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Lactic metabolism revisited: metabolism of lactic acid bacteria in food fermentations and food spoilage

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Sensory properties, shelf life, and safety of a majority of fermented foods are determined by the metabolic activity of food fermenting lactic acid bacteria. This communication reviews major metabolic routes of lactic acid bacteria, and indicates how metabolism is influenced by the environmental conditions or manipulated for improved control of food fermentations. Emphasis is placed on homofermentative and heterofermentative metabolism of carbohydrates, organic acids, and the conversion of amino acids with major impact on food safety and quality. In addition to the role of lactic metabolism in food fermentations, their implications for food spoilage are discussed.

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Introduction

The term 'lactic acid bacteria' (LAB) describes as group of Gram-positive bacteria that share metabolic and physiological characteristics [1–3]. Suitable criteria to define the term LAB have been lacking for most of the 20th century and the term has been associated with food-fermenting or probiotic organisms, often including bifidobacteria. Currently, the term LAB describes organisms in the order *Lactobacillales* [4], confirming the suggestion that LAB constitute a phylogenetically homogenous group [1]. LAB include environmental organisms, members of plant microbiota, commensals of humans and animals, and opportunistic or obligate pathogenic organisms [4]. Five of the six families of LAB also include food fermenting organisms [4]; *Lactobacillaceae* and *Leuconostococcaceae* comprise predominantly non-pathogenic organisms with a safe tradition of use in food fermentations (Figure 1) [4]. Food-fermenting LAB excel at exploitative competition and inhibit competitors by combining rapid utilization of abundant carbohydrates with accumulation of lactic and acetic acids. The evolution of LAB is shaped by reduction of genome size to achieve niche adaptation [5]. The reduction of the genome size was associated with abandoning the metabolic efficiency and versatility that are characteristic of the closely related bacilli. Abandoning the metabolic efficiencies of aerobic or anaerobic electron transfer chains, however, enables LAB to adhere to an 'iron free diet' and to occupy plant or animal associated ecological niches where lack of iron limits bacterial growth [6]. LAB dominate fermentation microbiota in a majority of fermented foods (Figure 1) but are also relevant as food spoilage organisms.

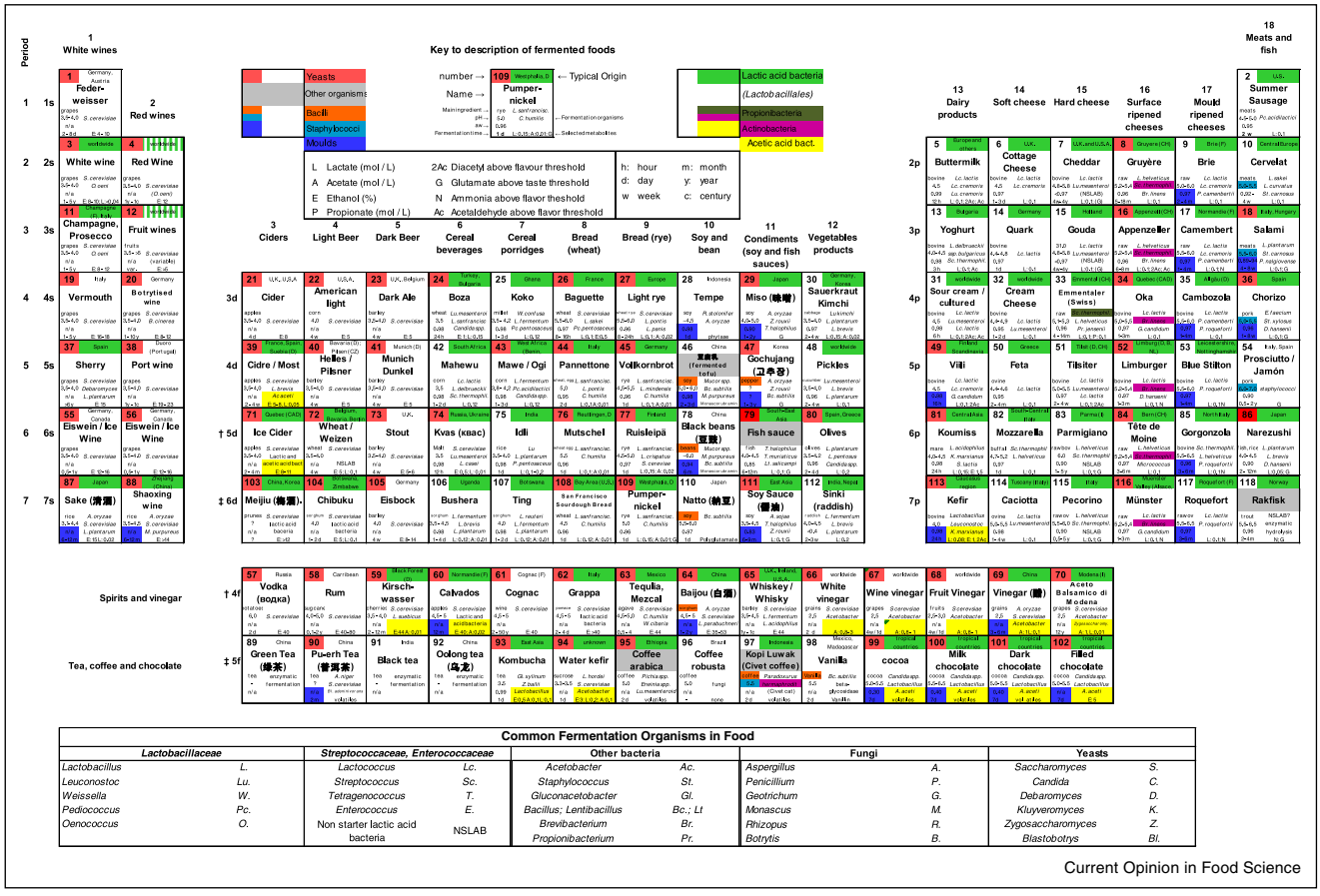
Metabolism of lactic acid bacteria: an overview

LAB have been classified as obligate homofermentative, facultative heterofermentative, and obligate heterofermentative [1–3]. The pentose phosphate pathway for homofermentative fermentation of pentoses (Figure 2) [7], however, is not accommodated in this classification. Moreover, major metabolic differences and branching points are dependent on the pathway employed for fermentation of hexoses rather than the ability to ferment pentoses (Table 1). In LAB fermenting glucose via the Emden–Meyerhoff pathway (Figure 2a), carbohydrates are preferentially transported by PTS systems, metabolism of sugars other than glucose is subject to carbon catabolite repression, pyruvate is the central branching point of metabolism, and fructose is exclusively used as carbon source (Table 1) [2,8,9]. In LAB fermenting glucose via the phosphoketolase pathway (Figure 2b), PTS systems are not functional, metabolism of disaccharides is preferred over glucose fermentation, acetyl-phosphate is the central branching point of metabolism, and fructose is preferentially or exclusively reduced to mannitol (Table 1) [8,10]. This communication aims to summarize recent advances related to lactic metabolism with emphasis on respiration, homolactic fermentation of pentoses, the utilization of lactate and diols, and their relevance for food quality.

Homolactic metabolism of hexoses and pentoses

Pyruvate is the key branching point of homolactic metabolism of hexoses (Figure 2). The fate of pyruvate depends on the availability of oxygen and substrates. Anaerobic metabolism under substrate limitation is

Figure 1



Periodic table of fermented foods providing an overview on the diversity of products, fermentation organisms, and raw materials. Fermented foods are grouped by product category and ranked within a group by flavour intensity or ripening time where applicable. Colour coding of specific fields indicates the presence of specific groups of fermentation organisms (see key on top of table); typical organisms, typical concentration of metabolites, and characteristic ripening/fermentation times are indicated. Water activities are not presented for dry foods or alcoholic beverages. Food products are generally listed in the language of origin; translations are provided where possible. The figure is formatted for large scale (A0) printing.

mediated mainly by pyruvate formate lyase (Figure 3a) [7,9]. Lactate is the main product of metabolism when the fermentable carbohydrates are abundant (Figure 3b). Aeration allows the alternative regeneration of co-factors (Figure 3c) but lactate generally remains the major metabolite of most LAB growing aerobically [11–13].

Many LAB are conditionally respiring [14]. LAB are auxotroph for heme (all LAB) and menaquinone (some LAB) but the availability of heme (and menaquinone) in the fermentation substrate supports cofactor recycling and proton export by respiration (Figure 3d) [15]. Respiration shifts homofermentative metabolism towards acetate and acetoin as major metabolites (Figure 4) [6,16].

Homolactic LAB occur as sole fermentation microbiota in many in meat and dairy fermentations and the fermentation of condiments at high salt concentrations; in vegetable and cereal fermentations, they are found in association with heterolactic LAB (Figure 1). Homofermentative metabolism of carbohydrates in food yields lactate as sole or major product of metabolism (Figure 1); exceptions include soy fermentations with *Tetragenococcus halophilus* where low concentrations of hexoses favour metabolism by pyruvate formate lyase (Figure 1). *Carnobacterium* spp., which grow on vacuum packaged meats and fish, preferentially metabolize hexoses via pyruvate formate lyase [4].

Food fermentations with LAB are not aerated (Figure 1) and thus do not support respiration. The cytochrome oxidase of LAB, however, is active at low oxygen concentrations and may contribute to oxygen elimination during initial stages of food fermentations [14]. Genes required for respiratory metabolism are expressed even in