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Interaction of starter cultures and nonstarter lactic acid bacteria in the cheese environment[1]

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ABSTRACT

The microbiota of ripening cheese is dominated by lactic acid bacteria, which are either added as starters and adjunct cultures or originate from the production and processing environments (nonstarter or NSLAB). After curd formation and pressing, starters reach high numbers, but their viability then decreases due to lactose depletion, salt addition, and low pH and temperature. Starter autolysis releases cellular contents, including nutrients and enzymes, into the cheese matrix. During ripening, NSLAB may attain cell densities up to 8 log cfu per g after 3 to 9 mo. Depending on the species and strain, their metabolic activity may contribute to defects or inconsistency in cheese quality and to the development of typical cheese flavor. The availability of gene and genome sequences has enabled targeted detection of specific cheese microbes and their gene expression over the ripening period. Integrated systems biology is needed to combine the multiple perspectives of post-genomics technologies to elucidate the metabolic interactions among microorganisms. Future research should delve into the variation in cell physiology within the microbial populations, because spatial distribution within the cheese matrix will lead to microenvironments that could affect localized interactions of starters and NSLAB. Microbial community modeling can contribute to improving the efficiency and reduce the cost of food processes such as cheese ripening.
Key words: cheese, interaction, starter culture, nonstarter lactic acid bacteria, metabolism

THE PLACE OF MICROBES IN CHEESE-MAKING

The potential for controlling the course of fermentation and ripening is a strong driver for developing defined cultures. Concurrently, there is consumer demand for traditional products. Both perspectives can benefit from a better understanding of microbial community interactions. According to their roles, the microbiota involved in the process of cheese manufacture and ripening can generally be divided into 2 groups: starter lactic acid bacteria (starter **LAB** or **SLAB**), such as mesophilic lactococci for Cheddar cheese, and adventitious nonstarter LAB (**NSLAB**), such as lactobacilli. The SLAB are mainly responsible for acid development during cheese production and contribute to the initial ripening process (Beresford et al., 2001). The NSLAB have been shown to play a somewhat contradictory role during ripening by enhancing flavor development or deteriorating cheese quality (Martley and Crow, 1993). The microbial succession during cheese ripening is related to the ability of the microbial populations to adapt to specific environmental conditions, influencing the features of cheeses. The microbiota of long-ripened cheeses has been widely studied (Neviani et al., 2013; Santarelli et al., 2013; Gatti et al., 2014).

Flavor develops in cheese by the combined metabolic activity of the microbial community on milk fat, proteins, and carbohydrates, accompanied by further enzymatic and chemical conversions in the cheese matrix. The major LAB metabolic pathways involved in cheese flavor formation are metabolism of lactose (or glycolysis) and citrate, as well as proteolysis and the subsequent catabolism of AA (Figures 1 and 2). The release of free fatty acids (lipolysis) and their metabolism can be also involved but to a lesser extent (Lazzi et al., 2016). Specifically, in the characterized aroma profile of Cheddar, one half of the potent odorants originate from lactose fermentation or citrate degradation (and a few from lipolysis), and the other half result from leucine and methionine degradation (Yvon and Rijnen, 2001). Methional and methanethiol, which are the major aroma compounds produced from methionine, contribute to the Cheddar aroma and the desirable garlic note, respectively (Yvon and Rijnen, 2001). This review will focus mainly on semihard and hard cheeses, and will not attempt to cover the advances made in understanding microbial interactions in smear-ripened and mold-ripened cheeses.

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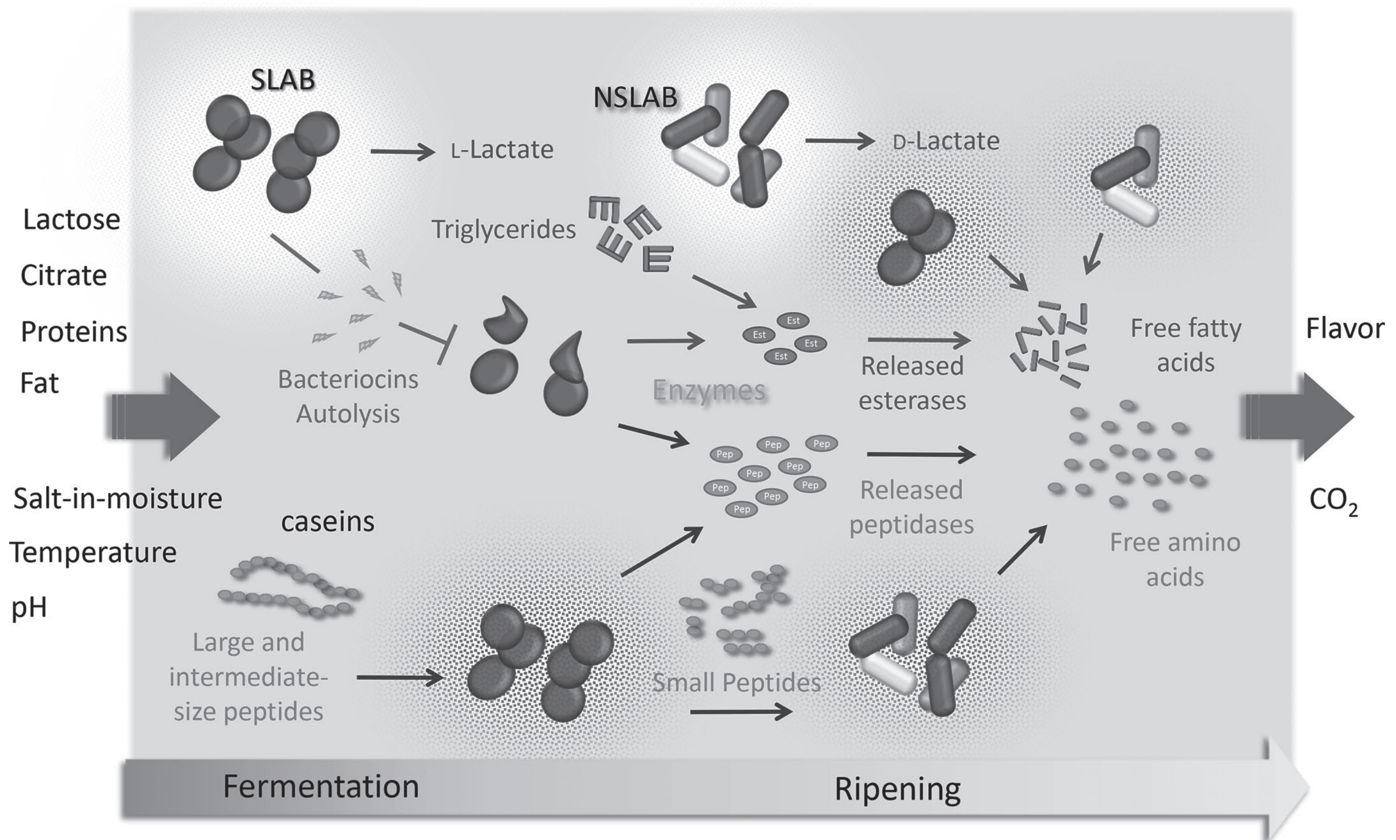

Figure 1. Factors influencing the ecological interactions among microorganisms in cheese. Schematic representation of possible interactions among starter lactic acid bacteria (SLAB) and nonstarter lactic acid bacteria (NSLAB) during cheese manufacture and ripening. Competition for residual lactose between SLAB and NSLAB depends on the salt-in-moisture (S/M) content. At low S/M, residual lactose is mainly converted to L-lactate by salt-sensitive SLAB in the absence of NSLAB. At high S/M, SLAB activity is reduced, so the greater residual lactose may be converted to D-lactate by NSLAB, particularly at higher ripening temperatures (top). The ability of SLAB and NSLAB strains to produce bacteriocins confers a competitive advantage. Cellular lysis induced by bacteriocins or autolysis leads to release of enzymes such as peptidases and esterases (center). The SLAB degrade large and intermediate-sized peptides, providing smaller peptides for the proteolytic system of NSLAB. Intracellular bacterial peptidases released after autolysis may degrade small peptides to free AA. Microbial and chemical conversion of metabolites and AA subsequently contributes to flavor formation (bottom). Color version available online.

Role of Starter Cultures

The LAB are gram-positive bacteria that produce lactic acid as a primary fermentation end product, so they are useful as starter cultures to aid in coagulation of milk proteins during the process of cheese making. For artisanal cheese products, the back-slopping technique has traditionally been used, which requires the inoculation of milk with whey or fermentate. Starter culture mixes consisting of unknown strains are termed "undefined starters." Further efforts in controlling starter quality have led to defined starter cultures, consisting of a specific number of strains of bacteria that may have been isolated from undefined starter cultures (Kelleher et al., 2015). The application of defined starter culture blends and rotation aims to ensure consistency of the fermentation process (Kelleher et al., 2015). However, when strain diversity is reduced, blends may become susceptible to several factors such as carbon and nitrogen constraints, salt stress, temperature and pH changes, as well as phage predation during milk fermentation (Gatti et al., 2014). Mixed-strain and undefined cultures may be more resilient and display a more robust performance (Erkus et al., 2013), which is enhanced by the presence of a rich consortium of microbes. In spite of increasing efforts to identify the microbial composition of mixed cultures, little is known about diversity at the strain level, mainly due to the need to develop molecular tools to investigate the presence of specific strains (Johansen et al., 2014). Metagenomics has been applied recently to study the structure of microbial communities in undefined and defined starter cultures; however, resolution at the strain level is still difficult to achieve (Erkus et al.,

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