Rychlik 2001). Studies have shown that rumen microbiota has an important effect on the growth, health, and immunity of the host (Jami et al. 2014; Huws et al. 2018). Liu et al. (2019) reported that dietary composition is the most important factor that affected the rumen microbial community and changed the rumen microbiota and their metabolites when cattle are fed with different diets. However, there are few studies about the effects of whole-plant corn silage and corn straw silage on rumen microbiota and metabolites (VFA) on beef cattle growth performance. Therefore, this study aimed to investigate the effects and potential mechanism of feeding whole-plant corn silage and corn straw silage on the growth performance of Simmental hybrid cattle from the perspective of rumen microbiota and metabolites. The investigation provided a theoretical basis for exploring the mechanism of rumen microbiota and its metabolites in regulating the growth performance of beef cattle, and provided a promising direction for the application of probiotics in improving the growth performance of beef cattle.

### Materials and methods

#### Animals, diet, and experimental design

All experimental procedures in this study were approved by the Institutional Animal Ethics Committee of Henan Agricultural University (approval number: HENAU-2016–015). The experiment was conducted at Henan Hengdu Xianan Cattle Development Limited Company (Henan, China). The whole-plant corn silage and corn straw silage were produced on the experimental cattle farm and were stored until the start of the experiment. The storage time was 75 days. Sixty healthy Simmental hybrid cattle (448.5 ± 18.37 kg) were selected and randomly divided into two groups (6 replicates in each group and 5 cattle in each replicate). Two diets were designed for the experiment. One diet was supplemented with 27.05% whole-plant corn silage (WS group), and the other diet was supplemented with 27.05% corn straw silage (CS group). The detailed ingredient composition and nutrient content of the investigated diets are presented in Table 1.

The pre-trial period was 10 days, and the formal trial period was 80 days. All cattle were kept under unified management. The feed and drinking water were supplied, with a feeding schedule at 8:30 and 14:30 every day. The barn spray disinfection and manure removal were carried out regularly to prevent the immune stress of the cattle. Then, the growth performance was determined in 60 cattle. Average daily feed intake (ADFI) was calculated by the amount of feed supplement subtracting the amount of leftover feed. Cattle of each replicate (5 cattle in each replicate) were weighed before the morning feeding on the first and 80th days of the formal trial, recorded as the initial weight and the last weight, to calculate average daily gain (ADG). Feed intake-to-weight gain ratio (F/G) was calculated by ADFI divided by ADG.

#### Sample collection

At the end of the experiment, one cattle from each replicate was randomly selected for slaughter (6 samples in each group). Ruminal fluid was collected 3 h after the morning feeding on the last day of this experiment using an oral stomach tube according to previous study (Shen et al. 2012). Fifty milliliters of rumen fluid was collected from each cattle, and the rumen fluid was filtered with four layers of gauze. The fluid pH was measured immediately. The samples were immediately flash-frozen in liquid nitrogen and stored at −80 °C for DNA extraction and measuring the volatile fatty acids (VFAs) according to the previous study (Xi et al. 2014).
Table 1 Composition and nutrient levels of diet of beef cattle (DM, dry matter, basis %)

| Items                        | WS%   | CS%   |
|------------------------------|-------|-------|
| Molasses                     | 4.36  | 4.36  |
| Bean dregs                   | 2.13  | 2.13  |
| Distiller’s grains           | 10.18 | 10.18 |
| Molasses                     | 2.13  | 2.13  |
| Concentrate supplement       | 43.63 | 43.63 |
| Total                        | 100.00| 100.00|

DNA extraction and 16S rRNA gene sequencing

DNA was extracted from rumen fluid using E.Z.N.A DNA Stool Mini kit (Omega, New York, USA). DNA concentration was determined using a Nano Drop 2000 (Thermo Fisher Scientific, Waltham, MA, USA), and DNA integrity was checked using 1% agarose gel electrophoresis. The V3–V4 hypervariable region of the bacterial 16S rRNA gene was amplified by PCR using primers 338F (5’–ACT CCTACGGGAGGCAGCAG-3’) and 806R (5’–GGACTACHVGGGTWTCTAAAT-3’) and the following program: denaturation for 3 min at 95 °C; 27 cycles of denaturation for 30 s at 95 °C, annealing for 30 s at 55 °C, and elongation for 45 s at 72 °C; and a final extension at 72 °C for 10 min. PCR reactions were performed in triplicate with each 20-mL reaction mixture containing 4 μL 5× FastPfu Buffer, 2 μL 2.5 mM dNTPs, 0.8 μL of each primer (5 μM), 0.4 μL FastPfu Polymerase, and 10 ng template DNA. The resulting PCR products were extracted from a 2% agarose gel and further purified using an AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA). The PCR products were mixed and sequenced as a single sample. A paired-end amplification library was constructed and sequenced using the Illumina Miseq platform (Illumina, San Diego, USA) according to the standard protocols by Majorbio Bio-Pharm Technology Co. Ltd. (Shanghai, China). The raw reads were deposited into the NCBI Sequence Read Archive (SRA) database under accession number SRP298526.

Bioinformatics analysis of sequencing data

Raw fastq files were quality-filtered by Trimmomatic and merged by FLASH: the reads were truncated at any site receiving an average quality score <20 over a 50-bp sliding window; sequences whose overlap was longer than 10 bp were merged according to their overlap with no more than 2-bp mismatch; sequences of each sample were separated according to barcodes (exact matches) and primers (allowing for two nucleotide mismatches). Reads containing ambiguous bases were removed. Operational taxonomic units (OTUs) were clustered with a 97% similarity cutoff using UPARSE (version 7.1; http://drive5.com/uparse/) with a novel “greedy” algorithm that performs chimera filtering and OTU clustering simultaneously (Edgar 2013). Sample biodiversity was calculated using the Chao1 and Shannon indices. R language tools were used to generate graphs and colony histograms. Changes in the relative abundance of bacteria are shown using column charts (Singh et al. 2015). Weighted UniFrac principal coordinate analysis (Lozupone et al. 2011) and hierarchical cluster analysis of Bray–Curtis samples based on OTU level were used to summarize the composition of rumen microbiota (Jiang et al. 2013).
determine the effect of posterior segment microbiota interacting with apparent performance, redundancy analysis (RDA) was performed at the genus level using the R language vegan packet (Mu et al. 2017). Three levels of metabolic pathway information were obtained using PICRUSt for Pathway (Langille et al. 2013) and abundance tables for each level were obtained and analyzed by majorbio Co., Ltd., China (Shanghai, China).

Statistics and analysis

Analyses of data were performed using the software SPSS18.0 (IBM, New York, USA). Differences between means were assessed using an independent sample t-test and \( P < 0.05 \) was considered statistically significant.

Results

Effects of different diets on growth performance of beef cattle

Beef cattle were fed either whole-plant corn silage (WS) or corn straw silage (CS) for 80 days. The effects of different treatments on the growth performance of beef cattle are presented in Fig. 1. There was no significant difference in ADFI between these two different diets group observed \( (P > 0.05, \text{Fig. 1a}) \). The ADG of cattle with WS treatment was significantly higher than that of cattle with CS treatment \( (P < 0.05, \text{Fig. 1b}) \). Moreover, F:G with WS treatment was significantly lower than that of cattle with CS treatment \( (P < 0.05, \text{Fig. 1c}) \). These results indicated that WS treatment could improve the growth performance of beef cattle.

Effects of different diets on the concentration of VFAs in beef cattle rumen

The effects of different diets on rumen VFAs of beef cattle were investigated. Rumen pH values in both treatment groups were in the normal range (Fig. 2a), and there was no significant difference observed in the total fatty acids, butyric acid, and propionic acid \( (P > 0.05, \text{Fig. 2b, c, and e}) \). However, the amount of acetic acid in CS treatment was significantly higher than that in WS treatment \( (P < 0.05, \text{Fig. 2d}) \). The acetate-to-propionate ratio \( (A/P) \) in WS treatment was significantly lower compared to that in CS treatment \( (P < 0.05, \text{Fig. 2f}) \).

Effects of different diets on the diversity and composition of rumen microbiota

After quality filtering, we obtained 578,207 microbial sequences from rumen samples, of which 4066 were chimeric reads that were removed from further analysis. The mean sequence read length was 253 bp. One thousand six hundred seventy-five OTUs were obtained by OTU clustering of sequences at a sequence-similarity level of 97%, which were divided into 19, 29, 57, 92, 214, and 440 known groups on phylum, class, order, family, genus, and species level, respectively. Of these, 1597 OTUs were found in both treatments, while 46 and 32 OTUs were specific to the CS and WS treatments, respectively (Fig. 3a). We analyzed the richness and diversity of the microbial community using the rarefaction curve, Shannon index, and Chao index. The rarefaction curve tended to be flat, indicating that the sequencing data reached saturation and the amount of data and depth of sequencing were sufficient (Fig. 3b). There was no significant difference in the Shannon index between the two groups while there was a significant difference in the Chao index between the two groups, indicating that the microbial abundance was significantly different between the two groups (Fig. 3c–d). Hierarchical cluster analysis and principal coordinate analysis (PCoA) of samples for β-diversity revealed a significant difference in rumen microbial composition between the two groups, with the first two principal components accounting for 56.28% and 24.55% of the total variation, respectively (Fig. 3e–f).

Analysis of rumen microbial community composition of two groups of beef cattle showed that *Bacteroidetes* accounted for 72.39% and 58.73%, *Firmicutes* accounted for...
for 19.20% and 24.24%, *Proteobacteria* accounted for 3.18% and 11.96%, respectively, in the WS group and the CS group on the phylum level. These three strains were the dominant strains in these two treatments and accounted for more than 90% of the total sequences (Fig. 4a). The abundance of *Bacteroidetes* in the WS treatment was significantly higher than that of in the CS treatment ($P = 0.005$), and the abundance of *Proteobacteria* in the WS treatment was significantly lower than that in the CS treatment ($P = 0.045$), but there was no significant difference in the abundance of *Firmicutes* between the two treatments ($P = 0.045$ and $P = 0.045$, respectively) (Fig. 4d).

**Effects of different diets on the correlation of bacterial genera and VFA concentrations**

The correlation between rumen microbiota and VFAs was analyzed. As shown in Fig. 5, *Prevotella_1* was positively correlated with A/P, *Succinivibrionaceae_UCG-002* was positively correlated with propionic acid and butyric acid, and negatively correlated with pH, *Succiniclasticum* was positively correlated with pH and A/P, and *norank_f__F082* and *Rikenellaceae_RC9_gut_group* were positively correlated with propionic acid and butyric acid (Fig. 5a–b).

**Effects of different diets on metabolic pathways in beef cattle**

To predict the functions of rumen microbiota, metabolic pathways of the microbiota involved were analyzed. There were much more microbiota associated with the functions of amino acid metabolism, nucleotide metabolism, and metabolism in the WS treatment than in the CS treatment ($P = 0.002$, $P = 0.018$, $P = 0.025$, respectively, Fig. 6a). There were much more microbiota associated with functions of membrane transport and genetic information processing in the CS treatment than in the WS treatment ($P = 0.007$, $P = 0.004$, respectively, Fig. 6a).
Fig. 3 Effects of different diets on rumen microbial alpha and beta diversity in beef cattle. a Venn chart of rumen microbial on OTU level in different groups. b Rarefaction curve of sequencing data. c Shannon index of rumen microbial in different groups. d Chao index of rumen microbial in different groups. e Hierarchical clustering tree on OTU level. f Principal coordinates analysis on OTU level. Abbreviations: whole-plant corn silage group (WS), blue; corn straw group (CS), red. The microbiota were determined in 12 cattle from two different groups (1 cattle each replicate), *0.01 < P ≤ 0.05, **0.001 < P ≤ 0.01, ***P ≤ 0.001

To analyze the specific association between rumen microorganisms and metabolic pathways, the correlation analysis was conducted. As shown in Fig. 6b, *Succinivibrionaceae_UCG-002* was negatively correlated with glycan biosynthesis and metabolism, metabolism of co-factors and vitamins, nucleotide metabolism, and translation. *Prevotellaceae_UCG-003* was positively correlated with amino acid metabolism, carbohydrate metabolism, energy metabolism, genetic information processing, lipid metabolism, membrane transport, metabolism of cofactors and vitamins, nucleotide metabolism, replication, and repair and translation. *Ruminococcus_2* was positively correlated with amino acid metabolism, carbohydrate metabolism, energy metabolism, genetic information processing, lipid metabolism, and translation.

Discussion

As the main source of nutrients for ruminants, roughage plays an important role in stimulating rumination and chewing, maintaining normal pH of rumen fluid and normal fermentation of rumen microbiota, and promoting digestion and metabolism of nutrients. Studies have shown that the utilization rate of animal feed can be improved by regulating the rumen microbiota through dietary alterations (Yang et al. 2017). Volatile fatty acids produced by fermentation of rumen carbohydrates are the main source of energy for ruminants, accounting for more than 70% of the total metabolic energy (Bergman 1990). Therefore, we investigated the effects of whole-plant corn silage and corn straw silage on growth performance, rumen microbiota, and VFAs of beef cattle. The daily gain of beef cattle with the CS treatment was lower than that of cattle with the WS treatment. This may be due to the low nutritional value of corn straw and the high content of neutral detergent fiber (NDF) and acid detergent fiber (ADF). ADF is a carbohydrate in plant material or feed that is insoluble in acid detergent, including cellulose and lignin which are more correlated with digestibility (digestibility refers to the percentage of digestible nutrients in the feed to the ingested nutrients) than with intake (Van Soest 1965; Mertens 1997). Neutral detergent fibers (NDF) are carbohydrate in plant material or feed that is insoluble in neutral detergents, including cellulose, hemicellulose, and lignin fractions of feeds which are highly correlated with feed volume and chewing activity than ADF (Mertens 1997). The feed intake and its digestibility have great impact over the ruminant weight gain (Carberry et al. 2012). The previous study has shown that lowest final body weights were observed in beef cattle fed rice straw diet with highest ADF and NDF intake (Chen et al. 2019). The digestibility of straw is only 20–30% (King et al. 2017). When beef cattle consume roughage comprising only corn straw silage, it is difficult for them to meet their maintenance requirement, which affects growth performance. Khaing et al. (2015) showed that replacing Napier grass with whole-plant corn silage increased goat weight gain, feeding, and digestion. Zaralis et al. (2014) showed that when whole-plant corn silage was added to the diet of fattening cattle, the feed intake of beef cattle could be increased, thus improving growth performance. In our experiment, feeding whole-plant corn silage improved the growth performance of beef cattle, which was similar to the results of the above study.

pH is an important indicator of rumen fermentation and can be used to determine whether rumen fermentation is normal or not. The normal pH of rumen fermentation is pH 6–7 (Nocek 1997). Rumen fluid pH lower than 5.8 is considered rumen acidosis (Penner et al. 2007). In this experiment, cattle rumen pH in the two treatments was in the normal range and had no negative effect on rumen fermentation. The final products of rumen fermentation of dietary carbohydrates are VFAs, mainly acetic acid, propionic acid, and butyric acid (Luo et al. 2001). With decreasing crude fiber content, the acetic acid drops while propionic acid increases (Kaufmann and Rohr, 1966). Acetic acid is the precursor of fat biosynthesis in ruminants while propionic acid is an important precursor of glucose biosynthesis (Liu et al. 2016; Aschenbach et al. 2010; Young 1977). Therefore, propionic acid fermentation can provide more energy for the body and help livestock gain weight. In our experiment, the amount of acetic acid was significantly lower in the WS treatment but the amount of propionic acid was higher in the WS treatment though without a significant difference. Thus, the A/P was significantly decreased in the WS treatment. Decreasing the roughage inclusion rate increased the proportion of propionate and decreased the A/P (Jeon et al. 2019). When the A/P decreases, CH4 production would decrease and energy retention by the cattle would increase (Russell 1998). The decrease of A/P in the WS group may be one reason for improving the growth performance of beef cattle with WS treatment.

Moreover, the rumen microbiota and its correlation with rumen metabolites were further evaluated. There was a significant difference in the Chao α-diversity index of rumen microbiota between the two treatment groups, and the
community compositions of the two treatments were distinctly separated in β-diversity analysis, indicating a significant difference in the structure and composition of microbial communities between the two treatments. On the phylum level, the dominant bacteria in the two treatment groups were *Bacteroidetes* and *Firmicutes*, which was similar to the results of an investigation by Ley et al. (2008). These two bacterial phyla are found in the rumen of different ruminants.

**Fig. 4** Analysis of the composition and difference of the rumen microbiota of beef cattle in different diets. a. Composition of microbiota community on phylum level. b. Microbiota community presented significantly different proportions (%) on phylum level. Proportions represented the average relative abundance of microbial in different groups. c. Composition of microbiota community on genus level. d. Microbiota community presented significantly different proportions (%) on the genus level. Proportions represented the average relative abundance of microbial in different groups. Abbreviations: whole-plant corn silage group (WS), blue; corn straw group (CS), red. The microbiota were determined in 12 cattle from two different groups (1 cattle each replicate), *0.01 < P ≤ 0.05, **0.001 < P ≤ 0.01, ***P ≤ 0.001

**Fig. 5** Association and model predictive analysis. a. RDA analysis of microbial in CS group. b. RDA analysis of microbial in the WS group. Abbreviations: whole-plant corn silage group (WS); corn straw group (CS). An acute angle between microbial (arrow) and VFA (arrow) indicated a positive correlation; an obtuse angle indicated a negative correlation. The length of the arrow can represent the degree of impact of environmental factors on species. The angle between the arrows of environmental factors represents positive and negative correlation (acute angle: positive correlation; obtuse angle: negative correlation; right angle: no correlation)
indicating that they play an important role in the rumen. The rumen of beef cattle fed with two different silages had a higher relative abundance of *Bacteroidetes* than that of *Firmicutes* and the rumen pH was about 6.51 in the WS group and 6.31 in the CS group, which was similar to the results of the report where the relative abundance of *Bacteroidetes* (50%) was higher than that of *Firmicutes* (43%) when the rumen pH was about 6.51 (Jami and Mizrahi 2012). *Bacteroidia* are capable of metabolic activities such as hydrolysis of polysaccharides and proteins, fermentation of sugars, and production of VFAs (Krieg et al. 2010). Species related to *Bacteroides* showed a high proportion of genes for debranching and oligosaccharide degrading enzymes, while species belonging to *Firmicutes* are rich in cellulase and hemicellulase (Gharechahi and Salekdeh 2018). *Bacteroidetes* and *Firmicutes* can be used as an important microbial indicator for evaluating the energy requirement of ruminants (Xue et al. 2017) because up to 70% of the host’s energy requirement is supplied by VFAs, while microbial species belonging to *Bacteroidetes* are responsible for acetate and propionate production and *Firmicutes* are responsible for butyrate production (Bergman 1990; Macfarlane and Macfarlane 2003; Den Besten et al. 2013). In this experiment, feeding whole-plant corn silage significantly increased the relative abundance of *Bacteroides*, which may improve the growth performance of beef cattle because *Bacteroidia* are capable of hydrolysis of polysaccharides and proteins, fermentation of sugars, and production of VFAs which could provide energy for the host (Krieg et al. 2010; Bergman 1990; Macfarlane and Macfarlane 2003; Den Besten et al. 2013). On the genus level, *Prevotella* is the most widespread and most abundant genus of bacteria in the rumen (Sharma et al. 2014). *Prevotella* function in hemicellulose degradation with high activity and can adjust the bacterial amount according to the difference in dietary structure (Li et al. 2015). Co-culture of *Prevotella* and fiber-degrading bacteria can improve the utilization of plant hemicelluloses (pectin and xylan), thus promoting the degradation of fiber in the rumen. *Prevotella* also play an important role in the degradation of non-fibrous polysaccharides and proteins in plants (Griswold 1999). *Succinivibrionaceae_UMC-002* can degrade non-fibrous carbohydrates in the rumen (Henderson et al. 2016). The main metabolites of *S. ruminis* were succinic acid, which can be converted into propionate (Van Gylswyk 1995). In this study, feeding whole-plant corn silage significantly increased the relative abundance of *Prevotella_1* and decreased the relative abundance of *Succinivibrionaceae_UMC-002*, indicating that feeding whole-plant corn silage could increase the degradation of the both fibrous and non-fibrous carbohydrates probably mainly by *Prevotella_1*. The concentration of VFAs in the rumen is related to the rumen microbiota (Griswold 1999). In this experiment, *Prevotella_1*, *Succinivibrionaceae_UMC-002*, and *Rikenellaceae_RC9_gut_group* were positively correlated with VFAs, indicating that these bacteria play an important role in the biosynthesis of VFAs and energy absorption and utilization, similar to the results of previous researches (Kovatcheva-Datchary et al. 2015; Holman and Gzyl 2019). However, the correlation needs to be further investigated. The research has shown that a small number of microbial species may have strong effects on rumen fermentation (Hanage 2014). Microbiota function in host metabolism mainly through the fermentation of carbohydrates that cannot be utilized and absorbed by the host itself, including plant polysaccharides (such as resistant starch, cellulose, hemicellulose, colloid), oligosaccharides (such as oligofructose and inulin), and insoluble sugars, as well as endogenous mucus produced by epithelial cells, producing final products that participate in the metabolic processes of the host body.
The rumen microbiota is a symbiotic complex of microorganisms, which is not only an important source of protein in ruminants but also the main energy source for ruminants to produce VFAs through fiber fermentation. Therefore, rumen microbiota represents a huge pool of biological resources, and it is very important to actively explore the functional genes of rumen microbiota that are closely related to important nutritional and physiological functions, such as carbohydrate transport and metabolism, amino acid transport and metabolism, and the production of VFAs. We analyzed the difference in metabolic pathways of rumen microbiota with the two different diet treatments and found that after feeding whole-plant corn silage, the functions of amino acid metabolism, nucleotide metabolism, and metabolism were significantly upregulated and carbohydrate metabolism tended to be upregulated \((P = 0.05896)\). This may be due to the higher relative abundance of \textit{Prevotella} in the WS group than in the CS group. \textit{Prevotella} play an important role in rumen protein metabolism (Broderick 1996). \textit{Prevotella} can eventually degrade protein into various peptides, which can be effectively absorbed by the rumen and promote the formation of bacterial protein. In addition, \textit{Prevotella} can degrade hemicellulose and starch (Ramšak et al. 2000). Furthermore, the results of correlation analysis between specific bacteria and metabolic pathways showed that ruminant metabolic pathways were closely related to \textit{Succinivibrionaceae_UCG-002}, \textit{Prevotellaceae_UCG-003}, and \textit{Ruminococcus_2}. \textit{Succinivibrionaceae_UCG-002} was negatively correlated with glycogen biosynthesis and metabolism, nucleotide metabolism, metabolism of co-factors and vitamins, and translation, which may cause the downregulation of these processes. \textit{Prevotellaceae_UCG-003} can use hemicellulose and play an important role in protein metabolism and starch degradation (Ramšak et al. 2000). Moreover, \textit{Prevotella} has been reported to be one of the most numerous and genetically diverse bacterial genera in the rumen (Purushue et al. 2010). In our correlation analysis, \textit{Prevotellaceae_UCG-003} was positively correlated with amino acid metabolism, carbohydrate metabolism, energy metabolism, genetic information processing, lipid metabolism, membrane transport, metabolism of cofactors and vitamins, nucleotide metabolism, replication and repair, and translation. \textit{Ruminococcus_2} can hydrolyze and ferment carbohydrates and play an important role in rumen fermentation (Rey et al. 2014). In our experiment, \textit{Ruminococcus_2} was positively correlated with amino acid metabolism and carbohydrate metabolism. In conclusion, feeding whole-plant corn silage can increase the daily gain and decrease the F/G of beef cattle. The improvement in growth performance of beef cattle fed whole-plant corn silage was related to changes in rumen microbiota that improve rumen metabolism by increasing the metabolism of amino acids, carbohydrates, and nucleotides. However, the specific mechanisms need to be further studied.

**Author contribution** Y. C. and H. L. performed experiments and analyzed data. Z. G., J. X., and B. L. participated in the data collection. M. G., X. Y., J. N., and X. Z. assisted with animal experimentation. S. M. and D. L. provided advice on the design and performance of experiments. Y. C. and H. L. wrote the manuscript draft. Y. S. and Y. H. S. supervised the study. All of us read and approved the final manuscript.

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**Data availability** The authors declare that data supporting the findings of this study are available within the article.

**Declarations**

**Ethics approval and consent to participate** Not applicable.

**Consent for publication** All authors consent for publication.

**Competing interests** The authors declare no competing interests.

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