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MINI REVIEW

Current approaches on the roles of lactic acid bacteria in crop silage

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Abstract

Lactic acid bacteria (LAB) play pivotal roles in the preservation and fermentation of forage crops in spontaneous or inoculated silages. Highlights of silage LAB over the past decades include the discovery of the roles of LAB in silage bacterial communities and metabolism and the exploration of functional properties. The present article reviews published literature on the effects of LAB on the succession, structure, and functions of silage microbial communities involved in fermentation. Furthermore, the utility of functional LAB in silage preparation including feruloyl esterase-producing LAB, antimicrobial LAB, lactic acid bacteria with high antioxidant potential, pesticide-degrading LAB, lactic acid bacteria producing 1,2-propanediol, and low-temperature-tolerant LAB have been described. Compared with conventional LAB, functional LAB produce different effects; specifically, they positively affect animal performance, health, and product quality, among others. In addition, the metabolic profiles of ensiled forages show that plentiful probiotic metabolites with but not limited to antimicrobial, antioxidant, aromatic, and anti-inflammatory properties are observed in silage. Collectively, the current knowledge on the roles of LAB in crop silage indicates there are great opportunities to develop silage not only as a fermented feed but also as a vehicle of delivery of probiotic substances for animal health and welfare in the future.

INTRODUCTION

Silage is known as “canned grass” for ruminants, providing them with green fodder throughout the year; it can aid in preserving green plants and has been studied for almost 180 years as recorded (Wilkinson et al., 2003). In conventional fermentation of silage, water-soluble carbohydrates (WSC) are primarily converted to organic acid mixtures by epiphytic lactic acid bacteria (LAB); this lowers pH and preserves forage under anaerobic conditions (Broberg et al., 2007). In order to further improve the fermentation quality, different silage LAB additives have been developed to improve the quality of silage fermentation and the effects of these LAB on silage fermentation, aerobic stability, and animal productivity have been well summarised (Kim et al., 2021; Muck et al., 2018; Shah et al., 2017, 2018). Lactic acid bacteria are involved in the preservation and fermentation of forage crops in inoculated silages.

Typically, the ensiling process of forage crops is dominated by LAB, and alterations in microbial communities are closely related to silage fermentation (Figure 1; Driehuis et al., 2018). In addition, poorly fermented or contaminated silage can serve as a source of pathogenic bacteria or other undesirable microbes (Driehuis et al., 2018; Queiroz et al., 2018). Lactic acid bacteria inoculants are widely used to ensure silage quality by improving the fermentation process and aerobic stability of silage. Numerous studies have demonstrated that the application of LAB inoculants during ensiling could reduce silage pH and enhance silage

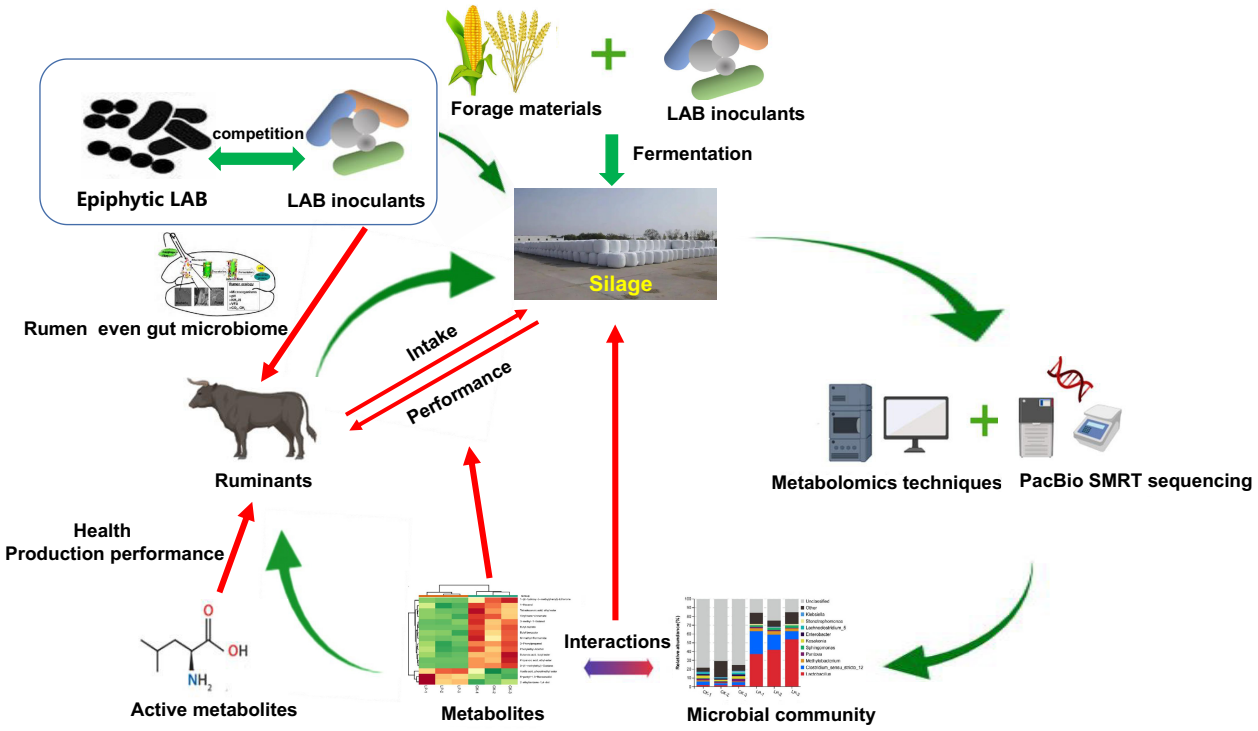

FIGURE 1 Associations among lactic acid bacteria, silage, and animals.

preservation (Muck et al., 2018). Thus, changes in silage bacterial communities must be profiled to enhance our understanding of the contribution of LAB inoculants to silage fermentation. Corroborating this notion, Bai et al. (2021) and Xu, Wang, et al. (2021) reported that LAB inoculants could modulate microbial community dynamics and functional shifts during the ensiling process. Moreover, the complex metabolic pathways during ensiling are regulated by inoculants through the degradation of forage substrates and the transformation of metabolites (Xu, Wang, et al., 2021). The metabolites produced by LAB in silage directly affect silage fermentation quality; furthermore, the assessment of metabolites of ensiling systems can provide important information regarding nutritional value and fermentation quality of the silage, and its impacts on animal health and welfare (Figure 1; Xu, Ding, et al., 2019). With advances in technology, the roles of LAB in silage can be explored continuously through studies of the microbiome and metabolome.

Currently, research on silage LAB is driven by novel innovations to fulfil human requirements, such as food safety, feed nutritional value, health benefits, and even animal welfare (Queiroz et al., 2018). For instance, at the XVIII International Silage Conference, Wilkinson and Muck (2018) proposed some approaches to using LAB during ensiling to improve silage hygiene and sustainably increase silage nutrient availability. Moreover, Leandro et al. (2021) suggested the investigation of novel strains of LAB with specific functions from infrequently explored sources, which may reveal strains that are more promising in terms of probiotic potential and may be useful for industrial and animal health applications. In this context, research on functional LABs, also known as silage LABs with such properties, has advanced significantly over the past few years. Besides organic acid, LAB produces 1,2-propanediol, bacteriocins, 3-phenyllactic acid, aromatic compounds, exopolysaccharides, enzymes, and vitamins, as well as exhibit other properties, such as pesticide degradability and relatively high antioxidant activity (Broberg et al., 2007; Ding et al., 2017; Florou-Paneri et al., 2013; Leroy & De Vuyst, 2004; Mohammadi et al., 2021). These LAB present at least one functional property, contributing in improving the fermentation process, enhance the silage quality, and increase the digestibility and safety of end silage to confer health benefits for both humans and other animals.

To this end, the present review discusses the impacts of LAB on silage microbiome and metabolome, which further affect silage fermentation quality and aerobic stability. Furthermore, we summarise the novel functions of silage LAB by screening and focussing on recent literature pertaining to silage production and its potential impacts on animal health and productivity as well as animal product quality. Therefore, the present review offers novel insights into and sheds light on the roles of LAB in crop silage.

LACTIC ACID BACTERIA MODULATING MICROBIAL COMMUNITY STRUCTURE AND FUNCTION IN SILAGE

To uncover the structure and composition of microbial communities in fresh and ensiled forages, molecular technologies, such as denaturing gradient gel electrophoresis (DGGE), real-time PCR, ribosomal intergenic spacer analysis, and terminal restriction fragment length polymorphism (Brusetti et al., 2011; Li & Nishino, 2011; Pang et al., 2011; Stevenson et al., 2006), have been used over past decades. However, these techniques only displayed partial microorganisms that researchers aimed to detect. Next-generation sequencing (NGS) and PacBio single-molecule real-time sequencing technology (SMRT) offer high-throughput and enable the discovery of a vast majority of microbiota and relative abundances of various microbes in the community to the genus and species precision (Mayo et al., 2014; McAllister et al., 2018; Schloss et al., 2016). The present section primarily focused on the roles of LAB in microbial communities in silages, as revealed by NGS and SMRT. Notwithstanding, many of the epiphytic microbiomes in forages before ensiling cannot be classified to the genus level.

Lactic acid bacteria modulating microbial communities in corn silage

Whole-plant corn silage is the predominant forage used in ruminant dairy ration worldwide and can be naturally fermented due to its high WSC content and sufficient epiphytic LAB abundance. Generally, most epiphytic bacteria of fresh whole-plant corn are undesirable microorganisms, such as *Xanthomonadaceae*, *Sphingobacteriaceae*, *Enterobacteriaceae*, *Moraxellaceae*, and *Meyerozyma*, *Acinetobacter*, *Klebsiella*, *Acremonium*, *Agrobacterium*, *Microbacterium*, *Chryseobacterium*, *Klebsiella*, and *Candida* genus (da Silva et al., 2020; Guan et al., 2018; Guan, Shuai, Yan, et al., 2020; Keshri et al., 2018; Xu, Ding, et al., 2019; Xu, Wang, et al., 2021). Although there are great differences in the composition of epiphytic microbial communities in whole-plant corn silage, the constellation of the microbiome, which develops during the ensilage process, differs markedly from that of the epiphytic one (Gharechahi et al., 2017); as such, the relative abundance of LAB often increases after ensiling, and they dominate silage fermentation at the later stages. NGS analysis revealed that corn silage is mainly dominated by the LAB genera *Lactobacilli*, *Leuconostoc*, *Pediococcus*, and *Weissella* at the initial stage of ensiling (Guan et al., 2018; Wang, Gao, et al., 2021; Zhang, Liu, et al., 2020); however, *Lactobacilli* becomes dominant bacteria at the later stages (Gharechahi et al., 2017; Sun, Bai, et al., 2021; Wang, Franco, et al., 2020).

Recent studies have investigated differences in the microbial communities of various LAB-inoculated versus untreated corn silages using SMRT. For instance, Xu, Yang, et al. (2019) found that the addition of *Lactobacillus* (*Lentilactobacillus*) *buchneri* combined with *Saccharomyces cerevisiae* did not affect total yeast, bacterial, and fungal communities in corn silage during ensiling and aerobic exposure. Meanwhile, the abundance of *Lactobacilli* in silages treated with *Lactobacillus acidophilus* and *Lactobacillus* (*Lactiplantibacillus*) *plantarum* was high after 45 and 90 days of ensiling (Jiang et al., 2020). Guan, Shuai, Yan, et al. (2020) found that inoculating *Lactobacillus* (*Ligilactobacillus*) *salivarius* 358 and *Lactobacillus* (*Lacticaseibacillus*) *rhamnosus* 753 in corn silage at 30°C affected bacterial communities throughout the ensiling process, resulting in a gradual shift in dominant bacterial genera from *Pediococcus* and *Lactobacilli* to just *Lactobacilli*. In addition, the *Lactobacillus* (*Lactiplantibacillus*) *plantarum* inoculant primarily modulated the bacterial communities at the early and middle stages of ensiling, while the *Lactobacillus* (*Lentilactobacillus*) *buchneri* inoculant modulated the bacterial communities at the late stages (Bai et al., 2021; Xu, Wang, et al., 2021). Moreover, the inoculants modulated the keystone species of LAB (independent of abundance) that affect the silage fermentation process. For instance, *Lentilactobacillus buchneri*, *Lentilactobacillus parafarraginis* (formerly *Lactobacillus parafarraginis*), and *Levilactobacillus hammesii* (formerly *Lactobacillus hammesii*) in untreated corn silage, *Limosilactobacillus panis* (formerly *Lactobacillus panis*) in *Lactobacillus* (*Lentilactobacillus*) *buchneri*-treated silage, and *Companilactobacillus crustorum* (formerly *Lactobacillus crustorum*) in *Lactobacillus* (*Lactiplantibacillus*) *plantarum*-treated silage were considered keystone taxa, which play crucial roles in the relevant LAB treatments of whole-plant corn silages (Xu, Wang, et al., 2021). Moreover, inoculants modified the interaction between fermentation quality and microorganisms. For instance, *Lactobacillus acetotolerans* in uninoculated silage, *Secundilactobacillus odoratitofui* (formerly *Lactobacillus odoratitofui*) and *Limosilactobacillus panis* in *Lactobacillus* (*Lentilactobacillus*) *buchneri*-inoculated silage, and *Lentilactobacillus parafarraginis* and *Lentilactobacillus kefiri* (formerly *Lactobacillus kefiri*) in *Lactobacillus* (*Lactiplantibacillus*) *plantarum*-inoculated silage were positively correlated with fermentation quality (Xu, Wang, et al., 2021). Furthermore, silages with improved fermentation quality following inoculant treatment exhibited simplified bacterial correlation structures (Bai et al., 2021).

Lactic acid bacteria modulating microbial communities in alfalfa silage

According to McAllister et al. (2018), microbial populations associated with alfalfa silages are more diverse than those associated with cereal silages; this results in the growth of undesirable microbes during ensiling and deterioration of fermentation quality. With advances in sequencing technology, studies have found that the composition of epiphytic microorganisms on the surface of fresh alfalfa is rather diverse due to differences in raw material varieties as well as harvesting areas and time; however, most of the epiphytic microorganisms are mainly undesirable bacteria, and the key species of LAB involved in silage fermentation account for only a small percentage (Guo et al., 2018; Hu et al., 2020; Yang et al., 2019, 2020). Undesirable microorganisms on the alfalfa surface before ensiling mainly include *Pantoea*, *Streptococcus*, *Enterobacter*, *Bacillus*, *Pseudomonas*, *Exiguobacterium*, *Massilla*, *Planococcus*, *Sphingobium*, *Acinetobacter*, and *Clostridium* (Bai et al., 2021). When fermentation is initiated, the dominant flora changes rapidly, and the community composition is completely altered from undesirable bacteria to LAB that dominate silage fermentation. Lactic acid bacteria that dominate alfalfa silage fermentation primarily include *Lactiplantibacillus* and *Lentilactobacillus* (formerly *Lactobacillus*), *Weissella*, *Lactococcus*, *Enterococcus*, and *Pediococcus* species (Guo et al., 2018; Hu et al., 2020; Yang et al., 2019, 2020).

The inoculation of LAB remarkably affects the composition and succession of microbial communities during the ensiling process of alfalfa silage. *Lactobacillus* (*Lactiplantibacillus*) *plantarum* is a common LAB additive to alfalfa silage. Moreover, when alfalfa was inoculated with *Lactobacillus* (*Lactiplantibacillus*) *plantarum*, *Lactobacilli* was the dominant bacterium associated with the fermentation of alfalfa silage (Yang et al., 2020). Even in high-moisture alfalfa silage, the inoculation of *Lactobacillus* (*Lactiplantibacillus*) *plantarum* increased the abundance of *Lactobacilli* and inhibited the growth of *Clostridium* (Yang et al., 2020; Zheng et al., 2017). A strain of *Lactobacillus* (*Lactiplantibacillus*) *plantarum* isolated from rumen fluid and dairy cow faeces could increase the relative abundance of *Lactobacilli* in alfalfa silage (Guo et al., 2020). Interestingly, when alfalfa silage was inoculated with *Pediococcus pentosaceus* or *Lactobacillus* (*Lactiplantibacillus*) *plantarum*, *Lactobacillus* (*Lactiplantibacillus*) *plantarum* decreased the relative abundance of *Pediococcus pentosaceus*, while *Pediococcus pentosaceus* promoted the growth of *Lactiplantibacillus plantarum* during the ensiling process. Furthermore, it was reported that different LAB inoculants altered the keystone taxa of alfalfa silage, further affecting microbiota structure and silage quality. Meanwhile, high-fermentation quality silage inoculated with LAB showed simplified bacterial correlation structures (Bai et al., 2021).

Lactic acid bacteria modulating microbial communities in grass silage

In addition to whole-plant corn and alfalfa silages, grass silages prepared from barley, ryegrass, oat, and other grasses are commonly used as ruminant feed worldwide. The ensiling characteristics of grasses differ from those of legumes (e.g. alfalfa) or whole-plant corn. Thus, the microbial composition and changes in grass silages are rather different from those in corn and alfalfa silages throughout the ensiling process. In addition, inoculants evidently affect the composition of microbial communities in grass silages.

Barley silage

Barley (*Hordeum vulgare*) is tolerant to diverse growth conditions and is widely cultivated worldwide. Owing to its excellent nutritional quality and high palatability, barley is mostly used as animal feed in the form of silage (Newton et al., 2011). Barley is relatively easy to ensile because of its low buffering capacity and abundant fermentable carbohydrates. Furthermore, LABs are often used to improve the aerobic stability of barley silage. Liu et al. (2019, 2020) reported that in barley silage, *Lactobacilli* inoculants (including *Lactobacillus* (*Lactiplantibacillus*) *plantarum*, *Lactobacillus* (*Lacticaseibacillus*) *casei*, and *Lactobacillus* (*Lentilactobacillus*) *buchneri*) decreased the diversity of bacterial communities during ensiling, while aerobic exposure increased the diversity of fungal communities. Spontaneous barley silages were dominated by *Lactobacilli*, *Weissella*, and *Pediococcus* species. The addition of *Lactobacilli* inoculants increased the abundance of *Lactobacilli* but decreased the abundance of *Pediococcus* and *Weissella* during ensiling, while aerobic exposure decreased the abundance of *Acinetobacter* and *Empedobacter* (Liu et al., 2019, 2020). Moreover, the addition of inoculants combined with molasses decreased the abundance of *Acinetobacter* and *Enterococcus* in barley silage following aerobic exposure of 5 and 7 days (Liu et al., 2020).

Ryegrass silage

Ryegrass is the principal grass used to produce silage in temperate regions. Annual ryegrass silage is dominated by *Lactobacilli* and *Pediococcus* species. Meanwhile, the inoculation of *Lactobacillus (Lactiplantibacillus) plantarum* plus *Lactobacillus* (*Lentilactobacillus buchneri*) inoculants increased the abundance of *Sporolactobacillus* but decreased the abundance of *Lactobacilli* and *Pediococcus* (Li, Zhang, et al., 2019). Epiphytic bacteria in Italian ryegrass include *Psychrobacter*, *Lactococcus*, *Lactobacilli*, *Pseudomonas*, and *Camobacterium*

species (Wang, Sun, et al., 2020; Yan et al., 2019). *Lactobacilli*, *Lactococcus*, and *Enterococcus* species are the dominant bacteria in spontaneous Italian ryegrass silage. Following the inoculation of *Lactobacillus (Lactiplantibacillus) plantarum* 694 or commercial *Lactobacillus (Lactiplantibacillus) plantarum*, bacterial diversity decreased, and *Lactiplantibacillus plantarum* became the dominant species (Yan et al., 2019). Wang, Shao, et al. (2022) investigated the effect of epiphytic microbiota from alfalfa and red clover on the composition of bacterial communities in Italian ryegrass silage and found that *Lactobacilli* was the dominant genus on days 3 and 60 of ensiling. Furthermore, Parvin et al. (2010) showed that the inoculation of LAB, such as *Lactobacillus (Lactiplantibacillus) plantarum* and *Lactobacillus* (*Levilactobacillus*) *brevis*, nearly eliminated indigenous bacterial communities in wilted Italian ryegrass silage, leaving the inoculated species as the dominant bacteria.

Oat silage

Oat (*Avena sativa* L.) is distributed in over 40 countries worldwide, being primarily concentrated in northern regions at approximately 40° north latitudes, including Asia, Europe, and North America. Oat silage is an ideal feed for providing energy to livestock in cold regions. Through high-throughput sequencing analysis, epiphytic microorganisms of fresh oat were found to mainly include *Pantoea*, *Pseudomonas*, *Sphingomonas*, *Clostridium*, *Anaerotruncus*, and *Lactobacilli* (Chen et al., 2020; Cheng, Chen, Chen, & Chen, 2021). After ensiling, the microbial composition was completely altered, and LAB became the dominant bacteria. According to Chen et al. (2020), the dominant bacteria of oat silage were *Lactobacilli* and *Leuconostoc* after 30, 60, and 90 days of ensiling. In addition, the effects of LAB inoculants on oat silage were evident. Inoculation with *Lactobacillus (Lactiplantibacillus) plantarum* decreased the bacterial diversity and increased the relative abundance of *Lactobacilli* in oat silage after ensiling (Cheng, Chen, Chen, & Chen, 2021; Xiong et al., 2022). Temperature strongly affects the composition of microbial communities in oat silage. *Enterococcus* was the only dominant bacteria in oat silage when stored at 5°C after 60 days of ensiling. The relative abundance of *Lactobacilli* increased and that of *Enterococcus* decreased with an increase in storage temperature (Li, Chen, et al., 2021).

Leymus chinensis silage

Leymus chinensis is a native cool-season perennial grass, which is primarily distributed throughout temperate northern Asia (Zhang & Yu, 2017). As a major forage source, *Leymus chinensis* has been used for silage production in meadows and typical steppes of Inner Mongolia in Northern China (Zhang et al., 2016). The microflora of fresh *Leymus chinensis* mainly includes *Pantoea*, *Escherichia*, *Kosakonia*, *Enterobacter*, and *Atlantibacter*, while *Enterobacteriaceae* dominate the bacterial community in spontaneous *Leymus chinensis* silage (Xu, Sun, et al., 2021).

In LAB-treated (including *Lactobacillus* (*Lactiplantibacillus*) *plantarum* and *Lactobacillus* (*Lacticaseibacillus*) *casei*) *Leymus chinensis* silage, *Lactobacilli* was the most prevalent bacterial genus (>97%); its abundance negatively correlated with that of the other major genera (such as *Pantoea*, *Escherichia*, *Atlantibacter*, *Kosakonia*, and *Enterobacter*) and with pH, but positively correlated with concentrations of lactic and acetic acid (Xu, Sun, et al., 2021). Zhang et al. (2016) also reported that high-quality *Leymus chinensis* silage could be obtained with the addition of LAB strains during ensiling.

Lactic acid bacteria modulating microbial communities in tropical silage

Silage preparation requires special consideration due to the peculiar climatic circumstances in tropical areas. *Clostridium* in tropical grass silages prefer humid environments to effectively inhibit the reduction in pH and lead to spoilage of silage. In addition, under warm conditions, silages are vulnerable to aerobic spoilage. These attributes are mainly affected by epiphytic microbial communities in tropical forages.

Tropical legume silage

Stylo and alfalfa are critical legume forages for ruminants and are widely cultivated in tropical and subtropical regions. However, a lower concentration of WSC in legumes renders the preparation of high-quality silage challenging (Li et al., 2017). *Exiguobacterium* was the dominant bacteria in tropical stylo and alfalfa before ensiling, whereas *Exiguobacterium*, *Lactobacilli*, and *Enterobacter* were abundant in spontaneous alfalfa silage (Wang, He, Xing, Zhou, Yang, et al., 2019). Zou et al. (2021) found that *Cronobacter*, *Methylobacterium*, and *Enterococcus* were the predominated genera in naturally fermented stylo silage, whereas Zi et al. (2022) reported *Weissella*, *Enterobacter*, and *Pantoea* dominate bacterial communities in untreated stylo silage. Inoculation of *Lactobacillus (Lactiplantibacillus) plantarum* increased the abundance of *Lactobacilli* to promote stylo ensiling (Chen et al., 2021).

Tropical grass silage

Corn silage is the most common energy source for dairy cows in tropical regions (de Oliveira et al., 2017),

although the fermentation quality is usually poorer than that in cool or temperate regions (Bernardes et al., 2018). However, many studies have focused on the effects of chemical or LAB inoculants on fermentation quality and aerobic stability; few have focused on microbial communities in corn silage under tropical climate conditions using NGS or SMRT. Hisham et al. (2022) reported that *Pseudomonas*, *Leuconostoc*, and *Weissella* were the major epiphytic bacteria of sweet corn silage, with *Lactobacilli* becoming the dominant genus after ensiling.

Napier grass is an important tropical grass used as animal feed because of its high biomass production and wide adaptability. *Acinetobacter*, *Pseudomonas*, *Lactococcus*, *Mrakiella*, and *Hannaella* were the dominant bacteria in Napier grass cultivated in Chongqing, China, while *Lactobacilli*, *Sphingomonas*, and *Methylobacterium* were the predominant bacteria in Napier grass cultivated in Guangzhou, China (Wang, Li, et al., 2022). In addition, *Weissella* and *Pantoea* were the dominant genera in Napier grass in Malaysia (Hisham et al., 2022). Interestingly, *Weissella* and *Lactobacilli* were the dominant genera in Napier grass silages from different regions, and LAB inoculants or wilting treatments regulated the structure of microbial communities (Hisham et al., 2022; Yin et al., 2021; Zi et al., 2021).

Sugarcane is a competitive forage with high biomass yield and nutritive value (Daniel et al., 2017). Muraro et al. (2021) reported that *Leuconostoc* and *Pseudomonas* were the dominant bacteria in fresh sugarcane, while many undesirable microorganisms were dominant during the ensiling process, with *Lactobacilli* accounting for <10% of all bacteria in silage. However, *Leuconostoc* was the dominant bacteria in sugarcane top silages during the early-to-middle (2–30 days) stages of ensiling, and *Lactobacilli* was dominant at the late stages (60–90 days) (Ren et al., 2019; Wang, Teng, et al., 2020); Lactic acid bacteria inoculants increased the abundance of *Lactobacilli*.

Tropical woody silage

Tropical woody plants have recently been explored as novel sources of fodder for ruminants (Du, Sun, Lin, et al., 2021; Wang, Cao, et al., 2021; Wang, He, Xing, Zhou, Pian, Yang, et al., 2019). Mulberry has been used as feed for ruminants and non-ruminants because of its high energy, crude protein content, and digestibility (González-García & Martín-Martín, 2017; Kabi & Bareeba, 2008). Chen et al. (2021) reported that most of the epiphytic microorganisms of mulberry leaf silage were unclassified, with *Methylobacterium* accounting for 5% of all bacteria. Following fermentation, silages from Sichuan, China, were dominated by *Lactobacilli*, while those from Guangdong were dominated by *Kosakonia* and *Lachnoclostridium*; gallic acid and *Lactobacillus (Lactiplantibacillus) plantarum* inoculation promoted the growth of *Lactobacilli* and *Weissella* during ensiling (Chen et al., 2021; Li, Chen, et al., 2022; Wang, Teng, et al., 2020). In addition, Li, Chen, et al. (2022) investigated microbial communities of mulberry silage from Guangdong, China, and found that mulberry silage was dominated by *Lactobacilli* species (96%), particularly dominated by *Lactobacillus acetotolerans*, *Levilactobacillus hammesii*, *Companilactobacillus farciminis* (formerly *Lactobacillus farciminis*), and *Lentilactobacillus buchneri*.

Moringa oleifera Lam. (MOL) is widely distributed almost worldwide, and its leaves are rich in vitamins, phenolics, fatty acids, and amino acids (Guillén-Román et al., 2018). MOL has been proven to improve animal feed utilisation, productivity, and health (Kholif et al., 2018). MOL silage has been exploited as a novel functional feed for ruminants. Regarding microbial communities in MOL before or after ensiling, Wang, He, Xing, Zheng, Zhou, et al. (2019), Wang, He, Xing, Zhou, Pian, et al. (2019) reported that *Lactobacilli*, *Enterobacter*, and *Xanthomonas* were the dominant genera in fresh MOL, while *Lactobacilli* became dominant during the ensiling process (Tian, Wang, et al., 2021; Wang, He, Xing, Zheng, Zhou, et al. 2019; Wang, He, Xing, Zhou, Pian, et al. 2019); Lactic acid bacteria inoculants promoted MOL fermentation by *Lactobacilli*. However, Wang et al. (2018) reported that *Exiguobacterium*, *Acinetobacter*, and *Pseudomonas* were the most abundant bacterial genera in MOL, both before and after fermentation, and that *Lactobacillus (Lactiplantibacillus) plantarum* inoculation did not affect microbial community composition. In addition, adding MOL could enhance fermentation quality by decreasing the abundance of *Clostridium* and *Enterobacter* and increasing the abundance of *Lactobacilli* in alfalfa, stylo, and rice straw silages (He, Lv, et al., 2020; He, Zhou, et al., 2020; Wang, He, Xing, Zhou, Yang, et al., 2019).

As a nutrient-rich woody plant, paper mulberry (*Broussonetia papyrifera* L.) has also been used as a novel forage source to cope with the challenges of feed shortage and rapid development of the livestock industry in the tropics (Du, Sun, Chen, et al., 2021; Zhang et al., 2019). Studies have shown that microbial diversity was higher in fresh paper mulberry than in silages (Du, Sun, Chen, et al., 2021). Silage fermentation resulted in a dynamic shift in dominant bacteria from gram-negative to gram-positive strains; for instance, lactic acid bacteria became the most dominant genera and species that affected fermentation quality in terminal silages (Du, Sun, Chen, et al., 2021). *Enterobacter*, *Enterococcus*, and *Lactobacilli* were identified as the major drivers of fermentation in spontaneous whole-plant paper mulberry silages (Cheng, Chen, Bai, et al., 2021; Hao et al., 2022), while *Lactobacilli* was a dominant genus

in LAB (including *Lactobacillus* (*Lacticaseibacillus*) *rhamnosus*, *Lactobacillus* (*Lentilactobacillus*) *buchneri*, and their combination) treatments (Cheng, Chen, Bai, et al., 2021; Sun et al., 2022). Guo et al. (2021) reported that wilting reduced the abundance of *Enterobacter* whereas increased the abundance of *Lactobacilli* in paper mulberry silage; they further detected *Lacticaseibacillus rhamnosus* after wilting, which showed a positive correlation with lactic acid content of silage.

Lactic acid bacteria modulating microbial community functions in silage

Investigation of functional shifts based on the functional predictions of the microbiome has allowed us to evaluate the metabolic pathways of microbial communities during ensiling. The major pathways closely related to silage fermentation include amino acid, carbohydrate, nucleotide, and energy metabolisms (Bai et al., 2022; Hisham et al., 2022; Liu et al., 2019, 2020; Wang, Shao, et al., 2022; Xu, Wang, et al., 2021). Amino acids and their utilisation play physiological roles of LAB, such as energy regulation and resistance to environment stress (Fernandez & Zuniga, 2006). Using KEGG pathway analysis, the fermentation process was separated into three phases based on bacterial metabolic pathways (Figure 2; 0–3 days was the I phase of fermentation; 3–14 days was the II phase of fermentation; 14–60 days was the III phase of fermentation) (Bai et al., 2022). During the initial 14 days of ensiling, functional genes-related nucleotide and carbohydrate metabolisms were rapidly upregulated, while those related to energy and amino acid metabolisms were rapidly downregulated, with day 3 being the intersection. After 14 days of ensiling, functional genes related to nucleotide and carbohydrate metabolisms tended to be downregulated, while those related to energy and amino acid metabolisms continued to be upregulated. *Lactobacillus* (*Lactiplantibacillus*) *plantarum* and *Lactobacillus* (*Lentilactobacillus*) *buchneri* enhanced the ensiling process by upregulating carbohydrate metabolism (Bai et al., 2022; Xu, Wang, et al., 2021). In addition, the bacterial community function was evidently affected by the storage temperature (Bai et al., 2022). However, the effects of inoculants or their combination on carbohydrate metabolism in alfalfa silages were different. In particular, the relative abundance of carbohydrate metabolism genes was relatively high on days 1, 3, and 14 of ensiling in *Lactobacillus* (*Lactiplantibacillus*) *plantarum* plus *Pediococcus pentosaceus*-treated silage and on day 60 of ensiling in *Lactobacillus* (*Lactiplantibacillus*) *plantarum* plus *Pediococcus pentosaceus* and *Enterococcus faecalis*-inoculated alfalfa silage (Bai et al., 2021). In a study on metabolic pathways during the ensiling process and after air exposure, lactic acid bacteria were found to alter the metabolic pathways in barley; the LAB inoculants enhanced fructose and mannose metabolism, pyruvate metabolism, pentose phosphate and glycolysis pathways, amino acid metabolism pathways of alanine aspartate and glutamate, and energy pathways of methane metabolism on day 5 of aerobic exposure (Liu et al., 2019). In addition, during the aerobic stage of barley silage, inoculants mixed with molasses enhanced the metabolism of starch, sucrose, and glycolysis, as well as amino acid (alanine aspartate and glutamate metabolism, pyruvate metabolism, and amino sugar and nucleotide sugar metabolism) (Liu et al., 2020).

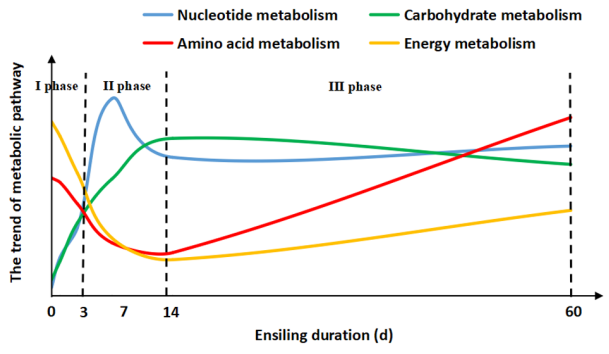

FIGURE 2 Dynamics of nucleotide, carbohydrate, amino acid, and energy metabolisms in whole-plant corn silage; the fermentation process (0–60 days) could be separated into three phases, 0–3 days was the I phase of fermentation; 3–14 days was the the II phase of fermentation; 14–60 days was the III phase of fermentation.

Ensiling is characterised by the transformation of carbohydrates to organic acids. The dominant LAB in ensiling can metabolise monosaccharides (glucose, galactose, xylose, and fructose) and some disaccharides (sucrose and maltose) in forages (Pahlow et al., 2003). The efficiency of polysaccharide degradation largely affects the fermentation process and final quality of silage. However, with very few exceptions, LAB is unable to ferment biomass like starchy or lignocellulosic feedstocks (Tarraran & Mazzoli, 2018). You et al. (2022) predicted the presence of carbohydrate-active enzyme (CAZyme) genes in the alfalfa silage microbiome and found that LAB in silage presented the highest abundance of glucoside hydrolases, with *Latilactobacillus curvatus* (formerly *Lactobacillus curvatus*), *Levilactobacillus brevis*, and *Lactiplantibacillus plantarum* and *Weissella* (e.g. *Weissella cibaria*, *Weissella hellenica*, and *Weissella kandleri*) carrying a higher number of CAZyme genes for degrading starch, arabinoxylan, and cellulose. In addition, silage bacteria have been found to contain the crucial enzymes oligosaccharide depolymerising β-xylosidases and endoacting-b-1,4-arabinoxylanases (Peng et al., 2016). This suggests that these species have the ability to break down starch, cellulose, and hemicellulose if starch, arabinoxylan and cellulose are degraded to hexoses or pentoses, which are homo- or

hetero-fermented by LAB to produce lactate, acetate, and ethanol (Figure 3; Gänzle, 2015; You et al., 2022). Although such predictions of functional pathways have offered information on functional shifts in microbial communities during ensiling, the precise details or mechanisms underlying these changes mediated by LAB inoculation remain unclear and warrant further research in the future.

ROLES OF FUNCTIONAL LAB IN SILAGE PREPARATION

In general, inoculants are selected for their ability to rapidly lower silage pH through the fermentation of WSC to lactic acids, which further inhibits proteolytic activity and preserves nutrients. At present, attempts are underway to design inoculants (functional inoculants) that not only improve silage quality but also positively affect animal health, production, stress tolerance and enhance silage intake and digestibility. Some studies have demonstrated that inoculated silages indirectly increased the milk production of cows compared with non-inoculated silages (Mayne, 1990; Meeske et al., 2002); however, the underlying mechanisms remain unclear. In this section, we introduce progress related to several attractive functional inoculants of silage. These inoculants positively affect silage safety while maintaining fermentation quality and decreasing pH. Moreover, these inoculants improve animal performance, increase feed intake and digestibility, and even enhance animal product quality (Figure 4).

Feruloyl esterase-producing LAB

The utilisation of dietary fibre fractions by ruminants depends on the ability of rumen microorganisms to produce cellulase and hydrolyse plant cell walls. However, the utilisation of feed with high dry matter (DM) and fibre content is generally inefficient (Badhan et al., 2018). Exogenous fibrolytic enzymes are applied as ruminant nutrients to alleviate this problem, particularly on ensiled materials, to improve feed utilisation. This strategy could indeed improve substrate availability in ensiled forages, ultimately increasing animal performance, in addition to the lactic acid concentration and nutritive quality of silage (Adesogan et al., 2014; Arif et al., 2019). They can be prepared using either a single enzyme group; combination of various enzyme groups, such as hemicellulases, cellulases, amylases, pectinases, and proteases; or combination of enzymes and bacterial inoculant. However, most of the enzyme additives available on the market are primarily composed of cellulases and hemicellulases, and their activity is limited to the corresponding cell wall fractions (Weinberg et al., 2007). None of these commercial additives contains enzymes that act on the lignin fraction of fibres.

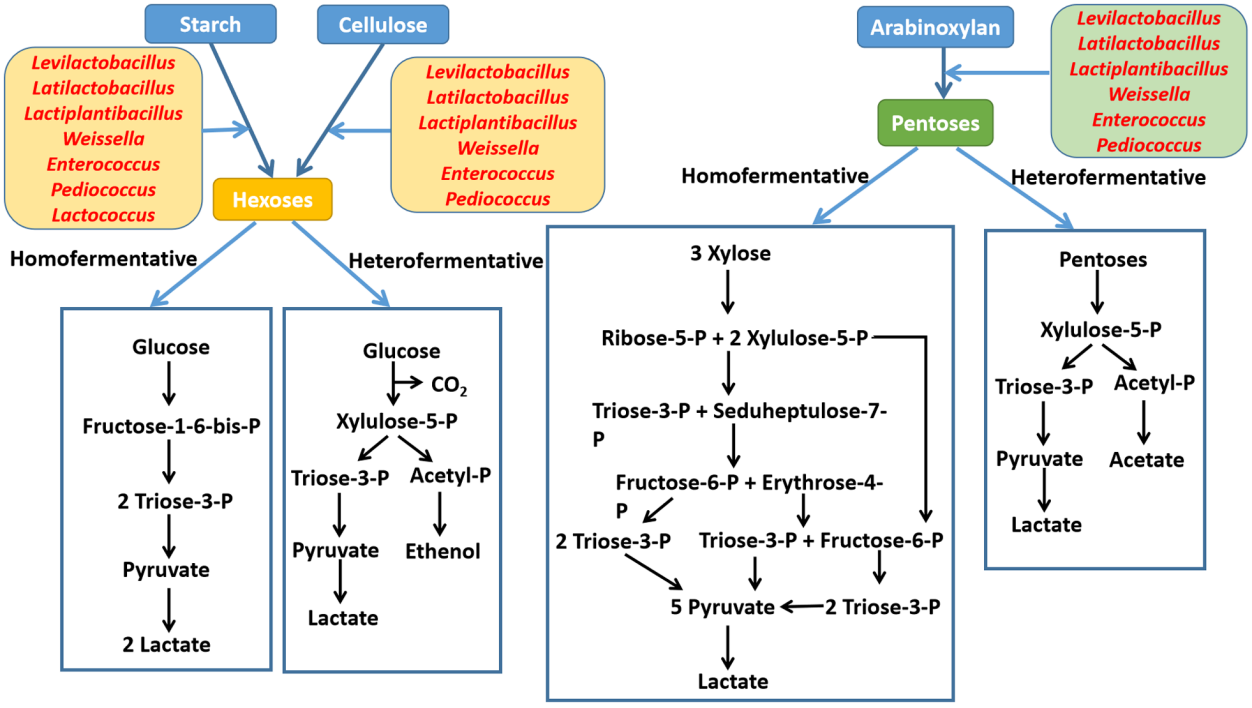

FIGURE 3 Schematic diagram showing simplified fermentation pathways of plant carbohydrate degradation; homofermentative metabolism of hexoses via the Emden–Meyerhoff pathway; heterofermentative metabolism of hexoses via the phosphoketolase pathway; homofermentative metabolism of pentoses via the pentose phosphate pathway; and heterofermentative metabolism of pentoses via the phosphoketolase pathway.

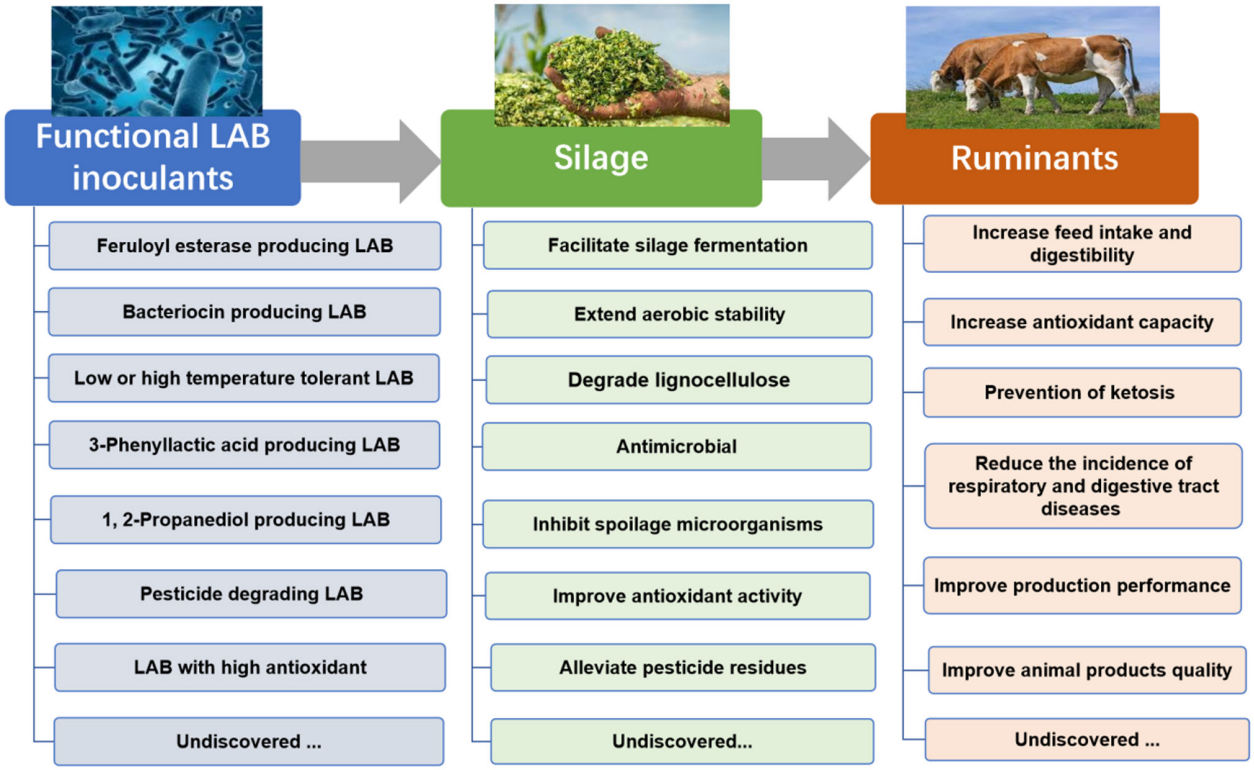

FIGURE 4 Functions of lactic acid bacteria and their effects on silage and ruminants.

Lignocellulose in plants is composed of cellulose, hemicellulose, lignin, and other components, which are cross-linked via feruloyl ester bonds (Yu et al., 2005). The feruloyl ester bonds between lignin and hemicellulose act as a physical barrier to microbial invasion, rendering the hydrolysis of lignocellulose by microbial enzymes difficult during ensiling and rumen fermentation (Aboagye et al., 2015; de Oliveira et al., 2015). Thus, to prepare high-quality silage with strong digestibility, degradation of the plant cell wall during ensiling is essential; this can be achieved by supplementing various biological additives that can effectively degrade the lignocellulosic structure of forages.

In recent years, extensive research has elucidated the positive effects of carboxylesterase on degrading feruloyl ester linkages and modifying the matrix structure of forage lignocellulose (Addah et al., 2012; Nsereko et al., 2008). Studies have shown that inoculation with feruloyl esterase-producing LAB during ensiling promoted forage lignocellulose degradation with a concomitant increase in silage-free ferulic acid concentration (Li, Ding, et al., 2021; Li, Ke, et al., 2020). In addition, breakage of the link between lignin and cell wall carbohydrates facilitated further degradation of forage in the rumen. Li, Ding, et al. (2019); Liu et al. (2020) and Usman et al. (2022) have confirmed the positive effects of feruloyl esterase-producing *Lactobacillus* (*Lactiplantibacillus*) *plantarum* A1 on silage enzymatic digestibility in vitro. Moreover, Kang et al. (2009) and Jin et al. (2015) have reported improvement in the DM and neutral detergent fibre (NDF) digestibility of silages treated with feruloyl esterase-producing *Lactobacillus* (*Lentilactobacillus*) *buchneri* in situ. Furthermore, animal trials have revealed that in addition to improving silage fermentation and digestion, feruloyl esterase-producing bacteria enhanced the antioxidant and immune properties of animals (Li, Zhang, et al., 2022). Addah et al. (2012) also demonstrated that inoculation of whole-crop barley silage with a mixed culture of homolactic bacteria and feruloyl esterase-producing *Lactobacillus* (*Lentilactobacillus*) *buchneri* at ensiling improved the efficiency of body weight (BW) gain in growing feedlot steers. In addition, in dairy goats that were fed alfalfa silage inoculated with feruloyl esterase-producing LAB, milk fat, and milk protein concentrations were increased (Li, Zhang, et al., 2022).

Lactic acid bacteria with antimicrobial properties

Excessive mycotoxins and massive amplification of pathogenic bacteria in silage are common public health concerns in animal husbandry (Ogunade et al., 2018). In general, lactic acid bacteria are used to facilitate fermentation and prevent mildew of silage by controlling microbial events during fermentation (Gallo et al., 2022; Wambacq et al., 2016). In particular, bacteriocin produced by LAB is an important antimicrobial product with biopreservation and antibacterial properties, which allows the bacteria to regulate the growth of

spoilage microorganisms in silage (Gollop et al., 2005; Li et al., 2015). As reported in previous studies, bacteriocin can form pores on the surface of cell membrane, increase the permeability of cell membrane, dissipate the cytoplasmic membrane potential and transmembrane pH gradient, and destroy the integrity of cell membrane, causing cell content to flow out and cell death (Wang et al., 2019; Zhang et al., 2016). These attributes may enhance the safety and quality of food/feed and their by-products (Balciunas et al., 2013; O'Sullivan et al., 2002). Thus, trials involving LAB inoculants with antimicrobial properties have garnered much attention in the global dairy industry. Moreover, strains producing bacteriocins have been proven useful in inhibiting spoilage microorganisms in silage. Some preliminary studies have indicated that bacteriocins produced by LAB may be a potential and an effective alternative to classical antibiotics used in animal husbandry (Joerger, 2003; Santoso et al., 2006; Shen et al., 2017). In a previous study, a selective bacteriocin, pediocin SA-1, could be used as an additive to control *Listeria monocytogenes* in maize silages (Amado et al., 2016). Forage inoculated with bacteriocin-producing bacteria, such as *Lactococcus lactis* CECT 539 and *Pediococcus acidilactici* NRRL B-5627, was more effective than non-inoculated controls in improving the fermentation quality of silages and inhibiting the growth of *Listeria monocytogenes* (Amado et al., 2012). Silva et al. (2016) reported that the inoculation of alfalfa silage with a potential bacteriocinogenic *Pediococcus pentosaceus* strain improved the fermentation profile under tropical conditions, although they did not observe any antimicrobial effect. Recently, Chikindas et al. (2018) suggested that bacteriocins are involved in different activities against similar bacterial species and other microorganisms, such as eukaryotic cells, some viruses, and mycobacteria. Similarly, Li, Ding, et al. (2020) reported that the inoculation of alfalfa silage with class IIa bacteriocin-producing LAB effectively inhibited the growth of yeast and moulds and improved the aerobic stability of the silage. Thus, it is important to explore promising LAB strains that possess antimicrobial properties and such inoculants may improve the microbial safety of silage. In addition, lactic acid bacteria strains that exhibit antifungal activity may serve as another tool to improve the quality of silage that is susceptible to fungal attack. However, it was not clear how the bacteriocin contributed to the inhibition of fungi since bacteriocins are known to inhibit homologous bacteria, but not fungi (Silva et al., 2016). Thus, more research is needed to confirm the role of bacteriocins in inhibiting the growth of spoilage fungi.

Furthermore, 3-phenyllactic acid is a small-molecule organic acid that is ubiquitous in nature. It presents antifungal activity and is an important preservative in the feed, food, pharmaceutical, and cosmetic industries (Dieuleveux et al., 1998; Strom et al., 2002). 3-phenyllactic acid has been reported to exhibit positive bioactivities when fed to animals. For instance, 3-phenyllactic acid could replace 70.1% phenylalanine in the diets of chicks and mice; furthermore, it showed positive effects on the immunity of hens and pigs (Boebel & Baker, 1982; Wang, He, Xing, Zhou, Yang, et al., 2019; Wang, Wang, Wang, Meng, Duan, et al., 2019). Reportedly, 3-phenyllactic acid is present in corn, alfalfa, and grass silages (Broberg et al., 2007; Wang, Gao, et al., 2020; Xu, Ding, et al., 2019). Furthermore, several LAB strains were found to produce 3-phenyllactic acid in grass silage (Broberg et al., 2007). Xu, Ding, et al. (2019) inferred that *Lactobacillus acetotolerans* could produce 3-phenyllactic acid in silage. Strom et al. (2002) isolated *Lactobacillus* (*Lactiplantibacillus*) *plantarum* MiLAB 393 from grass silage, and 3-phenyllactic acid produced by this strain suppressed the growth of *Fusarium sporotrichioides*, *Aspergillus fumigatus*, and *Kluyveromyces marxianus* in culture. Similarly, Wu et al. (2020) screened two 3-phenyllactic acid-producing strains, namely, *Lactobacillus* (*Lactiplantibacillus*) *plantarum* M1 and M2, from silages and pickles. Inoculation of these two strains improved fermentation quality and prevented protein degradation during the ensiling period. Therefore, similar to bacteriocin-producing LAB, 3-phenyllactic acid-producing LAB may serve as useful additives for improving the quality of silage fermentation and ensuring the quality and safety of forage grass in the future. In particular, as an alternative to antibiotics, these LAB hold great promise for preventing mildew of silage. The inhibition activity of 3-phenyllactic acid was related to its capacity to harm cell membranes and disrupt energy metabolism, which led to intracellular component leakage and decreased ATP synthesis, which in turn severely inhibited spore growth and even caused cell death (Li, Yao, & Meng, 2022). In addition, scanning electron microscope studies showed that the bacteria exposed to 3-phenyllactic acid had damaged, even broken cell wall structure (Mu et al., 2012).

Lactic acid bacteria with high antioxidant potential

Ruminants, such as dairy cows or dairy goats, are more susceptible to oxidative stress due to their intensive metabolic requirements for maintenance and production, resulting in metabolic and infectious diseases (Sordillo & Aitken, 2009; Tian et al., 2019). Thus, improving the antioxidant capacity of ruminants is of great significance to their health and productivity. The addition of exogenous antioxidants (e.g., ferulic acid, anthocyanins, catechin, pycnogenol, astaxanthin, and flavonoids) to ruminant diets is an effective strategy to mitigate oxidative stress (Khosravi et al., 2018; Nisar et al., 2013; Pandey & Negi, 2016; Wang, Wang, Wang, Meng, Duan, et al., 2019). Based on this, feed antioxidant additives are widely used for improving the survival rate

of newborn poultry, health and productivity of livestock, and shelf life of meat and milk products (Chew, 1996; Soberon, Cherney, et al., 2012; Soberon, Cherney, Liu, et al., 2012). However, the application of antioxidants is limited by their high cost and low output from extraction. Therefore, natural antioxidant compounds in ensiled forage have received considerable attention in recent years (Kotsampasi et al., 2017; Santos et al., 2014; Tian et al., 2019). The quality of silage affects all aspects of ruminant nutrition, ranging from voluntary intake, palatability, and nutritive value to animal health and product quality (Lozicki et al., 2015). A previous study has shown that extreme environmental conditions, such as high altitude, hypoxia, cold temperatures, and strong ultraviolet radiation in Qinghai-Tibet plateau provide an alternative and a readily available substrate to screen for LAB strains with attractive functional characteristics, particularly antioxidant properties (Ding et al., 2017). In recent studies, some LAB isolated from fermented food or silage have been confirmed to have good antioxidant properties (Ding et al., 2017; Pourramezan et al., 2018). It has been speculated that silage LAB with high antioxidant properties hold immense potential because their discovery has offered novel insights into the improvement of silage quality and animal antioxidant capacity. For instance, Zhang, Ke, et al. (2020, 2021) reported that the inoculation of alfalfa with the screened antioxidant strains *Lactobacillus* (*Lactiplantibacillus*) *plantarum* 24–7 or *Pediococcus acidilactici* J17 could improve the antioxidant status of silages with different DM contents. Zhang et al. (2022) tested six LAB strains with high antioxidant activity in alfalfa silage. All six strains improved the total antioxidant capacity of silages and reduced α-tocopherol and β-carotene losses compared with those observed in the reference strain. In addition, Li, Ding, et al. (2021) reported that feruloyl esterase-producing *Lactobacillus* (*Lactiplantibacillus*) *plantarum* A1 showed a high antioxidant capacity by degrading lignocellulose in alfalfa; this antioxidant capacity was attributed to free ferulic acid released during ensiling. Although Zhang, Ke, et al. (2020, 2021) and Zhang et al. (2022) have demonstrated that fermentation using LAB with high antioxidant activity improved the antioxidant capacity of alfalfa silage. However, whether silage treated with such inoculants can improve the antioxidant status of ruminants and ruminant products remain unclear. At present, only one of our previous studies proved that the application of feruloyl esterase-producing strain *Lactobacillus* (*Lactiplantibacillus*) *plantarum* A1 to silage could improve the antioxidant status of lactating dairy goats because of the free ferulic acid produced during ensiling (Li, Zhang, et al., 2022).

Pesticide-degrading LAB

Pesticides are frequently used to prevent or control pests, illnesses, and other plant pathogens in order to reduce the loss of green fodder caused by diseases and pests (Koli & Bhardwaj, 2018; Meissle et al., 2010). Hence, pesticides have played an important role in increasing the productivity and yield of forage crops. However, despite their significant role in agricultural activities, when pesticides are used excessively or inappropriately, their footprint on the ecosystem due to residual accumulation over time poses a serious health threat (Narenderan et al., 2020).

Pesticide residues in green fodder are the major source of pesticides in silage. In addition to the great health risk to ruminants and humans, the types and initial concentrations of pesticides affect the fermentation quality of silage (Ge et al., 2021). Zhang, Yu, et al. (2017) found that both chlorpyrifos and chlorantraniliprole increased the butyric acid concentration of alfalfa silage when these two pesticides were sprayed on the surface of alfalfa before ensiling. In recent years, strategies aimed at reducing or eliminating these naturally existing toxic compounds through biodegradation and biodetoxification have garnered attention, and some genera of LAB, such as *Lactobacilli* and *Leuconostoc*, have been proven to possess the metabolic ability to utilise insecticides as a source of carbon and energy (Cho et al., 2009; Choi et al., 2004; Islam et al., 2010; Kumral et al., 2020; Zhao & Wang, 2012). Thus, the use of LAB as detoxicants may offer an innovative strategy for the biodetoxification and biodegradation of toxic compounds in silage. Practically, some studies using different microbial strains as detoxification tools have been conducted on various fermented materials. For instance, Đorđević, Šiler-Marinković, et al. (2013) found that *Lactobacillus* (*Lactiplantibacillus*) *plantarum* could degrade 81% of pirimiphos-methyl (pesticide) during wheat fermentation without affecting bacterial growth and fermentation activity. In another study, Đorđević, Siler-Marinkovic, et al. (2013) found that *Lactobacillus* (*Lactiplantibacillus*) *plantarum* could degrade pyrethroid insecticides and bifenthrin during fermentation of milled wheat. The bifenthrin degradation activity was attributed to the metabolic hydrolysis of the carboxylic ester linkage. This result corroborates the report by Zhou et al. (2015) that *Lactobacillus* (*Lactiplantibacillus*) *plantarum* dissipated approximately 96.2–99.7% of four organophosphate pesticides, including chlorpyrifos, dichlorvos, phorate, and trichlorphon, in pickled Chinese cabbage. In silage, a novel strain, *Lactobacillus* (*Lacticaseibacillus*) *casei* WYS3, was screened for pesticide degradation in rice straw silage contaminated with chlorpyrifos, and the inoculation of this strain was found to promote chlorpyrifos removal after ensiling when compared with that after inoculation with control (Wang et al., 2016). Similarly, Liu et al. (2022) screened a novel beta-cypermethrin (beta-cyp)-degrading strain, *Lactobacillus* (*Lactiplantibacillus*) *pentosus* 3–27,

from beta-cyp-contaminated alfalfa silage; the strain could degrade 96% of beta-cyp (50 mg L^{-1}) in MSM medium after 4 days of culture. Moreover, when used as an inoculant, the strain not only improved the fermentation quality of alfalfa silage but also degraded beta-cyp. However, inconsistent with previous reports, Zhang, Yu, et al. (2017) indicated that the addition of *Lactobacillus* (*Lactiplantibacillus*) *plantarum* to silage delayed chlorpyrifos dissipation. Although the precise cause remains unclear, the strain may lack pesticide-degrading properties, as mentioned in previous studies. Therefore, screening and application of pesticide-degrading LAB are of great practical value to reduce pesticide residues in silage and improve fermentation quality.

Lactic acid bacteria producing 1,2-propanediol

Typically, *Lactobacillus* (*Lentilactobacillus*) *buchneri* is considered the dominant LAB for maintaining the aerobic stability of silage, as acetic acid produced by this bacterium plays an important role in improving the aerobic stability of silage (Nishino et al., 2003). In recent years, 1,2-propanediol has been found at high levels in screened *Lactobacillus* (*Lentilactobacillus*) *buchneri*-inoculated silages; but, naturally occurring populations of *Lactobacillus* (*Lentilactobacillus*) *buchneri* occasionally result in low concentrations of 1,2-propanediol in silages (Huang et al., 2021). Previous studies have indicated that at concentration between 0.25% and 1.5%, 1,2-propanediol in silage prolonged its aerobic stability (Kung et al., 2018). Huang et al. (2021) have successfully isolated and screened two strains of LAB, namely, *Lactobacillus* (*Lentilactobacillus*) *buchneri* 9–2 and 10–1, which produced a high concentration of 1,2-propanediol from baled alfalfa and corn silages stored for 1 or 2 years depending on physiological and biochemical characteristics. After 90 days of fermentation, the concentration of 1,2-propanediol in corn silages treated with *Lactobacillus* (*Lentilactobacillus*) *buchneri* 9–2 and 10–1 reached 34.7 and 34.6 g kg^{-1} DM, respectively, and these values were significantly higher than that (19.5 g kg^{-1} DM) in silages treated with the reference strain (*Lactobacillus* (*Lentilactobacillus*) *buchneri* 40,788). Furthermore, these bacterial strains improved the aerobic stability of silage compared with the reference strain. Likewise, Nishino et al. (2003) have reported that abundant 1,2-propanediol (49.4 g kg^{-1} DM) was accumulated in *Lactobacillus* (*Lentilactobacillus*) *buchneri* NK01-treated corn silage stored for 120 days. Interestingly, a previous study has shown that 1,2-propanediol exhibits no antifungal action (Driehuis et al., 2001). According to Krooneman et al. (2002) and Selwet (2020), 1,2-propanediol in silage is metabolised by other microorganisms to 1-propanol and propionic acid, and propionic acid is known to produce a stronger inhibitory effect than acetic acid against fungi. Thus, the prolonged aerobic stability of silage inoculated with 1,2-propanediol-producing *Lactobacilli* may be attributed to the increased concentration of propionic acid in the silage rather than the direct antifungal effect of 1,2-propanediol.

Nonetheless, glucogenic 1,2-propanediol is used in veterinary practice for the treatment of clinical ketosis (Zielińska et al., 2017). Upon consumption by dairy cows, 1,2-propanediol could be absorbed and converted to glucose in the liver or converted to propionic acid in the rumen (Kung et al., 2018). Thus, continuous intake of silage containing 1,2-propanediol may be a viable method for the prevention of ketosis in dairy cows (Nishino et al., 2003). Currently, 1,2-propanediol is produced using chemical methods; however, various microorganisms, such as LAB, can ferment sugars to 1,2-propanediol or degrade lactic acid to acetic acid and 1,2-propanediol under anaerobic conditions (Elferink et al., 2001). Regular consumption of such LAB-inoculated silages may affect the performance and energy efficiency of ruminants. Thus, screening of 1,2-propanediol-producing LAB and their application in silage production are of great importance for extending aerobic exposure time and alleviating dairy cow ketosis during practical production.

Low-temperature-tolerant LAB

Silage is the product of LAB-dominated fermentation. LABs grow at 5–50°C, with optima between 25°C and 40°C (Driehuis et al., 2003). However, in cold regions, there is a long and harsh winter following a short and cool growing season. Although the ambient temperatures are usually above 15°C during the day, they can drop significantly during the night (Bernardes et al., 2018). Bernardes et al. (2018) reviewed the challenges of silage preparation in cold regions and proposed ambient temperature as one of the major limiting factors for silage quality because fermentation triggered by epiphytic and inoculated LAB could be functionally impaired at lower temperatures. Moreover, Bai et al. (2022) reported that whole-plant corn silages stored at 30°C presented lower pH as well as lower bacterial diversity and network complexity than those stored at 20°C, indicating that low temperature (20°C) slowed down the fermentation of whole-plant corn silages. Thus, uncontrollable climate-related factors that are common or specific to cold regions can adversely affect silage production and utilisation.

Most efforts are focused on acid-based additives for preserving green forage in low-temperature

regions. Bernardes et al. (2018) have reviewed the effects of these additives on silage preparation in cold regions. In recent years, increasing attention has been paid to the development of low-temperature-tolerant silage LAB for forage preservation in cold regions. For instance, *Lactobacillus* (*Lacticaseibacillus*) *rhamnosus* GG6 and *Lactobacillus* (*Lactiplantibacillus*) *plantarum* GG7 isolated from Italian ryegrass silage could grow well at 5°C (Ali et al., 2017); the addition of these two inoculants at ensiling better promoted lactic acid fermentation at 10°C and 15°C than that seen with the reference LAB *Lactobacillus* (*Lactiplantibacillus*) *plantarum* MTD/1. Similarly, Wang et al. (2017) added four LAB strains isolated from straw silages to Italian ryegrass at ensiling and found that *Lactobacillus* (*Lactiplantibacillus*) *plantarum*, *Lactobacillus* (*Loigolactobacillus*) *coryniformis*, and *Pediococcus pentosaceus* improved silage fermentation quality at both 10°C and 15°C. Xu, Ke, et al. (2019) isolated *Pediococcus pentosaceus* Q6 from *Elymus nutans* growing on the Tibetan Plateau and reported that this strain could grow at 4°C and promote silage fermentation at low temperatures (10°C or 15°C). Zhang, Lv, et al. (2017) ensiled wheat straw with low-temperature-tolerant *Lactobacillus* (*Lactiplantibacillus*) *plantarum* strains, which improved silage fermentation at 5°C compared with the reference strain. However, all these ensiling experiments were conducted only in laboratory silos. In practice, Chen et al. (2020) treated oat silage with a low-temperature-tolerant LAB inoculant comprising *Lactobacillus* (*Lactiplantibacillus*) *plantarum* BP18, *Pediococcus pentosaceus* HS1, and *Lactobacillus* (*Lentilactobacillus*) *buchneri* LP22 in round bales and reported that the inoculant enhanced silage fermentation and optimised bacterial community structure at low-temperature environment. Overall, from these results, development of low-temperature-tolerant silage LAB strains is of great significance and a potentially promising method for controlling silage fermentation in cold regions in the future.

LACTIC ACID BACTERIA AFFECT METABOLITES OF SILAGE

The ensiling process of silage involves both the microbiome and metabolome. Using conventional methods, metabolites, such as lactic acid, acetic acid, butyric acid, propionic acid, and ethanol are commonly detected to evaluate fermentation quality and aerobic stability. As the key bacteria, lactic acid bacteria strains produce specific substances, such as 2,3-butadione, reuterin, acetaldehyde, 3-phenyllactic acid, and 3-hydroxydecanoic acid (Schnu, 2005; Sjögren et al., 2003; Strom et al., 2002). Moreover, LAB can produce a multitude of amino acids, fatty acids, vitamins, and oligosaccharides (Sun et al., 2012), suggesting that silages contain many other metabolites. Broberg et al. (2007) investigated metabolites produced by LAB in silage and detected *p*-hydrocoumaric acid, hydroferulic acid, and *p*-coumaric acid were produced by *Lactobacillus* (*Lactiplantibacillus*) *plantarum* MiLAB393 and MiLAB14 inoculants in grass. In addition, the results of Fourier-transform infrared spectroscopy conducted by Johnson et al. (2004) revealed that inoculants altered the characteristics of biochemical data; amides reflected the change in amino acids and proteins during ensiling, and these could be distinguished between control and inoculant-treated red clover and grass silages.

Recently, metabolomics has been applied to several studies on silage to identify novel bioactive metabolites that can serve as indicators of silage quality, including amino acids, fatty acids, vitamins, and flavour compounds, as well as bioactive substances that are beneficial to animal health and welfare. Various metabolites in different silages possess the potential to improve animal meat quality or alter the metabolomic profile of milk (Lanza et al., 2021; Wang, Zhao, et al., 2022). In silage, hundreds of metabolites have been detected, which are primarily composed of organic acids, sugars, amino acids, polyols, and volatile chemicals (Guan, Shuai, Ran, et al., 2020; Guo et al., 2018; Hu et al., 2020; Scherer et al., 2021; Xu et al., 2020; Xu, Ding, et al., 2019; Xu, Wang, et al., 2021). Lactic acid bacteria inoculants could modulate silage metabolome by modifying microbial communities (Zhang, Guo, et al., 2021). The inoculants *Lactobacillus* (*Lactiplantibacillus*) *plantarum*, *Lactobacillus* (*Lentilactobacillus*) *buchneri*, and *Lactobacillus* (*Lacticaseibacillus*) *casei* enhanced the relative concentrations of some organic acids and polyols in alfalfa silage, and the concentrations of most of the organic acids were positively correlated with the abundances of *Lactobacilli*, *Lactococcus*, *Weissella*, and *Enterococcus* (Guo et al., 2018; Hu et al., 2020). In whole-plant silage, *Lactobacillus* (*Lactiplantibacillus*) *plantarum* or *Lactobacillus* (*Lentilactobacillus*) *buchneri* inoculants increased the concentrations of some amino acids (e.g. phenylalanine, lysine, tyrosine, and glycine), phenolic acids (e.g. 4-hydroxycinnamic acid and 3,4-dihydroxycinnamic acid), flavour compounds (gluconic lactone), and organic acids (lauric acid, 3-hydroxypropionic acid, pentadecanoic acid, oxamic acid, and isocitric acid) (Xu, Ding, et al., 2019; Xu, Wang, et al., 2021). In a study of silage odour, Zhang, Guo, et al. (2021) focused on volatile chemicals in stylo and rice straw silages and found that *Lactobacillus* (*Lactiplantibacillus*) *plantarum* decreased the concentrations of certain volatile substances, which were positively correlated with the abundances of undesirable bacteria but negatively correlated with the abundance of *Lactobacilli*.

Interestingly, some biofunctional metabolites, such as bacteriostatic, antioxidant, anti-inflammatory compounds, and neurotransmitters have been detected in silage (Guo et al., 2018; Tian, Zhu, et al., 2021; Xia et al., 2022; Xu, Ding, et al., 2019; Xu, Wang, et al., 2021). Such metabolites may improve animal health and welfare, and inoculants may elevate their levels. For instance, levels of metabolites with anti-inflammatory (glycitin, lithospermic acid, and psoralidin), antioxidant (ferulic acid, isoferulic acid, sinapinic acid, and moslosooflavone), antimicrobial (phenyllactic acid), and anti-tumour (alnustone) activities were elevated by the LAB inoculation of mixed silage of *Sesbania cannabina* and sweet sorghum (Xia et al., 2022). Furthermore, metabolites with antimicrobial activity (methylbutanoic acid, 1,2-propanediol, and tiglic acid) were detected in LAB-treated Napier grass silage (Guan, Shuai, Ran, et al., 2020). Compounded LAB increased the relative concentrations of antioxidant substances (e.g. 7-galloylcatechin) and antibacterial compounds (e.g. ferulic acid) in *Cyperus esculentus* L. leaf silage (Sun, Wang, et al., 2021). In addition, our research group investigated comprehensive metabolome profiles of whole-plant corn silage inoculated with or without *Lactobacillus* (*Lactiplantibacillus*) *plantarum* using integrated metabolomics with solid-phase microextraction (SPME)–gas chromatography/mass spectrometry (GC/MS) as well as GC/MS and liquid chromatography/mass spectrometry (LC/MS). We identified 2087 metabolites in corn silage. Notably, inoculation with *Lactobacillus* (*Lactiplantibacillus*) *plantarum* remarkably altered silage volatile organic compounds as well as elevated the levels of some essential amino acids (L-isoleucine, lysine, and threonine), pyridoxine, acetylcholine, and compounds with antioxidant (alpha-linolenic acid and luteolin), anti-inflammatory (alpha-linolenic acid), and antimicrobial (3-phenyllactic acid and cinnamaldehyde) activities in corn silage (unpublished data). Correlation analysis between metabolites and bacterial species indicated that *Lactobacillus* (*Lentilactobacillus*) *buchneri* potentially produces specific amino acids, particularly the neurotransmitter of 4-aminobutyric acid (Guo et al., 2018; Xu, Ding, et al., 2019).

However, in some studies, lactic acid bacteria inoculants showed little effect on silage metabolome. For instance, Guan, Shuai, Ran, et al. (2020) reported that in Napier grass silage, differences in metabolome among treatments were more closely related to fermentation period rather than LAB inoculations. Moreover, *Lactobacillus* (*Lactiplantibacillus*) *plantarum* mainly affect metabolites related to carbohydrate and nitrogen pathways in sainfoin silage (Xu et al., 2020). However, additional details and mechanisms underlying the effects of LAB on the microbiome and metabolome should be explored in future studies.

SUMMARY

In summary, LAB plays pivotal roles in the forage ensiling process and are mainly dominated by *Lactobacilli*, *Weissella*, and *Pediococcus* species in corn, alfalfa, grass, and tropical crop silages. These LAB species serve various functions depending on forage type, microbial community, and storage practices. In various silages, LAB inoculants modulate microbial community composition through different routes depending on the epiphytic microbiota of fresh forage. Basically, LAB inoculants simplify the correlations among bacterial species to enhance the fermentation quality. It is worth noting that functional LABs are very promising sources of novel products and applications, specifically those that can satisfy the increasing consumer demands for natural products as well as functional silage and foods. Despite recent advances, research on silage LAB and their functional components remains at the nascent stage, and their full potential is yet to be realised, necessitating extensive efforts to explore the links of LAB with silage, animal, and animal products. Based on the current knowledge on silage metabolites, there are great opportunities to develop silage not only as a fermented feed but also as a vehicle of delivery of probiotic substances for animal health and welfare in the future.

AUTHOR CONTRIBUTIONS

Xusheng Guo: Conceptualization (lead); funding acquisition (lead); writing – review and editing (equal). **Dongmei Xu:** Conceptualization (equal); writing – original draft (equal); writing – review and editing (equal). **Fuhou Li:** Conceptualization (equal); writing – original draft (equal); writing – review and editing (equal). **Bai Jie:** Writing – original draft (equal). **Rina Su:** Writing – original draft (equal).

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CONFLICT OF INTEREST

None declared.

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