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Effects of cultivation media and NaCl concentration on the growth kinetics and biogenic amine production of *Lactobacillus reuteri*

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Abstract: We analysed and compared the ability of four strains of *Lactobacillus reuteri* of sheep origin ranked as NSLAB (non-starter lactic acid bacteria) to grow and produce biogenic amines (BA) under cultivation conditions varying in cultivation media and salt content. The production of biogenic amines was primarily dependent on the growth rate of *L. reuteri* under particular cultivation conditions. From among produced BA, tyramine appeared as the dominant one while *L. reuteri* CCM 3644 possessed the most potent aminogenic ability. The influence of NaCl on the growth and production of BA was dependent on their concentration. Higher salt concentration (≥ 3% w/v) significantly inhibited the production of BA. On the contrary, the addition of 1–2% of NaCl w/v significantly improved the production of BA by three tested strains of *L. reuteri* (CCM 3642, 3644, and 3645). Finally, to better describe the production of BA over time, the relations between selected variables were calculated using linear regression. The appropriate fitting and the corresponding equations suggested the polynomial (degree 2) or exponential relations between the increasing concentration of NaCl and the concentration or calculated specific production rates of produced BA.

Keywords: histamine; regression analysis; salt concentration; tyramine

Foodborne intoxications are mainly caused by the presence of toxins of microbial origin such as bacterial exotoxins, mould mycotoxins and biogenic amines (Benkerroum 2016). Fermented products, especially cheeses, belong among the most important exogenous sources of biogenic amines (Perin and Nero 2017). In cheeses, the content of the two most harmful biogenic amines (BA), histamine and tyramine, varies from 0 mg kg^{-1} (Mozzarella) to 996.5 mg kg^{-1} (Turkish Civil) and from 0 mg kg^{-1} (Pasta filata cheese from ewe's milk) to 1 585.4 mg kg^{-1} (Blue veined cheese), respectively (Benkerroum 2016). In general, BA represent a structurally heterogeneous group of biologically active low-molecular-weight nitrogenous compounds arising from decarboxylation of free amino acids in plants, animals and humans (Linares et al. 2012; Renes et al. 2014). Under the physiological condition, the human organism is able to metabolise the intake of a low amount of BA due to the detoxification system

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involving amino oxidases and transferases (Doeun et al. 2017). However, an excessively increased level of BA in the human organism causes nausea, headaches, urticaria, palpitations, changes in blood pressure, breathing difficulties and in some cases it may lead to development of anaphylactic shock (Benkerroum 2016). Although the increased presence of BA in food threatens human health, the European Union possesses no adequate legislation to limit the content of BA in dairy products (EFSA 2011).

Lactic acid bacteria are the main source of BA formation in dairy products (Perin and Nero 2017). The occurrence of *Lactobacillus reuteri* among the NSLAB (non-starter lactic acid bacteria) is rather rare, suggesting the contamination from faecal materials. However, their diverse metabolic production significantly contributes to the final quality, safety and organoleptic properties of dairy products (Gobbetti et al. 2015; Hou et al. 2015). Among others, these bacteria are capable of producing BA such as histamine and tyramine, the amines frequently responsible for foodborne intoxication in sensitive consumers (Ladero et al. 2010; Gobbetti et al. 2015). BA influence the quality of cheese as they cause an increase in pH and eye development due to the formation of carbon dioxide (Wüthrich et al. 2017). Consequently, we consider the BA-producing strains as potential spoilage organisms in cheese production. The objective of this study was to analyse and compare the ability of four strains of *L. reuteri* of sheep origin to grow and produce histamine and tyramine under different cultivation conditions varying in cultivation media and salt content (0–5% NaCl w/v). Moreover, we evaluated possible relations between BA production and cultivation parameters over time.

MATERIAL AND METHODS

Bacterial strains. Four *L. reuteri* strains were tested for their ability to produce BA (tyramine and/or histamine): *L. reuteri* CCM 3642 isolated from Pecorino Romano cheese; *L. reuteri* CCM 3643 isolated from sheep abomasum and two *L. reuteri* CCM 3644 and 3645 strains isolated from sheep milk. The strains were provided from the Czech Collection of Microorganisms (Brno, Czech Republic). Stocks of these cultures were kept in de Man, Rogosa and Sharpe (MRS) broth (MERCK, Darmstadt, Germany) at +4 °C.

Cultivation conditions. The tested lactobacilli were cultivated in MRS broth or in M17 broth (MERCK, Darmstadt, Germany) under aerobic condition at 37 °C for 72 h and 122 h. The lactose content in M17 broth was increased to 15 g L^{-1}. To evaluate the BA production, the corresponding cultivation media were supplemented with 0.2% of L-histidine w/v (MERCK, Darmstadt, Germany) and 0.2% of L-tyrosine w/v (Sigma-Aldrich, St. Louis, USA). The effect of NaCl (Centralchem, Banská Bystrica, Slovak Republic) on the production of BA was tested in both MRS and M17 broth with respective amounts of NaCl (0, 1, 2, 3, and 5% w/v). Overnight culture of tested strains was used in all experiments (input concentration ~10^6 CFU mL^{-1}).

Evaluation of growth kinetics. The growth of lactobacilli was evaluated by measuring the optical density (OD_{600nm}) using UV/VIS spectrophotometer (Spekol 1l Carl Zeiss; Jena, Germany) with plastic cuvettes (l = 1 cm). The non-linear fitting with the modified Gompertz equation published by Zwietering et al. (1990) was used to estimate the growth parameters of lactobacilli. The modified Gompertz equation described the logarithm of the relative optical density [$y = \ln (OD_\tau/OD_\tau = 0)$] and its dependence on the three main growth parameters: the lag phase of bacterial growth, the specific growth rate and the asymptote (Bargossi et al. 2015).

Determination of biogenic amine content. Quantitative and qualitative evaluation of BA production was analysed in cell-free supernatants acquired after centrifugation (9 000 RPM, 15 min) and performed by RP-HPLC with UV detector (Greif et al. 2006; Hladíková et al. 2012). The determination of BA required pre-column derivatisation with dansyl chloride (Sigma-Aldrich, St. Louis, USA). The production of BA was evaluated according to the modified Gompertz equation (Zwietering et al. 1990; Greif et al. 2006).

Statistical analysis. Each observed parameter was measured twice, expressed as mean ± SD. Student's *t*-test was used to determine the difference at each sampling group. Statistical analysis was based on a comparison of repeated measurements between two groups and the differences were considered significant when $P < 0.05$. In addition, the correlation analysis between various characteristics of lactobacilli growth and BA production was performed. The obtained data were processed using Microsoft Excel (Microsoft Corporation, Washington; USA) and Origin 8.1 (Microcal Software, Northampton, USA).

RESULTS AND DISCUSSION

Evaluation of growth characteristics. The growth of tested strains was monitored by measuring the optical density (OD_{600nm}) over time and the growth char-

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Table 1. The growth characteristics and the characteristics of biogenic amine production of tested *L. reuteri* strains cultivated in supplemented MRS broth that were calculated using the modified Gompertz equation (n = 2)

L. reuteri	Growth characteristics			NaCl (% w/v)	Biogenic amine production			
	A [ln (OD_∞/OD_0)]	μ_m (h^{-1})	λ (h)		λ_p (h)	n_p (mg $L^{-1}h^{-1}$)	c_{max} (mg L^{-1})	BA
CCM 3642	1.91 ± 0.03	1.12 ± 0.02	2.98 ± 0.04	0	6.03 ± 0.10	74.77 ± 0.06	1099.31 ± 9.53	tyramine
	1.88 ± 0.02	1.21 ± 0.02	2.99 ± 0.02	1	6.61 ± 0.04^a	89.39 ± 2.23^a	1187.58 ± 8.81^a	
	1.87 ± 0.02	0.79 ± 0.01^b	2.54 ± 0.03^a	2	5.79 ± 0.10	72.03 ± 0.04^c	1063.63 ± 10.53	
	1.88 ± 0.03	0.56 ± 0.01^b	2.16 ± 0.02^b	3	7.47 ± 0.09	54.38 ± 1.74^b	825.31 ± 6.97^b	
	1.90 ± 0.05	0.24 ± 0.02^b	30.21 ± 2.15^b	5	42.83 ± 0.53^c	27.52 ± 2.32^b	585.94 ± 0.98^c	
CCM 3643	1.88 ± 0.02	1.07 ± 0.02	3.20 ± 0.04	0	6.99 ± 0.13	98.10 ± 3.71	1102.57 ± 7.56	histamine
	1.85 ± 0.02	1.10 ± 0.02	3.13 ± 0.01	1	6.84 ± 0.23	108.11 ± 5.14	1131.07 ± 21.27	
	1.77 ± 0.02	1.02 ± 0.02	3.11 ± 0.03	2	6.87 ± 0.47	105.23 ± 4.76	1111.17 ± 28.43	
	1.70 ± 0.02^a	0.90 ± 0.04	3.20 ± 0.19	3	7.35 ± 0.36	96.79 ± 2.05	1150.18 ± 16.42	
	1.63 ± 0.03^a	0.09 ± 0.00^c	14.15 ± 0.01^c	5	26.75 ± 0.23^c	31.21 ± 0.93^b	675.93 ± 8.15^c	
CCM 3644	1.89 ± 0.01	0.88 ± 0.08	2.57 ± 0.01	0	6.01 ± 0.86	105.65 ± 0.06	898.08 ± 5.88	histamine
	1.91 ± 0.01	0.80 ± 0.03	2.22 ± 0.42	1	6.76 ± 0.68	131.98 ± 0.11^c	980.57 ± 9.18^a	
	1.85 ± 0.02	0.72 ± 0.02	2.12 ± 0.41	2	6.16 ± 0.78	132.46 ± 0.38^c	1012.09 ± 8.69^b	
	1.85 ± 0.02	0.50 ± 0.00^a	1.73 ± 0.01^c	3	8.80 ± 0.70	109.64 ± 1.75	976.46 ± 4.45^b	
	1.16 ± 0.02^c	0.19 ± 0.00^a	2.93 ± 0.15	5	45.03 ± 2.02^b	12.27 ± 1.14^c	363.97 ± 15.51^c	
				0	16.67 ± 0.41	11.74 ± 0.28	500.32 ± 10.98	tyramine
				1	18.50 ± 0.95	5.84 ± 0.28^b	523.15 ± 12.48	
				2	12.01 ± 1.20	3.09 ± 0.24^b	280.32 ± 9.96^b	
				3	4.45 ± 0.33^b	1.77 ± 0.00^c	75.83 ± 2.63^c	
				5	36.81 ± 1.06^b	0.87 ± 0.17^c	39.52 ± 1.85^c	
CCM 3645	2.06 ± 0.02	1.12 ± 0.02	3.24 ± 0.02	0	9.17 ± 0.06	19.90 ± 0.18	384.51 ± 3.24	tyramine
	2.00 ± 0.02	1.21 ± 0.02	3.00 ± 0.02^a	1	8.69 ± 0.05^a	16.51 ± 0.35^a	408.76 ± 3.46^a	
	1.95 ± 0.01^a	0.79 ± 0.01^b	3.48 ± 0.04^a	2	8.57 ± 0.08^a	14.51 ± 0.02^b	414.62 ± 4.01^a	
	1.94 ± 0.03	0.56 ± 0.01^b	3.38 ± 0.06	3	9.08 ± 1.03	12.83 ± 0.48^b	371.26 ± 4.78	
	1.93 ± 0.01^a	0.24 ± 0.02^b	25.08 ± 0.14^c	5	53.85 ± 1.06^c	0.04 ± 0.01^c	12.1 ± 0.12^c	

A – the asymptote describing the maximum value of the logarithm of the relative optical density reached; μ_m – the specific growth rate; λ – the lag phase; λ_p – the lag phase of metabolite production; n_p – the specific production rate; c_{max} – the asymptote describing the maximum metabolite concentration reached; n – number of parallels; means indicated by different lowercase letters in the same column differ significantly at $P < 0.05$; BA – biogenic amines

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acteristics were calculated by the modified Gompertz equation (Table 1). According to growth characteristics, changes in cultivation media and in salt concentration have already demonstrated presumptive intraspecies diversity among tested strains. In MRS broth, the corresponding asymptotes A [$A = \ln (OD_\infty/OD_0)$] were approximately the same among all tested lactobacilli. In M17 broth, *L. reuteri* CCM 3644 showed the highest growth potential (Figure 1). The maximum growth rate (μ_m) of lactobacilli cultivated in M17 broth was approximately 0.08 ± 0.03 h^{-1}. In M17 broth, lactose is the main source of carbon. It is known that many strains of *L. reuteri* are not able to ferment milk appropriately if they were primarily isolated from milk like two strains tested in this study: *L. reuteri* CCM 3644 and CCM 3645. But according to growth parameters, in particular the asymptote A, these two milk isolates grew significantly better ($P < 0.001$) in M17 broth than the other two isolates (Figure 1) suggesting that the milk origin itself may predetermine them to better metabolise lactose.

The major differences in growth characteristics were caused by the addition of an increasing content of salt. We observed that the addition of 3–5% NaCl w/v to MRS broth significantly decreased the asymptote A and slowed down lactobacilli growth ($P < 0.05$; 0.01; 0.001) (Table 1). However, the addition of 1% NaCl w/v to MRS broth slightly increased μ_m of *L. reuteri* CCM 3642, 3643, and 3645, suggesting that a small amount of salt in cultivation media could improve bacterial growth. The same effect was reported by Neysens et al. (2003). According to their observation, the cultivation of LAB in a medium supplemented with salt at a concentration higher than 3% w/v hinders bacterial growth, while a lower salt concentration (1–2% w/v) can exhibit a positive effect. Moreover, heterofermentative lactobacilli, such as *L. reuteri*, are in general more salt sensitive than homofermentative lactobacilli (Farnworth 2003).

By contrast, only *L. reuteri* CCM 3644 was able to grow in M17 broth containing an increasing amount of salt. In fact, differences in the values of the respective asymptotes A related to the salt content were still considerable. The most appropriate conditions were reached in M17 broth containing 1% of NaCl (w/v). However, the amount of 5% of NaCl (w/v) completely inhibited the growth of *L. reuteri* CCM 3644 in M17 broth.

Production of histamine and tyramine. The study of histamine and tyramine accumulation by *L. reuteri* strains implies that the above strains are able to produce L-histidine decarboxylase (EC 4.1.1.22) and/or L-tyrosine decarboxylase (EC 4.1.1.25), which convert L-histidine and L-tyrosine to histamine and tyramine, respectively. According to our results, the potential of tested lactobacilli to produce histamine and tyramine was closely related to their ability to grow under given cultivation conditions (Table 1). Gardini et al. (2001) emphasised the crucial role of the concentration of aminogenic cells in histamine/tyramine accumulation. The characteristics of BA production in MRS broth calculated according to the Gompertz

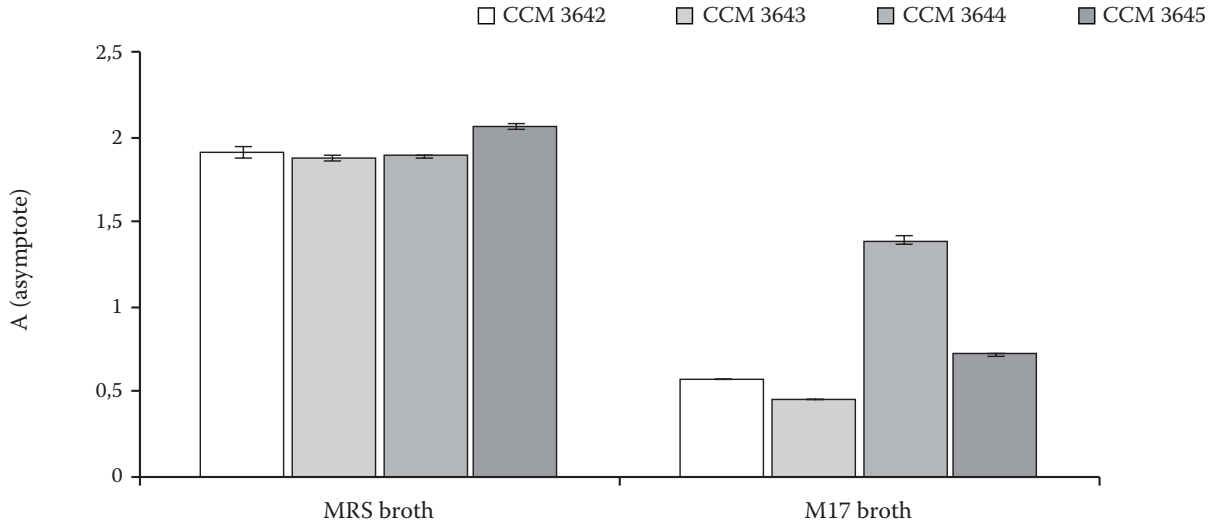

Figure 1. The growth of four *L. reuteri* strains under aerobic conditions (48 h; 37 °C) in supplemented MRS broth and in M17 broth is represented by the asymptote A [$A = \ln (OD_\infty/OD_0)$] calculated using the modified Gompertz equation

Number of parallels: $n = 2$

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equation are presented in Table 1. Among produced BA, tyramine appeared as the dominant one and *L. reuteri* CCM 3644 possessed the most potent aminogenic ability. As we expected, the production of BA in supplemented M17 broth was significantly reduced. Only *L. reuteri* CCM 3644 (milk origin) produced a comparable amount of histamine (638.18 ± 2.22 mg L^{-1}) like when cultivated in MRS broth, while the presence of tyramine was not detectable even after 122 h of cultivation similarly like the presence of histamine produced by *L. reuteri* CCM 3643. The strains *L. reuteri* CCM 3642 and CCM 3645 were able to produce tyramine (27.57 ± 0.86 and 15.22 ± 0.59 mg L^{-1}, respectively) after 122 h of cultivation.

The appropriate hazard level of ingested histamine is 50 mg, which represents the no-observed-adverse-effect level (NOAEL). Levels from 75 to 300 mg have been reported retrospectively to cause headache and flushing. In case of tyramine, an adult can tolerate 100–800 mg kg^{-1} bw (body weight) of dietary tyramine and levels > 1 080 mg kg^{-1} bw are toxic (FAO/WHO 2013). In conclusion, the toxic level of histamine was exceeded by all tested histamine producers cultivated in MRS broth. The toxic level of tyramine was not reached, but *L. reuteri* CCM 3642 was able to produce more than 1.0 g L^{-1} of tyramine after two days of incubation. Therefore these strains could significantly increase the content of tyramine and histamine in dairy products.

The addition of salt (1–5% w/v) to cultivation media strongly influenced the production of histamine and/or tyramine among the tested lactobacilli. Observing these changes, the addition of 1–2% NaCl w/v to MRS broth significantly increased the concentration of tyramine produced by *L. reuteri* CCM 3642 and CCM 3645 and of histamine produced by *L. reuteri* CCM 3644 together with their respective production η_{HA} and n_{TA} (Table 1). Several authors [Gardini et al. (2001); Greif et al. (2006); Buňková et al. (2011, 2012)] also observed the maximal production of BA in the presence of a lower concentration of NaCl (0.5–3.0% w/v) in cultivation media after cultivation of *Enterococcus durans*, *Lactococcus lactis, Enterobacter* spp., and *Enterococcus faecalis*, respectively.

Finally, the addition of higher amounts of salt (≥ 3% NaCl w/v) to MRS broth significantly reduced but it did not inhibit the production of BA in all tested lactobacilli strains ($P < 0.001$). In the same way, n_{HA}, and n_{TA} were significantly decreased and the lag phases of BA production were extended. According to the production of BA, the presence of NaCl in a cultivation medium at a concentration higher than 3% (w/v) is considered as inhibitive (Gardini et al. 2001; Suzzi and Gardini 2003).

The origin of our tested strains is closely connected with sheep milk and cheese manufacturing. In general, *L. plantarum* (32%), *L. brevis* (15%) and *L. paracasei* subsp. *paracasei* (12%) predominantly occur in sheep cheeses as NSLAB (De Angelis et al. 2001). The high content of tyramine or histamine in cheese could be due to the activity of non-starter lactic acid bacteria (NSLAB) of some *Lactobacillus* species, which are present at low numbers at the start of the manufacturing process and reach more than 6.0 log CFU g^{-1} at the end of ripening (Coda et al. 2006). Therefore, the presence of the tested *L. reuteri* strains in cheese could considerably increase the total amount of undesirable BA.

Relations between salt content and growth/production parameters of tested strains. To better understand possible relations between added salt (0–5% NaCl w/v) and the growth and BA production of tested lactobacilli, the regression analysis was conducted. We wanted to mathematically describe these relationships in order to be able to predict the future effect of added salt on the growth and BA production of tested lactobacilli under respective cultivation conditions. Gardini et al. (2001) published models describing relations between the concentration of NaCl, temperature and pH of cultivation media on the one hand and A, μ_m, λ of *Enterococcus faecalis* on the other hand. To our best knowledge, such models describing relations between environmental factors and growth and production parameters of *L. reuteri* strains have never been calculated.

We observed a strong negative correlation between NaCl concentration on the one hand and growth parameters (A; μ_m) as well as production parameters (c_{HA}, c_{TA}; n_{HA}, n_{TA}) on the other hand proving that increasing NaCl concentration may decrease the growth and production ability of tested lactobacilli. Figure 2 depicts the relations between μ_m, n_{HA}, n_{TA} and concentration of salt.

The appropriate fitting was performed and the corresponding equation was established (Table 2). The fitting suggested the polynomial relations between μ_m, n_{HA} and concentration of salt (c_{NaCl}) for the cultivation of *L. reuteri* CCM 3643 and CCM 3644 in MRS broth and exponential relation between n_{TA} and concentration of salt (c_{NaCl}) for the cultivation of *L. reuteri* CCM 3643. Moreover, in case of the cultivation of *L. reuteri* CCM 3644, a polynomial relation between concentration of produced histamine (c_{HA}) and

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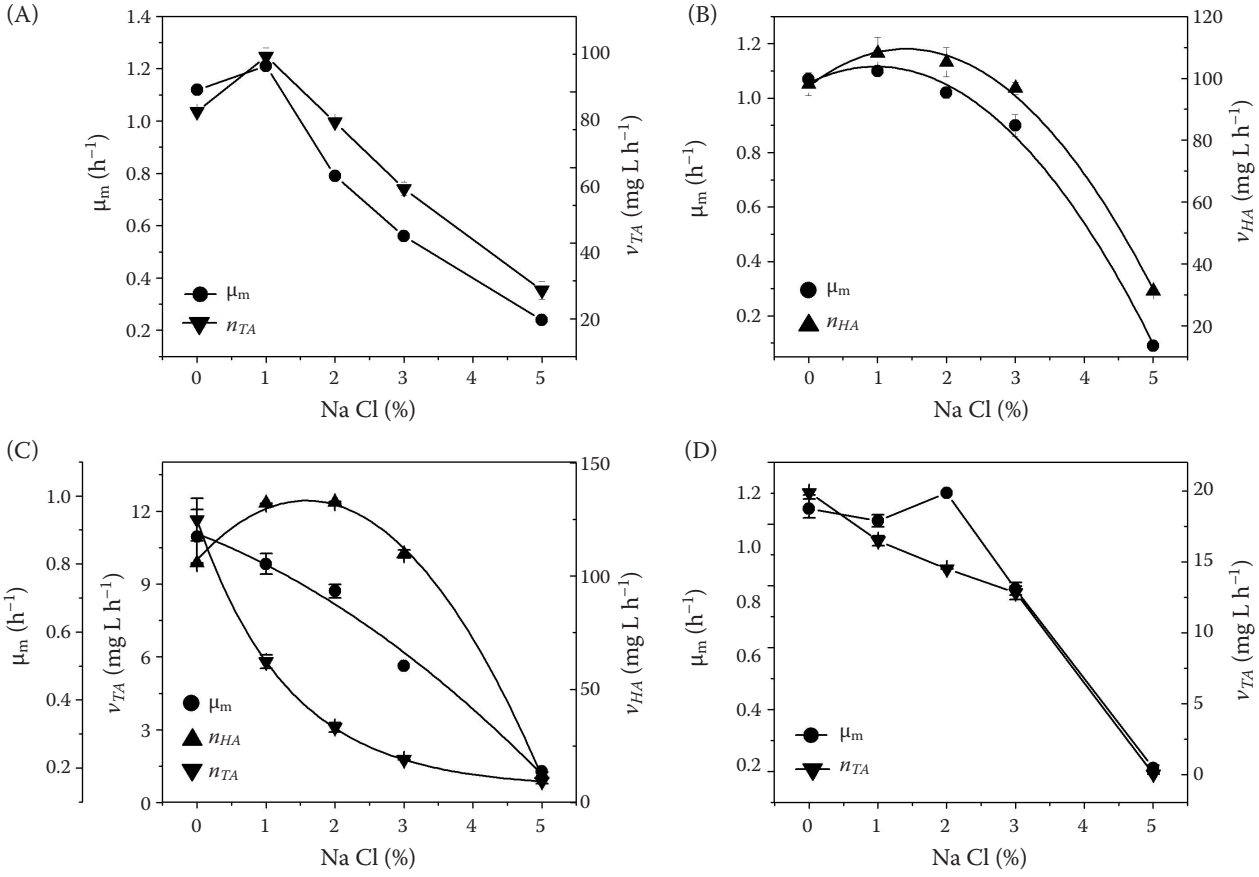

Figure 2. Graphical representation of relations between the concentration of NaCl (c_{NaCl}) and the growth and production characteristics of selected lactobacilli strains in MRS broth (n = 2); (A) *L. reuteri* CCM 3642, (B) *L. reuteri* CCM 3643, (C) *L. reuteri* CCM 3644, (D) *L. reuteri* CCM 3645

μ_m – the specific growth rate; ν_{HA} – the specific production rate of histamine; ν_{TA} – the specific production rate of tyramine

concentration of salt (c_{NaCl}) was determined (Table 2). In addition, a strong positive correlation between μ_m and parameters of BA production (c_{HA}, c_{TA}; n_{HA}, n_{TA}) was observed, confirming a strong relationship between cultivation conditions on the one hand and lactobacilli growth and production ability of lactobacilli towards BA on the other hand. According to these results, it is possible to regulate the final concentration of histamine and/or tyramine during fermentation processes more effectively.

Table 2. Mathematical relations between the concentration of NaCl (c_{NaCl}) in MRS broth and the growth and production characteristics of some lactobacilli strains (ν = 2)

Lactobacillus reuteri	Parameter	Equation of the model	R
CCM 3643	μ_m	$\mu_m = 1.055 + 0.123\ (c_{NaCl}) - 0.063\ (c_{NaCl})^2$	0.9913
	ν_{HA}	$\nu_{HA} = 99.63 + 20.13\ (c_{NaCl}) - 6.76\ (c_{NaCl})^2$	0.9983
CCM 3644	ν_{HA}	$\nu_{HA} = 107.43 + 31.98\ (c_{NaCl}) - 10.18\ (c_{NaCl})^2$	0.9981
	c_{HA}	$c_{HA} = 883.23 + 188.40\ (c_{NaCl}) - 58.16\ (c_{NaCl})^2$	0.9949
	ν_{TA}	$\nu_{TA} = 0.62 + 11.13 \times \exp[-0.76\ (c_{NaCl} - 0.01)]$	0.9992

R – correlation coefficient; μ_m – the specific growth rate; c_{HA} – the asymptote describing the maximum histamine concentration reached; ν_{HA} – the specific production rate of histamine; ν_{TA} – the specific production rate of tyramine

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CONCLUSION

The present study summarises the aminogenic potential of four strains of *Lactobacillus reuteri* under different cultivation conditions. In view of food safety, the contamination of dairy products by *L. reuteri* capable of producing histamine and/or tyramine poses a high risk for the end consumers. The parameters describing the time when the BA production reaches its maximum are relatively short in comparison with the duration of e.g. cheese-making processes. Together with the stability of histamine and tyramine produced in such manufacturing processes, the presence of aminogenic lactobacilli like NSLAB can finally cause serious health complications to sensitive consumers. Analysing and searching for relations between lactobacilli involved in manufacturing processes of dairy products and their growth and production abilities under such manufacturing processes will enable us to better predict the future composition of metabolites in final dairy products and to more effectively eliminate the potential health risk connected with the production of microbial metabolites.

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