

Article

Lignocellulolytic Enzymes and a Microbial Consortium Improve Lignocellulose Degradation, Fermentation Quality, and Bacterial Co-Occurrence in Forage Oat Silage

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Abstract

This study evaluated the effects of formic acid (A), lignocellulolytic enzymes (E), and a lignocellulose-degrading microbial consortium (M) on fermentation quality, lignocellulose degradation, carbohydrate conversion, bacterial community, and potential microbial associations in forage oat silage. Fresh forage oat was treated with *Lactiplantibacillus plantarum* alone (control) or combined with A, E, or M and ensiled for 60 days with three biological replicates per treatment. All additives improved silage fermentation quality. Compared with the control, E and M significantly increased lactic acid content, reduced pH, and decreased ammonia-N accumulation. E exhibited the highest water-soluble carbohydrate content (26.37 g/kg DM) and achieved the greatest degradation extent of hemicellulose, cellulose, and ADL, accompanied by increased release of glucose, fructose, and xylose. LEfSe and correlation analysis suggested that carbohydrate-utilizing bacteria and LAB-related taxa were closely associated with lignocellulose degradation, xylose release, and lactic acid production. M exhibited the highest observed co-occurrence network complexity, suggesting altered potential associations among bacterial taxa during ensiling. E primarily improved silage quality by promoting lignocellulose degradation and increasing carbohydrate availability, whereas M was associated with improved fermentation characteristics and changes in bacterial community composition and co-occurrence network complexity. These findings highlight lignocellulolytic enzymes and microbial consortia as effective strategies for improving lignocellulose utilization and fermentation quality in forage oat silage.

Keywords: forage oat silage; lignocellulolytic enzymes; microbial consortium; lignocellulose degradation; bacterial community; microbial co-occurrence network



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1. Introduction

Forage oat (*Avena sativa* L.) is an important annual forage crop widely cultivated in temperate and semi-arid regions because of its high biomass yield, strong environment

adaptability, and favorable nutritional value. However, forage oat is generally characterized by a high lignocellulose content and a relatively low population of epiphytic lactic acid bacteria (LAB), which may limit the rapid establishment of lactic acid fermentation during ensiling and reduce the utilization efficiency of structural carbohydrates. Consequently, improving lignocellulose degradation while maintaining favorable fermentation has become an important challenge in forage oat silage production.

Various additives have been developed to improve silage fermentation and nutrient preservation. In recent years, studies on lignocellulose degradation and conversion during the ensiling process have commonly categorized the underlying mechanisms into three major pathways: acid, enzymatic and microbial degradation [1]. Formic acid has been widely applied in silage production for its strong acidifying and antimicrobial effects, which helped limit nutrient losses and improve preservation during ensiling [2]. As a conventional chemical additive, formic acid is commonly used as a reference treatment for evaluating alternative silage improvement strategies because it rapidly decreases pH and inhibits undesirable fermentation. However, unlike chemical acidification, lignocellulolytic enzymes and microbial consortium may improve silage quality by modifying substrate availability and microbial community characteristics. Therefore, comparing these additives provides insights into the distinct mechanisms underlying chemical and biological approaches for improving forage oat silage preservation. Lignocellulolytic enzymes, particularly cellulase and xylanase, can hydrolyze cellulose and hemicellulose into a fermentable monosaccharide, increasing substrate availability for LAB fermentation and enhancing the utilization of structural carbohydrates. Mu et al. reported that cellulase and xylanase improved fermentation quality and increased the degradability of the mixed silage of agri-residue and alfalfa by promoting the hydrolysis of lignocellulosic components [3]. Similarly, Qiu et al. demonstrated that the enzyme addition enhanced carbohydrate release and bacterial community composition during ensiling [4]. Recently, lignocellulose-degrading microbial consortia have received increasing attention as a promising biological strategy for improving both lignocellulose conversion and silage fermentation. Unlike exogenous enzymes, microbial consortia can continuously colonize plant tissues and produce a diverse array of lignocellulolytic enzymes throughout the fermentation process. Li et al. isolated a lignocellulose-degrading microbial consortium from yak rumen and found that it exhibited high cellulase and xylanase activities, significantly reduced structural carbohydrate contents, and improved fermentation quality of rice straw silage [5]. Previous studies have demonstrated that microbial consortia can enhance lignocellulose degradation by promoting synergistic associations among functional microorganisms and increasing lignocellulolytic activities [6]. These findings suggest that microbial consortia may improve fermentation characteristics through both substrate transformation and microbial community assembly.

Advances in high-throughput sequencing technologies have greatly improved our understanding of microbial succession during ensiling. Previous studies have demonstrated that shifts in bacterial communities are closely associated with fermentation characteristics, nutrient preservation, and carbohydrate transformation in silages [7]. In addition, high-throughput sequencing has enabled the identification of key bacterial taxa involved in substrate utilization and fermentation processes, providing deeper insights into the microbial mechanisms underlying silage preservation. Beyond bacterial succession, microbial co-occurrence network analysis has emerged as an effective tool for exploring ecological relationships among microorganisms. Network topology analysis can characterize the structural complexity and statistical associations among microbial taxa within a community, thereby providing ecological information that cannot be obtained from taxonomic analyses alone. Previous studies have shown that potential microbial associations are closely linked to fermentation performance and may influence the establishment of desir-

able LAB-dominated ecosystems during ensiling [8]. Furthermore, co-occurrence patterns among microorganisms may reflect potential associations related to substrate conversion and metabolite production. Although lignocellulose-degrading microbial consortia have shown potential for improving lignocellulose conversion in crop residues, their effectiveness and underlying mechanisms in forage oat silage remain unclear. Forage oat differs from crop residues because it contains relatively high structural carbohydrates but limited epiphytic lactic acid bacteria, which may influence the establishment of lignocellulose degradation and lactic acid fermentation. Moreover, previous studies have mainly focused on fermentation characteristics or degradation efficiency, while how microbial consortia reshape bacterial community organization and potential co-occurrence patterns during forage oat ensiling remains insufficiently understood.

Therefore, the objectives of this study were to evaluate the effects of formic acid, lignocellulolytic enzymes, and a lignocellulose-degrading microbial consortium on fermentation characteristics, lignocellulose degradation, carbohydrate conversion, bacterial community, and microbial co-occurrence networks of forage oat silage. We further aimed to elucidate the potential relationships between key bacterial taxa, lignocellulose degradation, and fermentation performance, thereby providing theoretical support for improving both lignocellulose utilization and silage quality of forage oat. Although previous studies have demonstrated the potential of chemical additives or enzyme preparations to improve silage fermentation, the comparative effects and underlying mechanisms of conventional acidification, lignocellulose degradation, and microbial consortium-based strategies remain insufficiently understood in forage oat silage. In particular, whether a lignocellulolytic microbial consortium can simultaneously promote carbohydrate transformation and induce distinct bacterial community characteristics compared with conventional additives remains unclear. Therefore, we hypothesized that (1) formic acid would enhance fermentation stability by promoting rapid acidification and inhibiting undesirable microbial activity; lignocellulolytic enzymes would improve carbohydrate availability by enhancing structural carbohydrate degradation; and the lignocellulolytic microbial consortium would improve forage oat silage quality by enhancing structural carbohydrate transformation and promoting lactic acid fermentation; and (2) these improvements would be associated with specific changes in bacterial community composition and co-occurrence patterns.

2. Materials and Methods

2.1. Raw Material Preparation

Forage oat was cultivated in the experimental fields (37.67° N, 102.85° E, altitude 1780 m, mean annual temperature 8 °C, average annual precipitation 200 mm) in Huangyang Town of Wuwei (Gansu, China) in August 2024. Fresh forage oat was harvested at the heading stage using a small forage harvester, chopped to approximately 2 cm, and immediately transported to the laboratory for further processing. The microbial and chemical composition of the fresh material is shown in Table 1. The treatments were as follows: (1) *Lactiplantibacillus plantarum* alone (control); (2) *L. plantarum* + formic acid at 0.5% of fresh weight (A); (3) *L. plantarum* + lignocellulolytic enzymes at 0.12% of fresh weight (E); (4) *L. plantarum* + lignocellulose-degrading microbial consortium at 1×10^6 colony-forming units/g of fresh weight (M). The lignocellulolytic enzymes consisted of cellulase (50,000 U/g), xylanase (3×10^5 U/g), and β -glucosidase (100 U/g), which were mixed at a mass ratio of 6:3:1 and dissolved in sterile water. The microbial consortium used in this work was the same consortium previously established and characterized by Li et al. [5], which was composed of *Enterococcus*, *Streptococcus*, *Lactobacillus*-related taxa, *Clostridium*, *Bacillus* and *Lactococcus*. The preserved consortium was reactivated prior to use following the procedures described by Li. The application rates for formic acid, lignocellulolytic

enzymes, and the microbial consortium were selected based on previous studies [9–11]. After being dissolved in sterile water, all additives were evenly sprayed onto the forage oat at 30 mL/kg of fresh weight. Approximately 200 g of the mixed material was then manually packed into polyethylene bags as laboratory silos and vacuum sealed. Each treatment included three replicates, and the silos were stored at room temperature (25 ± 3 °C) for 60 days.

Table 1. Chemical composition and LAB population of fresh forage oat.

Items	<i>Avena sativa</i> L.
pH value	6.85 ± 0.13
DM (g/kg FW)	271.9 ± 5.03
CP (g/kg DM)	144.66 ± 8.36
BC (mEq/kg DM)	125.2 ± 9.76
WSC (g/kg DM)	55.91 ± 4.36
NDF (g/kg DM)	577.29 ± 4.91
ADF (g/kg DM)	313.81 ± 5.15
ADL (g/kg DM)	36.93 ± 3.04
Hemicellulose (g/kg DM)	263.48 ± 5.94
Cellulose (g/kg DM)	276.88 ± 3.58
LAB ($\log_{10}$ CFU/g FW)	3.92 ± 0.14
Aerobic bacteria ($\log_{10}$ CFU/g FW)	6.69 ± 0.138
Yeast ($\log_{10}$ CFU/g FW)	7.11 ± 0.14

DM, dry matter; CP, crude protein; BC, buffering capacity; mEq, milliequivalent; WSC, water-soluble carbohydrates; NDF, neutral detergent fiber; ADF, acid detergent fiber; ADL, acid detergent lignin; LAB, lactic acid bacteria.

2.2. Fermentation Characteristics and Microbial Counts

The fresh material or fermented silage was thoroughly mixed before subsampling. Briefly, a 20 g sample was mixed with 80 g of sterile water and extracted at 4 °C for 24 h. The extract was then filtered through four layers of gauze to obtain the filtrate. The pH of the filtrate was immediately measured using a digital pH meter (HANNA HI 2221, Hanna Italia Srl, Padova, Italy). The filtrate was then stored at -20 °C for the determination of organic acid, including lactic acid, acetic acid, butyric acid, and propionic acid measured by a high-performance liquid chromatograph (HPLC 1260, Agilent Technologies, Santa Clara, CA, USA) as described by Huang et al. [12]. Ammonia-N content was determined according to Broderick and Kang [13]. To determine dry matter content, another 100 g of fresh or fermented sample was freeze-dried in a vacuum freeze dryer at -40 °C to -20 °C for 72 h. The dried samples were then ground and passed through a 1 mm sieve for further analysis. The ground samples were used to determine water-soluble carbohydrates (WSCs), total nitrogen (TN), lignocellulose contents, and mono- and disaccharide contents. WSC content was determined according to Murphy [14]. TN content was determined according to Krishnamoorthy et al. [15], and crude protein content was calculated by multiplying TN by 6.25. A portion of the freeze-dried and ground samples was used to determine mono- and disaccharides, including fructose, glucose, xylose, arabinose, and sucrose, according to the method described by Weiß and Alt [16]. Neutral detergent fiber (NDF) and acid detergent fiber (ADF) contents were determined according to Van Soest et al. [17], using a fiber analyzer (ANKOM 200i, ANKOM Technologies, Macedon, NY, USA). The acid detergent lignin (ADL) content was determined following the procedure described by Coblentz et al. [18]. The hemicellulose content was obtained by subtracting ADF from

NDF, and cellulose content was determined as the difference between ADF and ADL. The cellulose degradation rate (CDR) was calculated according to Equation (1) [19]:

$$CDR(\%) = 1 - \frac{DM_{amount\ 60d} \times Cellulose_{content\ 60d}}{DM_{amount\ 0d} \times Cellulose_{content\ 0d}} \times 100\% \quad (1)$$

where the degradation rates of hemicellulose (HDR), ADL (ADLDR), and lignocellulose (LDR) were calculated using the same method. Lignocellulose content was defined as the sum of hemicellulose, cellulose, and ADL.

Fresh material (10 g) was mixed with 90 mL of sterile 0.85% saline and shaken at 120 rpm for 40 min. The extract was serially diluted from 10^{-1} to 10^{-4} , and aliquots were spread onto the corresponding media. LAB were cultured on MRS agar under anaerobic conditions, yeasts were cultured on potato dextrose agar, and aerobic bacteria were cultured on nutrient agar. All plates were incubated at 37 °C for 48 h, and microbial counts were expressed as $\log_{10}$ cfu/g of fresh matter.

2.3. 16S rRNA Sequencing

Microbial DNA was extracted from microbial pellets collected by centrifugation at $10,000\times g$ for 5 min at 4 °C and used for 16S rRNA gene sequencing. The full-length 16S rRNA gene was amplified using the universal bacterial primers 27F (5'-AGRGTITYGATYMTGGCTCAG-3') and 1492R (5'-RGYTACCTTGTTACGACTT-3'). The target regions were amplified using barcoded primers, and each sample was amplified in triplicate to reduce PCR bias. Purified PCR products were used to construct DNA libraries with the SMRTbell® Express Template Prep Kit 2.0 (Pacific Biosciences, Menlo Park, CA, USA). The purified SMRTbell libraries were sequenced on PacBio Sequel II platform (Pacific Biosciences, Menlo Park, CA, USA) by Shanghai Majorbio BioPharm Technology Co., Ltd. (Shanghai, China) Following sequencing, the raw reads were subjected to quality control, and chimeric sequences were identified and removed using UCHIME (v 4.2.40). The resulting clean reads were clustered into operational taxonomic units (OTUs) at 97% sequence similarity using UPARSE (v 7.1). Taxonomic classification was performed using an RDP classifier against the SILVA database (v 138.2) with a confidence threshold of 75%.

2.4. Construction and Analysis of Microbial Co-Occurrence Networks

Microbial co-occurrence networks were generated based on bacterial correlation matrices provided by the sequencing company. The correlations among bacterial taxa were calculated using Spearman correlation analysis, and significant associations were selected according to the criteria of $|r| \geq 0.7$ and $p < 0.05$. Network visualization and topological characteristics, including nodes, edges, and positive/negative correlation ratios, were analyzed using Gephi software (v 0.10.1).

2.5. Statistical Analysis

Chemical composition and fermentation characteristics data were analyzed using one-way ANOVA with the general linear model procedure in SPSS 22.0. Before conducting ANOVA, the normality of data distribution was assessed using the Shapiro–Wilk test, and the homogeneity of variance was evaluated using Levene's test. Differences among treatment means were compared using Tukey's test, and statistical significance was declared at $p < 0.05$. Alpha diversity indices were calculated using MOTHUR software (v 1.30.2). Beta diversity was evaluated based on the Bray–Curtis distance matrix, and principal coordinates analysis (PCoA) was performed in QIIME 2 for visualization. Bar plots were generated using R software (v 4.5.1). LEfSe analysis was performed to identify bacterial biomarkers with significant differences among treatments. Features with a Kruskal–Wallis test α value < 0.05 and an LDA score > 2 were considered significant biomarkers. Spearman's correlation

analysis was used to assess the associations between microbial communities and chemical composition or fermentation characteristics, and the results were visualized as a heatmap using R software (v 4.5.1).

3. Results

3.1. Fermentation Characteristics of Silages

As shown in Table 1, fresh forage oat was characterized by low WSC and high lignocellulose content. In addition, the population of epiphytic lactic acid bacteria was low ($3.92 \pm 0.14 \log_{10}$ CFU/g FW). Table 2 shows that all treatments significantly decreased the pH value and increased the lactic acid content, while AA content was not significantly affected. E (51.57 g/kg DM) and M (54.04 g/kg DM) significantly increased lactic acid content compared with the control and A ($p < 0.05$). The acetic acid content did not differ significantly among treatments (Table 2). The LA/AA ratio tended to increase in E and M compared with A, although the differences were not statistically significant ($p = 0.085$). PA remained low across treatments, ranging from 2.27 to 2.59 g/kg DM. Additives decreased BA ($<0.2\%$) contents to an acceptable level. E exhibited the highest WSC content (26.37 g/kg DM), significantly exceeding that of the control, whereas A also maintained high WSC level. The AN content of additives decreased to 37.55 (A), 50.44 (E), and 31.33 (M) g/kg TN, respectively, and the DML ranged from 6.33% to 12.35% among treatments, while no significant differences were observed ($p = 0.212$) (Table 3).

Table 2. Effects of different additives on the fermentation quality of forage oat silage.

Items	Treatments				SEM	p Value
	Control	A	E	M		
pH	4.55 a	4.20 b	4.24 b	4.16 b	0.04	0.015
LA (g/kg DM)	33.03 b	33.52 b	51.57 a	54.04 a	3.06	<0.001
AA (g/kg DM)	11.23	9.05	9.13	12.06	0.58	0.197
LA/AA	2.97	3.76	6.13	4.48	0.46	0.085
PA (g/kg DM)	2.37 b	2.27 b	2.36 b	2.59 a	0.19	<0.001
BA (g/kg DM)	7.51 a	1.88 b	0.91 b	0.37 b	0.57	<0.001

a,b Means within a row with different superscripts differ ($p < 0.05$). SEM, standard error of the mean. LA, lactic acid; AA, acetic acid; LA/AA, lactic acid:acetic acid ratio; PA, propionic acid; BA, butyric acid. Treatment: control = *L. plantarum* alone; A = *L. plantarum* + formic acid; E = *L. plantarum* + lignocellulolytic enzymes; M = *L. plantarum* + lignocellulolytic microbial consortium.

Table 3. Effects of additives on the chemical composition of forage oat silage.

Items	Treatments				SEM	p Value
	Control	A	E	M		
WSC (g/kg DM)	15.09 c	22.34 ab	26.37 a	18.36 bc	1.30	0.011
DM (g/kg FW)	240.15	254.69	238.31	241.09	2.89	0.212
DML (%)	11.68	6.33	12.35	11.33	1.06	0.212
AN (g/kg TN)	82.81 a	37.35 b	50.44 b	31.33 b	4.80	0.002

a–c Means within a row with different superscripts differ ($p < 0.05$). SEM, standard error of the mean. WSC, water-soluble carbohydrates; DM, dry matter; DML, dry matter loss; AN, ammonia nitrogen. Treatment: control = *L. plantarum* alone; A = *L. plantarum* + formic acid; E = *L. plantarum* + lignocellulolytic enzymes; M = *L. plantarum* + lignocellulolytic microbial consortium.

3.2. Changes in Lignocellulose Degradation and Carbohydrate Content

Additives significantly reduced NDF and ADF contents compared with the control (Table 4). E showed the lowest level of hemicellulose and cellulose contents (Figure 1A). No significant difference in ADL content was observed among treatments. All additives increased the degradation rate of hemicellulose and cellulose. E showed the best performance, followed by M, whereas A exhibited the weakest effect (Figure 1B). Additive treatments increased soluble carbohydrate contents, with E showing the highest total level, followed by M and A (Figure 1C). Glucose, fructose, and xylose were detected as the major monosaccharides after ensiling. Fructose concentrations ranged from 3.06 to 4.60 g/kg DM, while glucose concentrations ranged from 2.14 to 5.89 g/kg DM across treatments. The fructose concentration was comparable to glucose in the control, A, and M, whereas glucose showed a higher concentration than fructose in E.

Table 4. Effects of different additives on the carbohydrate composition of forage oat silage.

Items (g/kg DM)	Treatments				SEM	p Value
	Control	A	E	M		
NDF	608.54 a	562.14 b	542.16 b	565.51 b	6.66	0.031
ADF	335.86 a	312.93 b	303.55 b	312.76 b	3.39	0.039
ADL	41.10	38.85	41.10	40.88	0.45	0.302

a,b Means within a row with different superscripts differ ($p < 0.05$). SEM, standard error of the mean. NDF, neutral detergent fiber; ADF, acid detergent fiber; ADL, acid detergent lignin. Treatment: control = *L. plantarum* alone; A = *L. plantarum* + formic acid; E = *L. plantarum* + lignocellulolytic enzymes; M = *L. plantarum* + lignocellulolytic microbial consortium.

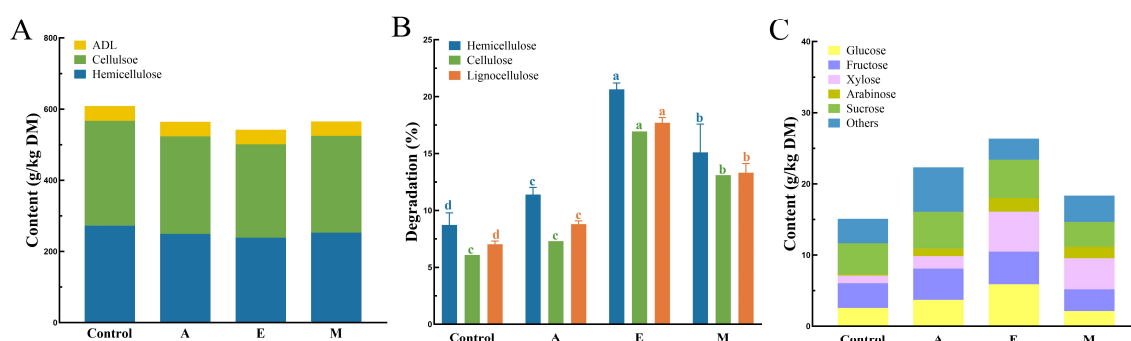


Figure 1. Effects of different additives on lignocellulose degradation and carbohydrate conversion of forage oat silage. (A) Contents of hemicellulose, cellulose, and ADL; (B) degradation rates of hemicellulose, cellulose, ADL, and total lignocellulose; (C) soluble carbohydrate composition. Control = *L. plantarum* alone; A = *L. plantarum* + formic acid; E = *L. plantarum* + lignocellulolytic enzymes; M = *L. plantarum* + lignocellulolytic microbial consortium. Different lowercase letters indicate significant differences among treatments ($p < 0.05$).

3.3. Changes in Bacterial Community Composition

The Shannon index of all silage was lower than fresh material, whereas M showed the highest Chao1 index (Figure 2A,B). Figure 2C,D exhibited the relative abundance of bacteria at the genus and species levels. Among all treatments, *L. plantarum* was the predominant species. The bacterial community in M was the most concentrated, with *L. plantarum* showing absolute dominance and accounting for approximately 90%. PCoA analysis showed a clear separation between FM and all silages. The control, A, and E were positioned close to each other, while M was separated from them (Figure 2E). LEfSe analysis in Figure 2F revealed distinct bacterial biomarkers among treatments. The control was enriched in

Levilactobacillus, *Bacillus*, *Enterococcus* and *Pseudomonas*, whereas A was mainly associated with *Hafnia* and *Obesumbacterium*. E showed higher abundances of *Lentilactobacillus*, *Weissella* and *Pantoea vagans*, while M was characterized by *Methylobacterium*, *Sphingomonas*, *Weissella cibaria* and *Pantoea agglomerans*. Notably, the biomarkers enriched in E mainly included LAB associated with carbohydrate fermentation, whereas those enriched in M included taxa previously reported to participate in plant organic matter utilization and lignocellulose degradation. The Spearman's correlation heatmap indicated that *Pantoea vagans*, *Rahnella* sp. AN3-3W3, *Weissella koreensis* and *Leuconostoc mesenteroides* were positively correlated with LA, LDR and xylose. Notably, *Rahnella* sp. AN3-3W3, *Weissella koreensis* and *L. mesenteroides* were negatively correlated with hemicellulose and cellulose.

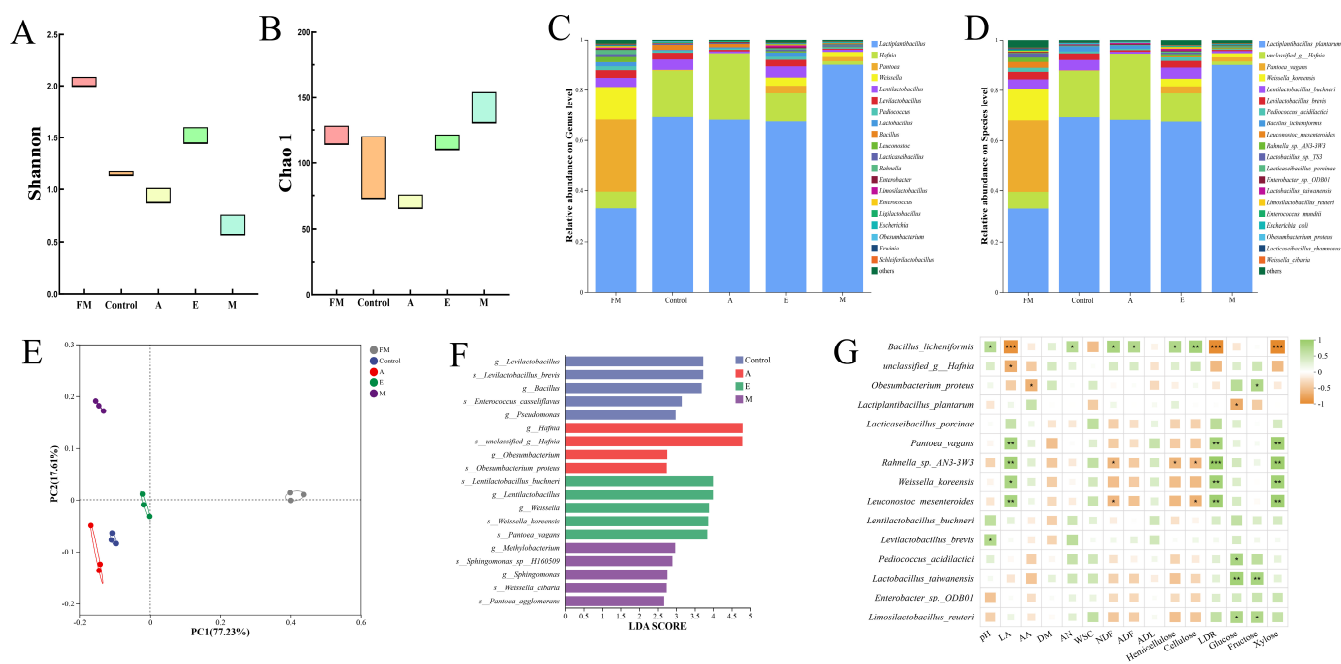


Figure 2. (A) Shannon diversity index; (B) Chao1 index; (C) relative abundance of dominant bacterial genera; (D) relative abundance of dominant bacterial species; (E) principal coordinates analysis (PCoA) of bacterial community structure; (F) LEfSe analysis of bacterial biomarkers; (G) Spearman's correlation heatmap between dominant bacterial taxa and fermentation characteristics, lignocellulose degradation, and carbohydrate conversion parameters. Asterisks indicate significant correlations (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). FM = fresh material of forage oat; control = *L. plantarum* alone; A = *L. plantarum* + formic acid; E = *L. plantarum* + lignocellulolytic enzymes; M = *L. plantarum* + lignocellulolytic microbial consortium.

3.4. Characteristics of Microbial Co-Occurrence Networks

Microbial co-occurrence network complexity was evaluated using topological parameters, including the numbers of nodes and edges, as well as the proportions of positive and negative correlations (Figure 3). Although the node number was similar across treatments, the edge number varied, with M showing the highest edge number, followed by E, control, and A. The negative/positive correlation ratio was highest in A and lowest in E. At the taxonomic level, *L. plantarum*, *unclassified Hafnia*, *P. agglomerans*, *L. lactis*, and *Escherichia coli* were highly connected in the M network, whereas the A network showed fewer connections among bacterial taxa. Overall, M exhibited the highest network complexity based on edge number.

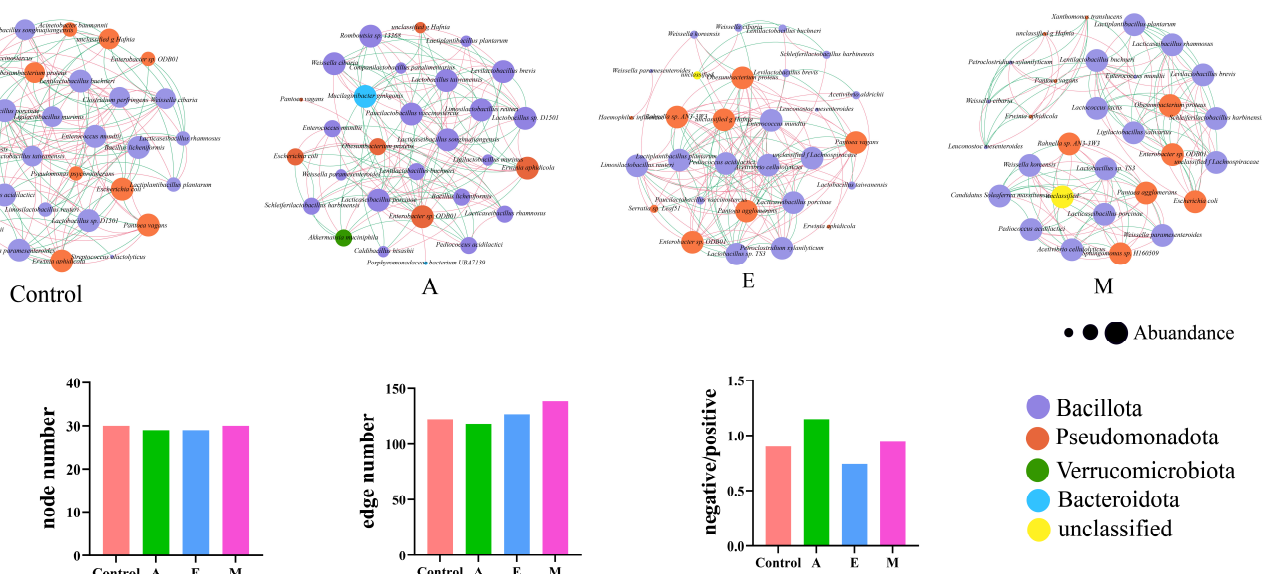


Figure 3. Co-occurrence networks and topological characteristics of bacterial communities in forage oat silages treated with different additives. Nodes represent bacterial taxa, and node size corresponds to relative abundance. Different colors indicate bacterial phyla. Green and red edges indicate positive and negative correlations, respectively. The numbers of nodes and edges were used to evaluate network complexity, whereas the negative/positive correlation ratio was used to assess network potential association. Control = *L. plantarum* alone; A = *L. plantarum* + formic acid; E = *L. plantarum* + lignocellulolytic enzymes; M = *L. plantarum* + lignocellulolytic microbial consortium.

4. Discussion

4.1. Fermentation Quality

Forage oat carried a high lignocellulose content and relatively low population of epiphytic LAB, which limited the rapid dominance of lactic acid fermentation, and additives were needed to regulate the ensiling process. The initial microbial population of forage oat may have influenced fermentation progression and storage stability. In the present study, the fresh forage contained relatively high epiphytic yeast and aerobic bacteria populations, indicating substantial microbial activity before ensiling. These microorganisms may rapidly consume available oxygen and soluble carbohydrates during the early ensiling phase, thereby affecting fermentation dynamics and potential aerobic stability. Lignocellulolytic enzymes in E and the microbial consortium in M may have contributed to lignocellulose degradation and released more fermentable carbohydrates, thereby providing additional substrates for LAB fermentation, increased LA content and reduced pH value [20,21]. The higher LA/AA ratio in E and M indicated that the enzymes and microbial consortium favored homofermentation, which was a more desirable fermentation pattern. The highest WSC content in E was mainly attributed to the addition of lignocellulose degradation enzymes, which disrupted the lignocellulosic structure and released more carbohydrates. In addition, the strong antimicrobial effect of formic acid reduced WSC consumption and exhibited the lowest DML in A during ensiling [22]. The lower AN content suggested that additives reduced protein degradation and deamination during ensiling, thereby contributing to protein preservation and improve fermentation quality, which was consistent with the findings of Zhang et al. [23].

4.2. Lignocellulose Degradation and Carbohydrate Content

The complex and recalcitrant structure of lignin limits its biodegradation during ensiling [24]. Different additive treatments may have degraded NDF, ADF, and ligno-

cellulose through distinct mechanisms. Exogenous lignocellulolytic enzymes (E) acted directly on structural carbohydrates by cleaving the β -1,4-glycosidic bonds in cellulose and hemicellulose/xylan, increasing the accessibility of fermentable carbohydrates for LAB during fermentation [3]. Previous studies have also demonstrated that cellulase addition can enhance cellulose hydrolysis and provide additional soluble carbohydrates for *Lactobacillus* growth, thereby improving fermentation performance during ensiling [25]. However, the released sugars were not completely converted into lactic acid because part of the carbohydrates remained as residual soluble sugars or were diverted to other microbial metabolic pathways. In M, the enhanced lignocellulose degradation was likely associated with the enrichment of lignocellulose-degrading microorganisms. Li et al. [11] reported that a lignocellulose-degrading microbial consortium M2 isolated from yak rumen exhibited high CMCase and xylanase activities, reduced structural carbohydrate contents and pH, increased WSC, monosaccharide and disaccharide contents in rice straw silage, and produced the highest lactic acid content and lignocellulose degradation when combined with LAB. These findings suggest that E mainly enhanced lignocellulose degradation via direct enzymatic hydrolysis, whereas M may be related to microbial community regulation and the potential contribution of lignocellulose-degrading microorganisms. All additives increased the degradation rates of hemicellulose and cellulose, indicating that the treatments enhanced carbohydrate accessibility during ensiling. Among them, E showed the greatest effect, probably because exogenous lignocellulolytic enzymes could directly hydrolyze cellulose and hemicellulose, thereby enhancing the degradation of structural carbohydrates. In contrast, formic acid mainly possessed an acidification effect, whereas it only had a weak hydrolytic effect. Compared with the control, E markedly increased all monosaccharide contents, suggesting that exogenous lignocellulolytic enzymes promoted the hydrolysis of structural carbohydrates and released more soluble sugars. Previous studies have shown that cellulase and xylanase can decompose cellulose into monosaccharides, providing substrates for LAB fermentation and improving carbohydrate utilization during ensiling [4]. The hemicellulose/xylan degradation accounted for the increasing of xylose content in E and M. Sun et al. reported that xylanase-secreting *Pediococcus pentosaceus* improved xylan degradation efficiency and increased hemicellulose degradation during alfalfa ensiling [26]. Meanwhile, *L. plantarum* is a homofermentative LAB that preferentially utilizes hexoses; therefore, cellulose-derived sugars were likely consumed rapidly during ensiling.

4.3. Microbial Community

The different additives reshaped the microbial community structure during ensiling. All silages showed a lower Shannon index than fresh material, indicating that ensiling reduced bacterial diversity. This decrease was likely associated with the anaerobic and acidic conditions created during fermentation, which favored LAB dominance and suppressed many epiphytic microorganisms. In contrast, M showed the highest Chao1 index, suggesting that the microbial consortium increased bacterial richness, possibly by introducing or stimulating lignocellulose-degrading microorganisms. At the genus and species levels, the bacterial community structure changed markedly after ensiling. *L. plantarum* was the dominant bacterial species in all silage treatments, indicating that *L. plantarum* played a central role in lactic acid fermentation and pH reduction. The highest dominance of *L. plantarum* in M may be explained by the addition of a microbial consortium, which promoted lignocellulose degradation and increased substrate availability. These released carbohydrates may not only support the growth of lignocellulolytic microorganisms themselves but also provide substrates for LAB and other carbohydrate-utilizing bacteria through potential co-occurrence, thereby facilitating the establishment of a LAB-dominated fermentation system [27]. In addition, the rapid accumulation of lactic acid and continuously decreased

pH further suppressed competing microorganisms and promoted the strong dominance of *L. plantarum*. This interpretation was supported by Dong et al. [28] and suggested that M not only affected lignocellulose degradation but also optimized the bacterial community structure, leading to a LAB-dominated fermentation system. PCoA analysis indicated that ensiling was the major factor driving bacterial community succession, while M exerted a distinct effect on community structure. LEfSe analysis revealed distinct bacterial biomarkers among treatments. *Lentilactobacillus* and *Weissella* in E were LAB genera that may contribute to heterofermentation, while *Pantoea* may participate in plant-derived carbohydrate utilization. Enzyme addition released more monosaccharides, including pentoses that favored the growth of heterofermentative LAB. This may explain their enrichment in E, although homofermentative fermentation remained dominant. *Sphingomonas* [29] and *Methylobacterium* [30], which were enriched in M, may be associated with lignin-derived compound degradation of plant-derived organic matter utilization, while *Pantoea* strains have been reported to possess lignocellulolytic potential [31]. In addition, *W. cibaria* may contribute to acid production and fermentation improvement. Notably, the high dominance of *L. plantarum* indicated the microbial consortium promoted the establishment of an efficient LAB-dominated fermentation system, thereby contributing to improved fermentation quality. The relationships among bacterial taxa, lignocellulose degradation, and fermentation characteristics were assessed using Spearman's correlation analysis and visualized with a heatmap. *P. vagans*, *R. sp.* AN3-3W3, *W. koreensis*, and *L. mesenteroides* were positively associated with LA, lignocellulose degradation rate, and xylose, suggesting that these taxa may be involved in hemicellulose degradation and lactic acid fermentation. *Rahnella* and *Pantoea* were commonly associated with plant-derived carbohydrate utilization, which may explain their positive correlations with xylose, the major product of hemicellulose/xylanase hydrolysis [32]. Taken together, these associations suggest that the microbial consortium may have contributed to improved ensiling performance through a synergistic two-pronged strategy, simultaneously enhancing lignocellulose degradation and improving fermentation characteristics.

4.4. Microbial Co-Occurrence Network Analysis

Microbial co-occurrence network analysis was used to explore the co-occurrence among bacterial taxa (Figure 3). The number of nodes was similar across all treatments, indicating a comparable richness of taxa included in these networks. However, the number of edges differed among treatments, reflecting differences in the co-occurrence network topology. The M treatment exhibited the highest edge numbers, followed by E, control, and A, which suggested a more complex co-occurrence pattern in the M treatment. At the taxonomic level, *L. plantarum*, unclassified *Hafnia*, *P. agglomerans*, *L. lactis*, and *E. coli* were highly connected in M, indicating that these taxa occupied central positions within the network. In contrast, the network of A showed fewer connections, implying similar and fewer potential associations among bacterial taxa. The negative/positive correlation ratio was the highest in A and the lowest in E, indicating different balances between negative and positive associations among treatments. Based on this metric, E showed the lowest negative-to-positive correlation ratio, whereas M exhibited the highest network connectivity. Overall, these results suggest the M showed a higher co-occurrence network complexity, which may reflect enhanced potential associations among bacterial taxa. This may facilitate lignocellulose degradation and lactic acid fermentation quality during ensiling. However, these inferences were based on co-occurrence network and correlation analyses. Future studies integrating functional validation and multi-omics approaches will be valuable for elucidating the mechanisms underlying microbial consortium-mediated lignocellulose degradation during ensiling.

5. Conclusions

Both lignocellulolytic enzymes (E) and the microbial consortium (M) effectively improved the fermentation quality of forage oat silage by enhancing lignocellulose utilization and promoting lactic acid fermentation. E exhibited the greatest lignocellulose degradation and carbohydrate release, demonstrating the high efficiency of direct enzymatic hydrolysis in converting structural carbohydrates into fermentable substrates. In contrast, M more effectively reshaped the bacterial community and exhibited higher co-occurrence network complexity, whereas E showed a lower negative/positive correlation ratio. These network characteristics suggest that the enzyme and microbial consortium treatments were associated with different bacterial community organization patterns. Overall, E primarily improved silage quality through direct lignocellulose degradation, whereas M was associated with pronounced changes in bacterial community composition and co-occurrence patterns. These findings suggest that the microbial consortium represents a promising strategy for improving the preservation and utilization of high-lignocellulose forage oat silage, although the underlying microbial mechanisms require further investigation.

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Abbreviations

The following abbreviations are used in this manuscript:

A	<i>Lactiplantibacillus plantarum</i> + formic acid treatment
AA	Acetic acid
ADF	Acid detergent fiber
ADL	Acid detergent lignin
ADLDR	Acid detergent lignin degradation rate
AN	Ammonia-N
BA	Butyric acid
CDR	Cellulose degradation rate
Control	<i>Lactiplantibacillus plantarum</i> alone
CP	Crude protein
DM	Dry matter
DML	Dry matter loss
E	<i>Lactiplantibacillus plantarum</i> + lignocellulolytic enzyme treatment
FM	Fresh material
HDR	Hemicellulose degradation rate

LAB	Lactic acid bacteria
LA	Lactic acid
LDR	Lignocellulose degradation rate
M	<i>Lactiplantibacillus plantarum</i> + lignocellulose-degrading microbial consortium treatment
NDF	Neutral detergent fiber
PA	Propionic acid
TN	Total nitrogen
WSC	Water-soluble carbohydrates

References

1. Muck, R.E.; Nadeau, E.M.G.; McAllister, T.A.; Contreras-Govea, F.E.; Santos, M.C.; Kung, L., Jr. Silage Review: Recent Advances and Future Uses of Silage Additives. *J. Dairy Sci.* **2018**, *101*, 3980–4000. [[CrossRef](#)] [[PubMed](#)]
2. Kung, L.; Shaver, R.D.; Grant, R.J.; Schmidt, R.J. Silage Review: Interpretation of Chemical, Microbial, and Organoleptic Components of Silages. *J. Dairy Sci.* **2018**, *101*, 4020–4033. [[CrossRef](#)] [[PubMed](#)]
3. Mu, L.; Wang, Q.; Wang, Y.; Zhang, Z. Effects of Cellulase and Xylanase on Fermentative Profile, Bacterial Diversity, and in Vitro Degradation of Mixed Silage of Agro-Residue and Alfalfa. *Chem. Biol. Technol. Agric.* **2023**, *10*, 40. [[CrossRef](#)]
4. Qiu, C.; Liu, N.; Diao, X.; He, L.; Zhou, H.; Zhang, W. Effects of Cellulase and Xylanase on Fermentation Characteristics, Chemical Composition and Bacterial Community of the Mixed Silage of King Grass and Rice Straw. *Microorganisms* **2024**, *12*, 561. [[CrossRef](#)] [[PubMed](#)]
5. Li, J.; Wu, Y.; Zhao, J.; Wang, S.; Dong, Z.; Shao, T. Bioaugmented Degradation of Rice Straw Combining Two Novel Microbial Consortia and Lactic Acid Bacteria for Enhancing the Methane Production. *Bioresour. Technol.* **2022**, *344*, 126148. [[CrossRef](#)] [[PubMed](#)]
6. Puentes-Téllez, P.E.; Falcao Salles, J. Construction of Effective Minimal Active Microbial Consortia for Lignocellulose Degradation. *Microb. Ecol.* **2018**, *76*, 419–429. [[CrossRef](#)] [[PubMed](#)]
7. Ni, K.; Wang, F.; Zhu, B.; Yang, J.; Zhou, G.; Pan, Y.I.; Tao, Y.; Zhong, J. Effects of Lactic Acid Bacteria and Molasses Additives on the Microbial Community and Fermentation Quality of Soybean Silage. *Bioresour. Technol.* **2017**, *238*, 706–715. [[CrossRef](#)] [[PubMed](#)]
8. Bai, J.; Ding, Z.; Su, R.; Wang, M.; Cheng, M.; Xie, D.; Guo, X. Storage Temperature Is More Effective Than Lactic Acid Bacteria Inoculations in Manipulating Fermentation and Bacterial Community Diversity, Co-Occurrence and Functionality of the Whole-Plant Corn Silage. *Microbiol. Spectr.* **2022**, *10*, e00101-22. [[CrossRef](#)] [[PubMed](#)]
9. Baytok, E.; Aksu, T.; Karsli, M.; Muruz, H. The Effects of Formic Acid, Molasses and Inoculant as Silage Additives on Corn Silage Composition and Ruminal Fermentation Characteristics in Sheep. *Turk. J. Vet. Anim. Sci.* **2005**, *29*, 469–474.
10. Liu, W.; Si, Q.; Sun, L.; Wang, Z.; Liu, M.; Du, S.; Ge, G.; Jia, Y. Effects of Cellulase and Xylanase Addition on Fermentation Quality, Aerobic Stability, and Bacteria Composition of Low Water-Soluble Carbohydrates Oat Silage. *Fermentation* **2023**, *9*, 638. [[CrossRef](#)]
11. Li, J.; Ding, H.; Zhao, J.; Wang, S.; Dong, Z.; Shao, T. Characterization and Identification of a Novel Microbial Consortium M2 and Its Effect on Fermentation Quality and Enzymatic Hydrolysis of Sterile Rice Straw. *J. Appl. Microbiol.* **2022**, *132*, 1687–1699. [[CrossRef](#)] [[PubMed](#)]
12. Huang, Y.; Zhang, S.; Hu, M.; Yang, S.; Hui, A.; Zhang, W.; Wu, Z. Effects of Biological Additives on the Fermentation Quality and Microbial Community of High-Moisture Oat Silage. *Agriculture* **2024**, *14*, 2275. [[CrossRef](#)]
13. Broderick, G.A.; Kang, J.H. Automated Simultaneous Determination of Ammonia and Total Amino Acids in Ruminal Fluid and In Vitro Media. *J. Dairy Sci.* **1980**, *63*, 64–75. [[CrossRef](#)] [[PubMed](#)]
14. Murphy, R.P. A Method for the Extraction of Plant Samples and the Determination of Total Soluble Carbohydrates. *J. Sci. Food Agric.* **1958**, *9*, 714–717. [[CrossRef](#)]
15. Krishnamoorthy, U.; Muscato, T.V.; Sniffen, C.J.; Van Soest, P.J. Nitrogen Fractions in Selected Feedstuffs. *J. Dairy Sci.* **1982**, *65*, 217–225. [[CrossRef](#)]
16. Weiß, K.; Alt, M. Determination of Single Sugars, Including Inulin, in Plants and Feed Materials by High-Performance Liquid Chromatography and Refraction Index Detection. *Fermentation* **2017**, *3*, 36. [[CrossRef](#)]
17. Van Soest, P.J.; Robertson, J.B.; Lewis, B.A. Methods for Dietary Fiber, Neutral Detergent Fiber, and Nonstarch Polysaccharides in Relation to Animal Nutrition. *J. Dairy Sci.* **1991**, *74*, 3583–3597. [[CrossRef](#)] [[PubMed](#)]
18. Coblenz, W.K.; Akins, M.S.; Kalscheur, K.F.; Brink, G.E.; Cavadini, J.S. Effects of Growth Stage and Growing Degree Day Accumulations on Triticale Forages: 1. Dry Matter Yield, Nutritive Value, and in Vitro Dry Matter Disappearance. *J. Dairy Sci.* **2018**, *101*, 8965–8985. [[CrossRef](#)] [[PubMed](#)]
19. Luo, X.; Liu, Y.; Wang, X.; Lei, L.; Shen, J.; Zhang, Q.; Wang, Y.; Ruan, R.; Cui, X. A Co-Ensiling Strategy of Food Wastes: Peanut Shell as an Additive to Distillers' Grains to Improve Efficiency of Energy Conversion. *J. Clean. Prod.* **2023**, *423*, 138710. [[CrossRef](#)]

20. Xu, J.; Zhang, K.; Lin, Y.; Li, M.; Wang, X.; Yu, Q.; Sun, H.; Cheng, Q.; Xie, Y.; Wang, C. Effect of Cellulase and Lactic Acid Bacteria on the Fermentation Quality, Carbohydrate Conversion, and Microbial Community of Ensiling Oat with Different Moisture Contents. *Front. Microbiol.* **2022**, *13*, 1013258. [[CrossRef](#)] [[PubMed](#)]
21. Chen, C.; Xin, Y.; Li, X.; Ni, H.; Zeng, T.; Du, Z.; Guan, H.; Wu, Y.; Yang, W.; Cai, Y. Effects of *Acremonium* Cellulase and Heat-Resistant Lactic Acid Bacteria on Lignocellulose Degradation, Fermentation Quality, and Microbial Community Structure of Hybrid Elephant Grass Silage in Humid and Hot Areas. *Front. Microbiol.* **2022**, *13*, 1066753. [[CrossRef](#)] [[PubMed](#)]
22. Lei, Y.; Li, M.; Liu, Y.; Wang, J.; He, X.; Zhao, Y.; Chen, Y.; Cheng, Q.; Chen, C. Lactic Acid Bacteria and Formic Acid Improve Fermentation Quality and Beneficial Predicted Functional Characteristics in Mixed Silage Consisting of Alfalfa and Perennial Ryegrass. *Fermentation* **2024**, *10*, 43. [[CrossRef](#)]
23. Zhang, X.; Meng, Y.; Xu, L. Lactic Acid Bacteria Additives Effectively Regulate Nitrogen Compounds and Related Bacterial Communities in Silage Infected with Leaf Spot Disease. *Front. Anim. Sci.* **2025**, *6*, 1577383. [[CrossRef](#)]
24. Hsin, K.-T.; Lee, H.; Huang, Y.-C.; Lin, G.-J.; Lin, P.-Y.; Lin, Y.-C.J.; Chen, P.-Y. Lignocellulose Degradation in Bacteria and Fungi: Cellulosomes and Industrial Relevance. *Front. Microbiol.* **2025**, *16*, 1583746. [[CrossRef](#)] [[PubMed](#)]
25. Xiong, H.; Zhu, Y.; Wen, Z.; Liu, G.; Guo, Y.; Sun, B. Effects of Cellulase, *Lactobacillus plantarum*, and Sucrose on Fermentation Parameters, Chemical Composition, and Bacterial Community of Hybrid Pennisetum Silage. *Fermentation* **2022**, *8*, 356. [[CrossRef](#)]
26. Sun, J.; Zhang, Y.; Zhao, Y.; Wang, Z.; Miao, X.; Huo, W.; Chen, L.; Liu, Q.; Wang, C.; Guo, G. Enhancing Alfalfa Hemicellulose Degradation by Anaerobic Bioprocessing with Engineered Xylanase-Secreting *Pediococcus pentosaceus*. *J. Agric. Food Chem.* **2025**, *73*, 22563–22576. [[CrossRef](#)] [[PubMed](#)]
27. Guo, X.; Xu, D.; Li, F.; Bai, J.; Su, R. Current Approaches on the Roles of Lactic Acid Bacteria in Crop Silage. *Microb. Biotechnol.* **2023**, *16*, 67–87. [[CrossRef](#)] [[PubMed](#)]
28. Dong, J.; Li, S.; Chen, X.; Sun, Z.; Sun, Y.; Zhen, Y.; Qin, G.; Wang, T.; Demelash, N.; Zhang, X. Effects of *Lactiplantibacillus plantarum* Inoculation on the Quality and Bacterial Community of Whole-Crop Corn Silage at Different Harvest Stages. *Chem. Biol. Technol. Agric.* **2022**, *9*, 57. [[CrossRef](#)]
29. Li, X.; Li, Z.; Li, M.; Li, J.; Wang, Q.; Wang, S.; Li, S.; Li, H. Transcriptomic and Metabolomic Analysis Reveals the Influence of Carbohydrates on Lignin Degradation Mediated by *Bacillus amyloliquefaciens*. *Front. Microbiol.* **2024**, *15*, 1224855. [[CrossRef](#)] [[PubMed](#)]
30. Tao, X.; Feng, J.; Yang, Y.; Wang, G.; Tian, R.; Fan, F.; Ning, D.; Bates, C.T.; Hale, L.; Yuan, M.M.; et al. Winter Warming in Alaska Accelerates Lignin Decomposition Contributed by *Proteobacteria*. *Microbiome* **2020**, *8*, 84. [[CrossRef](#)] [[PubMed](#)]
31. Yao, Q.; Huang, M.; Bu, Z.; Zeng, J.; Wang, X.; Liu, Z.; Ma, J.; Zhang, K.; Liu, X.; Zhu, Y. Identification and Characterization of a Novel Bacterial Carbohydrate Esterase from the Bacterium *Pantoea ananatis* Sd-1 with Potential for Degradation of Lignocellulose and Pesticides. *Biotechnol. Lett.* **2020**, *42*, 1479–1488. [[CrossRef](#)] [[PubMed](#)]
32. Pineda-Mendoza, R.M.; Zúñiga, G.; López, M.F.; Hidalgo-Lara, M.E.; Santiago-Hernández, A.; López-López, A.; Orduña, F.N.R.; Cano-Ramírez, C. *Rahnella* sp., a Dominant Symbiont of the Core Gut Bacteriome of *Dendroctonus* Species, Has Metabolic Capacity to Degrade Xylan by Bifunctional Xylanase-Ferulic Acid Esterase. *Front. Microbiol.* **2022**, *13*, 911269. [[CrossRef](#)] [[PubMed](#)]

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