The combined role of microbes and forages in animal productivity

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Abstract

Agricultural systems, particularly ruminant systems, are underpinned by diverse, functional microbial communities—in the soil, forage, silo, and rumen. We have relied on the jobs they perform on our behalf, but only recently have we been able to look "under the hood" at the membership and mechanisms within these microbiomes and begin to think about optimization. Ensiling is a common method of forage preservation globally and represents a highly intensive intersection between forage and microbiology, which has been shown to have beneficial effects on forage quality and dairy animal performance. However, observations of enhanced productivity, especially in the context of inoculated silages, are inconsistent. A greater understanding of the functions of, and interactions between, forage, silo, and rumen microbiomes are needed to develop best practices that align the interests of producers and their microbial communities.

Introduction

Microorganisms are an important, but historically inscrutable, component of all agricultural systems. Forages are critical to maintaining healthy rumen function and can be produced and fed sustainably. Silage is the intersection of forage and microbial action where wet forage is fermented without oxygen to preserve the crop. Silage is traditionally produced in North America and Europe as a method of animal feed preservation in wet, cool climates where forage production cannot sustain livestock year-round and the production of hay is challenging. Its use as a preservation method is growing rapidly in Africa, Asia, and South America as well. (Pahlow et al., 2003) Typically, forage fermentation is the product of lactic acid bacteria (LAB) consuming water soluble carbohydrates (WSC) present in harvested forage and metabolizing it to a mix of organic products, including the desirable lactic and acetic acids, as well as CO2 and ethanol. A well-preserved silage relies on rapid fermentation for retention of optimal feed quality because insufficient or slow acidification is associated with increased protein degradation, additional dry matter loss, and increased risk of spoilage. (Pahlow et al., 2003; Muck, 2013).

A common practice for increasing the likelihood of a good fermentation is to directly inoculate harvested forage with select species and strains of LAB. These silage inoculants were introduced as a means of producing rapidly fermented, aerobically stable silage without the uncertainty of relying on favorable weather conditions or the wild microbiome living on the forages in the field. Initially, silage inoculants focused on fast, efficient LAB that produced lactic acid as their only fermentation product. However, silages containing only lactic acid are prone to poor aerobic stability that deteriorates quickly when exposed to oxygen during feeding or at the face of the silo. Research efforts on LAB inoculants have focused primarily on the challenges of balancing rapid fermentation with aerobic stability between homofermenters, rapidly producing only lactic acid, and heterofermenters, producing a variety of products at the cost of greater dry matter loss, and the usefulness of these inoculants across varied climates and crops. The discovery and application of *Lactobacillus buchneri* and other LAB-carrying biochemical pathway that converts lactic acid to acetic acid and 1,2-propanediol offered an efficient compromise for striking a balance between rapid ensiling and aerobic stability (Muck, 1996).

As inoculation has grown in popularity, observations of animal performance benefits from inoculation have also increased. A review by Kung and Muck (1997) howed that, between 1990-1995, approximately half of the studies including microbially inoculated silages observed significant increases in gain and milk production (Kung et al., 1997). The average observed increase in milk yield for these studies was 1.37 kg/day. A recent meta-analysis of data from previously published studies revealed a significant and consistent effect of improved milk yield and numerical increases in milk fat and protein associated with bacterial inoculation of ensiled forages (Oliviera et al., 2017). However, performance improvements from inoculated silage are not consistently observed and the underlying mechanism(s) of animal performance benefits remain unclear.

Forage quality effects

Microbial inoculation has a pronounced positive effect on grass and legume silage fermentation, with increased lactic and acetic acid concentrations, improved dry matter preservation, and decreased proteolysis, but not necessarily for corn, sorghum, and sugarcane silages. (Kung et al., 1997; Oliviera et al. 2017) And yet, observed increases in animal performance in response to silage inoculation are present regardless of forage species. Four main forage quality mechanisms could potentially explain animal responses to silage inoculation: 1) digestibility, 2) increased DMI, 3) reduced proteolysis, 4) and improved conservation of nutritional value.

There is evidence that ensiling, particularly when ensiled for longer periods, can increase forage digestibility. (Danley et al., 1973; However, the effect of inoculation on improvement in dry matter digestibility was not significant in the 2017 meta-analysis by Oliviera et. Al (2017). This is not necessarily indicative that inoculation does not affect DM digestibility, however, as ensiling time was not accounted for and DM digestibility had the smallest dataset of the forage parameters analyzed.

Dry matter intake (DMI) is the most likely parameter to affect animal performance even in the absence of observed differences in silage quality. Most studies individually have found minimal or no significant effect of inoculation on DMI (Muck et al., 2018). However, themeta-analysis (Oliviera et al., 2017) showed a trend of increased DMI (RMD – 0.37kg/d; $P = 0.08$), but also high variability between studies. Taken together, these observations may indicate that inoculation can drive DMI patterns, but that effects depend on properties that are difficult to control or measure. This may be attributable to a reduction in spoilage organisms and associated compounds like ammonia and butyrate that reduce intake. Investigations of the effects of inoculation on the formation of intake-reducing compounds like biogenic amines, butyric acid, and ammonia might provide targets to measure that better connect silage inoculation and DMI.

Forage protein degradation is a continuous process that starts at harvest. It begins with plant proteases and is slowed by acidification. Proteolysis also produces byproducts that can reduce intake as mentioned above. This process is limited by minimizing time to silo sealing and ensuring robust fermentation to discourage Clostridial growth. The goal of inoculation is to dominate the fermentation community with beneficial microbes and to use available water-soluble carbohydrates (WSC) for organic acid production. In the 2017 meta-analysis, ammonia concentrations, an indicator of protein degradation, were higher in uninoculated forages. In addition, farm-scale silages showed far more variable, and higher, ammonia values when compared to laboratory-scale silages. This is likely due to variable weather conditions and longer times from cutting to ensiling at the farm scale.

Observed trends in animal performance benefits from inoculation may be attributable to a forage nutritive factor that is not always measured. Water-soluble carbohydrates are easily lost from harvested forages due to leaching or from CO_2 respiration. Similarly to proteolysis, this is largely influenced by the time from field to the silo. Interestingly, WSC levels differe strongly between inoculated laboratory-scale silages (higher WSC) and forage inoculated on-farm (lower WSC). (Oliviera et al., 2017) There is also new evidence that, while inoculated alfalfa produced changes in milk production and rumen dry matter digestibility, lack of effect on rumen N metabolism resulted in no detectable change in energy-cdorrected milk yield. (Monteiro et al., 2021)

Direct Microbial Effects

It is also likely that some direct microbial effects of inoculation contribute to observed increases in animal performance. LAB could compete directly with other microorganisms through the production of a variety of small molecules to inhibit competitors and pathogens (Axelsson, 2004; De Vuyst, 1994; Madigan et al., 2015). They have also been observed to produce bacteriocins, which have previously been shown to inhibit pathogenic bacteria including Clostridial species (Gollop et al., 2005; Bali et al., 2016). While present, the role of bacteriocins and other defense molecules in the preservation of silage is inconclusive (Broberg et al., 2007). However, if active, these metabolites have the potential to alter both the silage microbial community as well as the rumen microbial community.

The choice of inoculant plays a role in the efficacy of inoculation and it is difficult to measure its impact. LAB inoculants differ greatly in their efficacy between strains. Specific strains are often best suited to specific forage species and conditions and are marketed accordingly. LAB appear to demonstrate autochthonous characteristics derived from their original environment, which may help explain the wide variety in the efficacy of silage inoculants between strains of the same species (Ávila et al., 2020).

Conclusions

Silage quality is determined by both the forage and the microbial community of the silo. While the forage makes up the vast majority of the feed by weight, its conservation through fermentation has a major effect on its nutritional profile. Making good silage quickly ensures that the maximum value of fresh forage is preserved, but inoculation may hold benefits beyond the conservation of forage quality. In addition to lactic, acetic, and propionic acids, hundreds of other organic molecules are produced during fermentation. Some of these may be directly inhibitory to spoilage or pathogenic organisms. All of these factors likely contribute to observed improvements in animal performance in response to silage inoculation. Further work is needed to elucidate the specific mechanisms and to potentially harness these benefits more consistently for animal production.

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