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Mini-Review: The current role of lactic acid bacteria in beer spoilage

Few bacteria and yeast species are able to tolerate the antibacterial hurdles of beer and change its sensory properties such as smell, appearance, and texture. Tolerance to hop acids in particular is considered to be crucial to the survival of microorganisms in this hostile environment. Thus, the spectrum of beer-spoiling microorganisms is limited, but subject to slight changes in composition. Lactic acid bacteria (LAB) of the *Lactobacillus* and *Pediococcus* genera constitute the major part of this restricted group. Depending on their beer-spoilage potential and frequency of occurrence, each beer-spoiling species has its individual hazard potential. This hazard potential characterizes the danger the single species exerts on beer. The most dangerous beer spoiler is still the species *L. brevis*. It is vital for brewing microbiologists to be up to date with all the species with beer-spoilage ability. In the past decade, two beer-spoiling species, *L. cerevisiae* and *L. curtus*, have been newly described and two further species, *L. acetotolerans* and *L. rossiae*, were discovered to contain isolates with beer-spoilage potential. The mini-review gives an overview of all currently known LAB species with beer spoilage potential highlighting their species specific traits and their distribution in brewing environment. In addition to the species-specific approach, brewing microbiologists focus on species-independent strategies to reliably detect single isolates with beer-spoilage potential. A promising approach is the examination of genes located on mobile genetic elements such as plasmids that constitute a large portion of the beer-spoilers' genomes and are taken up by horizontal gene transfer.

Descriptors: beer spoilage, brewing, lactic acid bacteria, *Lactobacillus*, microbiology, *Pediococcus*

1 The two faces of lactic acid bacteria in brewing

Lactic acid bacteria (LAB) play an important role in the food industry – a positive role if deployed purposefully like yeast in the baking and brewing industry or a negative role as food-spoilage organisms by reducing the generated products' quality. In the brewing industry, LAB also exert positive or negative effects on the product depending on their intentional application or unintentional appearance in beer and its preliminary stages.

Some LAB species, especially those with hop-sensitive, thermophilic and homofermentative character and that are unable to produce diacetyl and biogenic amines (e.g. *Lactobacillus (L.) amylolyticus*), can be added to wort or the mash [16, 88]. The subsequent pH decrease results in numerous positive effects during the preliminary stages of beer production and increases the final beers' quality [9, 27, 56]. LAB can also be regarded as positive effectors if deployed as starter cultures in the production of specific beer (e. g. Belgian lambic beer or German Berliner Weisse sour beer) and modern craft beer styles [15, 91]. Another characteristic of LAB that has been the subject of research in the past decade is the ability to produce low-molecular and heat-stable proteins called bacteriocins that are able to restrict the growth of spoilage microorganisms without affecting the brewing yeast [45, 59, 88].

The more important role of LABs in the brewing industry is their role as spoilage organisms. Thus, it is worth noting that beer is protected from microbially triggered spoilage by different intrinsic and extrinsic factors. Process steps that reduce the germ load in beers, such as cold storage and filtration, are designated extrinsic factors in brewing science. The intrinsic factors of beer, called 'hurdles' according to *Leistner* [52, 53], are the ethanol and hop content, the low beer pH value, the presence of carbon dioxide and absence of oxygen as well as the lack of nutrients such as fermentable carbohydrates, vitamins and amino acids [57, 76]. Those intrinsic factors prevent the growth of pathogens such as members of the *Bacillus* and *Staphylococcus* genera in beer [17, 57]. Beer types with reduced intrinsic properties such as alcohol-free beer or low-hopped wheat beer are generally considered to be more susceptible to non-pathogen microbial spoilage [64]. The chemical and physical modes of action of the different intrinsic and extrinsic factors on beer-spoilage microorganisms are described in various publications [10, 57, 78, 86, 90, 94].

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2 The distinct group of beer-spoiling lactic acid bacteria

A few species can tolerate the adverse milieu, which is characterized by the presence and degree of expression of the particular

Table 1 Overview of beer-spoiling species, additional brewery-specific properties and related literature sources (excerpt from [43, 44, 66])

Species name	Beer-spoilage potential	Occurrence frequency	Primary/secondary contamination	Species-related literature sources
L. acetotolerans	+	ND	s	[31]
L. backii	++	↑↑	p	[85]
L. brevis	++	↑↑↑	p/s	[61, 63]
L. (para-)buchneri	+	↑↑	s	[32, 41]
L. (para-)casei	+	↑↑	p	[21, 60]
L. cerevisiae	+	ND	p	[51]
L. (para-)collinoides	++	↑	p	[18, 79]
L. coryniformis	+	↑↑	s	[1]
L. curtus	ND	ND	ND	[2]
L. harbinensis	+	↑↑	p/s	[55, 58]
L. lindneri	++	↑↑	s	[41, 54]
L. paucivorans	++	ND	p	[29]
L. (para-)plantarum	+	↑↑	s	[24, 61]
L. rossiae	+	↑	p/s	[22, 68]
Pd. damnosus	++	↑↑	p	[20, 23, 49]
Pd. claussenii	+	→	p	[20, 26]
Pd. inopinatus	+	→	p	[3, 46]

++ = very high / strong, + = high / strong or positive, ND = not determined;
↑↑↑ = mean percentage of incidents ≥ 15 %; ↑↑ = mean percentage of incidents 5 – 15 %, ↑ = mean percentage of incidents 1 – 5 %, → = mean percentage of incidents < 1 %; p = more primary contamination observed, s = more secondary contamination observed, p/s = nearly identical distribution between primary and secondary contamination

hurdles, and proliferate therein. In addition to several yeast species, called ‘wild yeasts’ to describe their unintentional appearance as opposed to the culture brewing yeast, and a few gram-negative species of the *Pectinatus* and *Megasphaera* genera, the gram-positive LAB form the largest group of beer-spoiling microorganisms (BSM). In contrast to non-spoilage members, spoilage LAB possess numerous active (= energy consuming) and passive (= energy neutral after build-up and/or activation) defense mechanisms [11, 76, 77, 89]. The tolerance towards the antimicrobial effects of hop-derived iso-α-acids is considered to be the crucial characteristic of gram-positive beer-spoilage bacteria [70, 71, 75, 77]. Consequences of bacterial growth in beer can be alterations in smell, taste, texture and/or appearance of the contaminated beers, depending on the inhabiting species, strain and cell count [76]. The source of contamination is characterized as primary if contamination occurs in the early stages of the brewing process (from the brewhouse to bright beer tanks) or as secondary if contamination occurs in later stages (after filtration) [5-7].

The beer-spoiling (BS) LAB belong to the *Lactobacillales* order that comprises six families to date (see: List of prokaryotic names with standing in nomenclature, http://www.bacterio.net). In addition to a few species of the *Leuconostoc* and *Lactococcus* genera with little beer-spoilage potential (BSP), certain members of the *Lactobacillaceae* family, which comprises the rod-shaped *Lactobacillus* [13] and the coccoid *Pediococcus* (*Pd.*) [20] genera, have an impact as BSM. Up to now, the heterogeneous LAB group of strictly fermentative bacteria list more than 200 species [33, 65, 86, 93] with only a minor fraction possessing the potential to spoil beer to some extent. From a phylogenetic point of view, BS species do not cluster together but are interspersed with non-spoiling species [25, 30, 33, 65, 66, 69, 72-74, 77, 87].

3 Current state of knowledge about beer-spoiling LAB species

It is essential to note that the group of BSM is not self-contained, but subject to certain compositional alterations caused by re-namings, new descriptions and technological advances in beer production. For example, two species with BSP, *L. cerevisiae* and *L. curtus*, were newly described in 2017 [2, 51]. It is of exceptional relevance for brewing microbiologists that certain species can acquire the ability to tolerate the adverse conditions of beer milieu over time as part of adaptive evolution [19, 35]. This acquisition is associated with the uptake of small mobile DNA units such as plasmids and transposons by horizontal gene transfer, which may lead to selective advantages [28, 34, 39, 78, 80, 92]. *L. rossiae* may serve as an example as this species was described in 2005, but was only recently characterized as beer spoiling [22, 43, 68]. Consequently, it is vital for brewing-microbiological quality control staff to be up to date with all species that pose a risk to their product.

Table 1 shows a current overview of the BS LAB species compiled from numerous literature sources [4, 8, 5-7, 42-44, 50, 66, 67].

A very high BSP (see Table 1) corresponds to the classification “obligate beer-spoiler” as characterized by *Back* and a high BSP to “potential beer-spoiler” [5]. As a consequence of BSP and frequency of occurrence, the most hazardous species in the brewing industry is *L. brevis*, followed by *L. backii*, *L. lindneri* and *Pd. damnosus* [66].

In brewery quality control, the species-dependent approach is the method of use as, in most cases, the knowledge about the contaminating species results in information about the possible risk to beer quality. However, several BS species comprise spoiling and non-spoiling strains (like the most dangerous beer spoiler *L. brevis* [11, 48, 62, 63, 89]). Based on this knowledge, species-independent approaches focus on diagnostic marker genes (DMG) which reliably separate BS from non-BS strains faster than the beer inoculation or challenge test, which is currently in use but very time consuming [34, 81]. No correlation was found between the metabolic capabilities in terms of the carbohydrate, amino acid and organic acid metabolisms of BS and non-BS strains [14, 34-36, 77]. These analyses also revealed that brewery-specific genes were not found within the core genome of a strain, but within conserved clusters on plasmids. Plasmid-encoded brewery-specific genes were, in particular, located between genes related to the key characteristic hop tolerance, but also between genes related to fatty acid biosynthesis or metabolic traits like the arginine deiminase pathway [34-36]. Prominent DMGs are *horA*, *horC*, *hitA*, *bsrA*, *bsrB*, ORF5 and *fabZ* [12, 37, 38, 40, 47, 48, 82-84]. A combination of species-specific, chromosomally encoded and plasmid-encoded traits seems likely to be the main reason why some strains are able to overcome the beer-specific hurdles.

Author contributions

All authors contributed to the study conception and design. The first draft of the manuscript was written by Jennifer Schneiderbanger and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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