



Could endophytic bacteria *Pantoea agglomerans* isolated from hop cones contaminate beer?

Tomas Hasek¹, Lenka Mravcova², Karel Krofta², Petra Patakova¹

¹ Department of Biotechnology, University of Chemistry and Technology Prague, Technická 5, 166 28 Prague 6, Czech Republic

² Hop Research Institute Co., Ltd., Kadaňská 2525, 438 01 Žatec, Czech Republic

*corresponding author: hasekt@vscht.cz

Abstract

Gram-positive bacteria, particularly lactic acid bacteria, are generally considered the primary potential contaminants of beer. However, given recent publications on the isolation of Gram-negative bacteria from hop pellets, it is important to also consider whether endophytic bacteria found in the above-ground parts of the hop plant, such as the facultatively anaerobic bacterium *Pantoea agglomerans*, might pose a potential risk during so-called dry hopping of beer. To find an answer to this question, we conducted practical experiments in which we intentionally inoculated various types of alcoholic and non-alcoholic beers, as well as culture media mimicking the beer environment. We subjected the inoculated beers to a 5-day incubation at two temperatures: 7 °C in a refrigerator and 30 °C in a thermostat. Our observations revealed that the main factor preventing the development of this type of contamination is the low pH of the beer, which is unsuitable for bacteria. Other contributing negative factors that prevent contamination are alcohol content and oxygen limitation. The only theoretical risk of contamination could be associated with improper storage of non-alcoholic dry-hopped beer at high temperatures.

Keywords: *Pantoea agglomerans*; hop endophyte; risk of beer contamination

1 Introduction

Hop, *Humulus lupulus*, has been used all over the world for more than a millennium and is a useful ingredient in the production of beer. It is valued not only for its bitter taste, but also because it protects beer from microbial spoilage (Bocquet et al., 2018). Of the various substances isolated from hops, xanthohumol exhibits the highest antimicrobial activity, followed by α - and β -bitter acids, but inhibition is limited to Gram-positive bacteria and selected yeasts (especially *Candida parapsilosis*) (Bogdanova et al., 2018).

Traditionally, hops are added to the wort during the wort boiling (kettle hopping) or to whirlpool tank (late hopping). However, dry hopping has recently gained popularity, as it allows a greater amount of aromatic substances, especially essential oils, to be added to the beer (Jelinek et al., 2018). This technique is based on adding

extra hops to already hopped wort and allows the extraction of volatile as well as non-volatile substances into the beer, which contributes to the final aroma and flavour of the brewed beer. The hop is added during fermentation or lagering/maturation in range of temperature 0–20 °C, so that the brewing process does not lead to loss of aromatic compounds (Hrabia et al., 2022).

The hop plant can be colonized by various microorganisms, including bacteria (such as from genera *Bacillus*, *Pantoea*, *Pseudomonas*, *Yersinia*) and fungi (such as from genera *Alternaria*, *Aspergillus*, *Fusarium*, *Penicillium*, *Rhizopus*, *Talaromyces*) (Riccioni et al., 2025; Krofta et al., 2021). Some of these can attack the plant, others can be tolerated by the plant and live with it in a delicate balance, and still others can be beneficial to the plant

(Young et al., 2023). Various strains of the bacterium *Pantoea agglomerans* have been repeatedly isolated from the above-ground parts of hop plants (Patakova et al., 2024; Kolek et al. 2021). *P. agglomerans* is a microorganism with dual properties and, in relation to plants, both pathogenic strains and strains with beneficial properties have been described, even used for plant protection (Dutkiewicz et al., 2016).

In dry hopping, hops are most often added in the form of granules (pellets). Pelletization is a process that facilitates the transport and storage of hops during beer brewing and standardizes the amount of hops added to beer (Jelinek et al., 2018). It was assumed that the pelletization of hop cones could eliminate the microorganisms present due to the high pelletizing temperature of up to 55 °C together with the high pressure used to form the pellets, which are packed into carbon dioxide-nitrogen-filled bags. These conditions should prevent the persistence of any microorganisms, together with a low water content of less than 10% (Young et al., 2023). Nevertheless, facultatively anaer-

obic bacteria *Pantoea agglomerans* were found to be able to grow in a sealed bag of hop pellets protected with nitrogen/inert atmosphere, if the bags of pellets were stored at an unsuitable temperature (Kolek et al., 2021), which is basically higher than 4 °C. *Pantoea agglomerans*, Gram-negative bacterium, has been

identified as relatively common cause of beer spoilage during fermentation, as well as yeast slurry spoilage (Manzano et al., 2011).

Given that *P. agglomerans* bacteria are often found on hops and can survive the pelletization process, and also due to the popularity of dry hopping, which does not destroy bacteria through heat, we decided to conduct a practical test. The aim of the test was to find out whether the bacterial strain *P. agglomerans* DBM 3797, isolated as an endophyte from hop leaves (Patakova et al., 2024), can grow in different types of beer stored under different conditions and thus answer the question of whether endophytes of this species can cause beer spoilage.

2 Materials and methods

2.1 Characterization of beer types tested

Brands of beer and their characteristics important for the tests are given Table 1.

2.2 Media preparation

For *Pantoea agglomerans* DBM 3797 growth, two types of media were prepared: the glucose medium (G) containing [g/L]: Glucose 20 (Penta), Peptone 0.5 (Carl ROTH), Yeast extract 0.2 (Merck), NaCl 1 (Penta), KCl 0.2 (Lachner), $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ 0.4 (Penta), $\text{CaCl}_2 \cdot 2\text{H}_2\text{O}$ 0.2 (Lachner), NH_4NO_3 1.5 (Honeywell Fluka) and the LB medium containing [g/L]: Tryptone 10 (Sigma Aldrich), Yeast extract 5 (Merck), NaCl 5 (Penta). Both types of media were sterilized in autoclave (3870ELV, Tuttnauer) for 20 min at 121 °C as well as other modified G media with identical content of glucose (G Birell medium

and G Krušovice medium) and also identical content of ethanol (G Gambrinus 10° medium) as in tested beers. Media characteristics are also given in Table 1. Ethanol was added into media after sterilization in an autoclave. The pH of the media was set at 4.65 to be similar to average pH of all beers tested.

Table 1 Brands of beer and their characteristics; selected characteristics of culture media mimicking beer

Beer/culture medium	Glucose (g/l)	Ethanol (% v/v)	Sugars* (g/L)	comment
Svijany 10°	–	4	0	non-pasteurized
Svijany 11°	–	4.8	0	non-pasteurized
Svijany 12°	–	5.0	0	non-pasteurized
Gambrinus 10°	–	4.3	<5	pasteurized
Birell NA	–	0.5	24	pasteurized
Krušovice NA	–	0.5	21	pasteurized
Glucose medium (G)	20	–	–	sterilized
Glucose medium (G) 5 % EtOH	20	5	–	sterilized
LB medium	–	–	–	sterilized
LB medium 4.0 %	–	4	–	sterilized
LB medium 4.8 %	–	4.8	–	sterilized
LB medium 5.0 %	–	5	–	sterilized
G Gambrinus 10° medium	5	4.3	–	sterilized
G Birell medium	24	0	–	sterilized
G Krušovice medium	21	0	–	sterilized

NA – non-alcoholic; *Sugars mean total amount of mono- and disaccharides given by the producer on the product. G Gambrinus 10°, G Birell and G Krušovice have the same composition as Glucose medium with the exception of glucose and ethanol.

and G Krušovice medium) and also identical content of ethanol (G Gambrinus 10° medium) as in tested beers. Media characteristics are also given in Table 1. Ethanol was added into media after sterilization in an autoclave. The pH of the media was set at 4.65 to be similar to average pH of all beers tested.

2.3 Beer preparation for experiment

Before inoculation, all beers were left in sterile Erlenmeyer flask for 10 minutes in ultrasonic bath for degassing of carbon dioxide. After that the beer was prepared for the cultivation. The pH of all tested beers was measured before inoculation.

2.4 Bacterial inoculum

The bacteria *Pantoea agglomerans* DBM 3797 stock cultures were maintained at -80°C in 30% glycerol as cryopreserved stocks. Bacteria were reactivated from this stock in fresh LB medium. The culture was performed in 250 mL Erlenmeyer flasks with 100 mL of media placed on a rotary shaker under the following conditions: 30°C , 150 rpm, 24 h. The culture was used as a 1% v/v inoculum for microbial cultivation in the particular beer or in fresh LB or glucose medium according to the setup mentioned above. The inoculum size was selected based on previous experience with the bacterial culture (Patakova et al., 2024) and in accordance with gen-

eral recommendations, which consider the range of 0.5–5% to be the optimal inoculum size (Sood et al., 2011).

2.5 Cultivation

The 250 mL Erlenmeyer flask filled with 100 mL of particular beer or prepared medium were inoculated by 1 mL (1% v/v) of overnight culture with the OD 2. The cultivation took part in thermostat with temperature set at 30°C and in refrigerator set at $6\text{--}8^{\circ}\text{C}$ for 168 hours. All beer brands and all types of culture media were tested in triplicate.

2.6 Sampling

The sampling was done every 24 h. The pH was measured in samples stored in 1.5 mL Eppendorf tubes by using pH meter (Eutech Instruments) and optical density (OD) was measured in microwell plates by multimode plate reader (Infinte® M200 Pro, Tecan) with set wavelength at 600 nm and shaking before the measuring. Absorbance at 600 nm was also measured in the culture medium before inoculation, and this value served as a blank. The marker of growth was considered to be the difference in absorbance between the value measured after inoculation and the value measured at the end of the culture. All the samples were monitored under optical microscope with the set magnification at $1000\times$ and use of an immerse oil.

2.7 Statistical analysis

All measurements were performed in triplicate; their means and standard deviations were evaluated using MS Excel software (Microsoft, USA).

3 Results and discussion

The research was conducted to determine the possible bacterial growth in beer contaminated with *Pantoea agglomerans* DBM 3797. Two types of media, as is shown in Table 1, were selected to mimic beer: a medium with glucose as a carbon source and LB medium, where bacteria use amino acids as a carbon source. Both types of media have already been confirmed as suitable for the

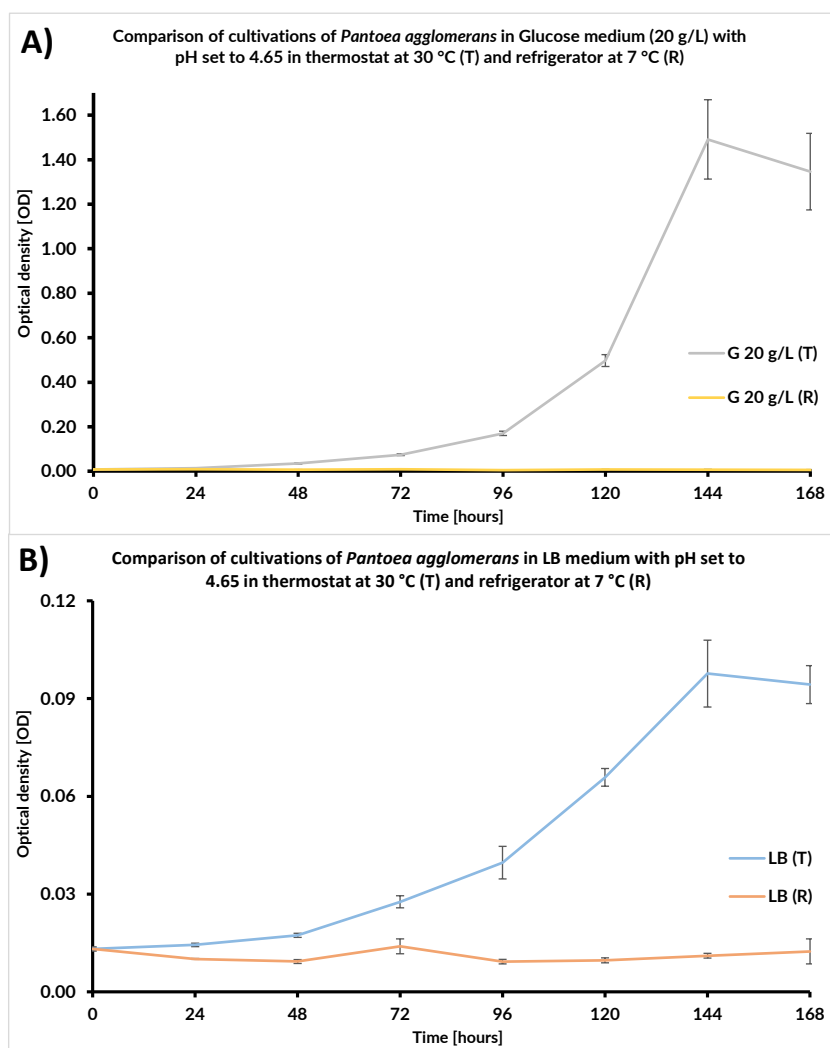


Figure 1 Growth of *P. agglomerans* in Glucose (A) and LB (B) media in thermostat (T) and refrigerator (R). (Please note that the y-axes in graphs A and B have different scales.)

growth of *P. agglomerans* (Patakova et al., 2024). Growth in beer and in synthetic media without hops, but containing equal amounts of ethanol or sugar (glucose) as tested beers was determined based on changes in optical density and pH. The tests were performed in thermostat (at 30 °C – optimal growth temperature for *P. agglomerans*) and in the refrigerator (at 7 °C) which was selected as an environment suitable for long-term beer storage, see Figure 1A and 1B. Unlike standard cultivation, where the initial pH is typically in the range of 6.5–7.0 (Patakova et al., 2024), in this experiment the pH in both media was adjusted to 4.65 to match the pH of beer. This low pH value led to a prolongation of the lag phase to 48–72 hours in both media. The combination of low pH and low temperature then led to nearly complete inhibition of growth in both media. Cultivation of *P. agglomerans* in LB medium is typically performed under aerobic conditions on a shaker. Because the cultures were static and unstirred at both cultivation temperatures, the resulting growth was more than 10 times higher in the case of glucose medium (Figure 1A and 1B) which shows that oxygen limitation significantly impaired the utilization of amino acids as carbon sources in LB medium. Shaken culture leads to more efficient supply of oxygen (Takahashi and Aoyagi, 2018)

necessary for growth in LB medium as demonstrated in inoculum preparation where sufficient concentration of cells for inoculation was reached after 24 h.

Growth was further tested in selected alcoholic beers and in modified culture media designed to mimic the beer environment, again in a thermostat at 30 °C and in a refrigerator at 7 °C; see Figure 2A–D. The highest growth was achieved in unpasteurized Svijany 10° beer both at 30 °C and in the refrigerator. A difference in growth was demonstrated between unpasteurized and pasteurized beer (compare Svijany 10° and Gambrinus 10°) which, however, were also manufactured using different methods. Furthermore, the data indicates that as alcohol concentration increased, the ability to grow decreased in both beers (Svijany 10°, 11°, and 12°) and in media with corresponding ethanol additions (LB 4.0%, LB 4.8%, and LB 5%). In addition, it was found that *Pantoea agglomerans* bacteria behaved differently in alcohol-glucose medium than in other cultivation environments, see Figure 3A, 3B. Filamentous growth demonstrated in Figure 3B suggests that glucose together with ethanol resulted in sub-lethal stress. The stress response in form of cell prolongation has already been documented in bacteria (e.g. Jones et al., 2013). An independent experiment conduct-

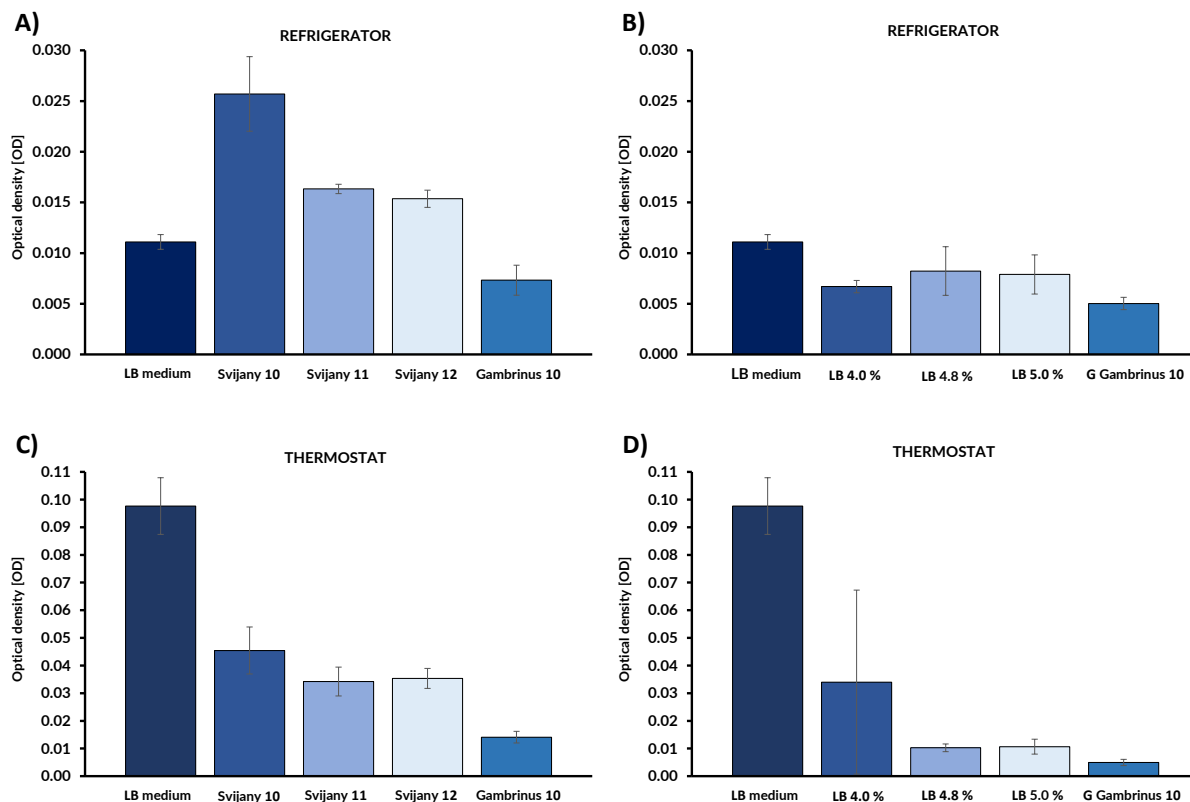


Figure 2 Growth in selected alcoholic beers (A, C) and in modified culture media designed to mimic the beer environment (B, D), in the thermostat at 30 °C (C, D) and in the refrigerator at 7 °C (A, B). (Please note that the y-axes in graphs A, B and C, D have different scales.)

ed at the Hop Research Institute, where the same bacterial strain was inoculated into 12° Budvar lager and 12° Pilsner Urquell lager, and after 48 h of cultivation in a BIOSAN RTS-C laboratory minibio-reactor (Biosan SIA, Latvia), confirmed our results, i.e. no growth was observed (data not shown, the experiment was performed just once).

In the case of non-alcoholic beers, a significant increase in *P. agglomerans* growth was observed in both Birell and Krušovice non-alcoholic beer, particularly at 30 °C, but also in the refrigerator when compared to alcoholic beers; see Figure 4A and 4B and compare with Figure 2A and 2B. To determine whether the growth in non-alcoholic beers is due to the absence of alcohol or to a higher concentration of carbohydrates, we also prepared model G medium with added ethanol at concentrations corresponding to 10-, 11-, and 12-degree beer. The results are shown in Figure 4 for medium G containing 5% (v/v) ethanol; media containing 4% (v/v) and 4.8% (v/v) ethanol showed a similar trend, but the data are not shown. Compared to media without added alcohol, the added ethanol had a slightly inhibitory effect on growth. Compared to alcoholic beers, non-alcoholic beers contain substantially more utilizable carbohydrates, see Table 1; however, it is questionable whether sugar content is truly the factor that promoted bacterial growth, because in simulated media with added glucose (G Birell, G Krušovice), growth was lower than in corresponding non-alcoholic beers (Figure 4B). A possible explanation could be the unfavorable initial acidic pH, which prevents the fermentation of carbohydrates into acids due to the inhibition of the relevant enzymes involved in metabolic pathways

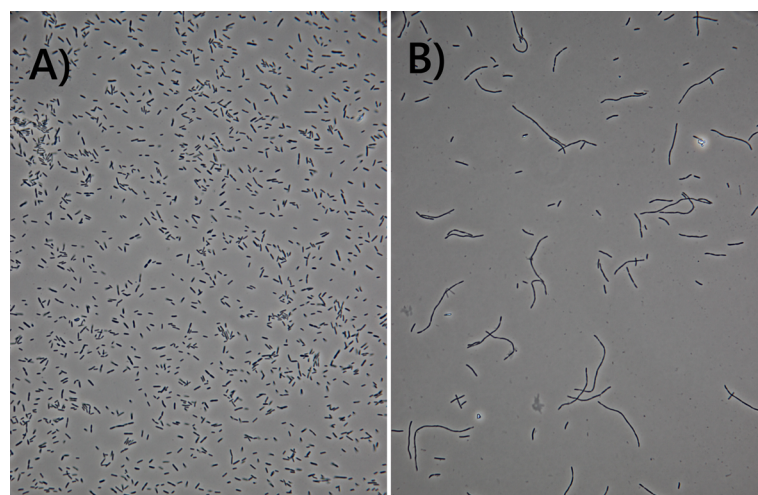


Figure 3 Growth in non-alcoholic Birell beer (A) and in G Gambrinus 10° culture medium (B) containing glucose and ethanol after 5 days of culture at 30 °C, magnification approx. 1000×

or lowering glucose consumption under low pH (Andersen et al., 2009). Another possibility may be the different buffering capacity of individual culture media, where even a small change in the concentration of alkaline substances (again, especially ammonium ions) in G medium can lead to a sudden increase in pH and the improvement of conditions for growth.

It is clear that the main factor inhibiting bacterial growth is the pH of the beer. In all cases, the pH value rose from the initial 4.65 to a higher value, indicating at least a minimal ability of *P. agglomerans* bacteria to adapt to the given environment, see Table 2. If significant growth occurred, whether in beer or in a simulated medium, the pH increased during growth also significantly; see bold values in Table 2. Maximum growth corresponded to a pH increase of up to 7.39 during bacterial growth in non-alcoholic Birell and Krušovice beers in a thermostat at 30 °C. The increase in pH may correspond to the previ-

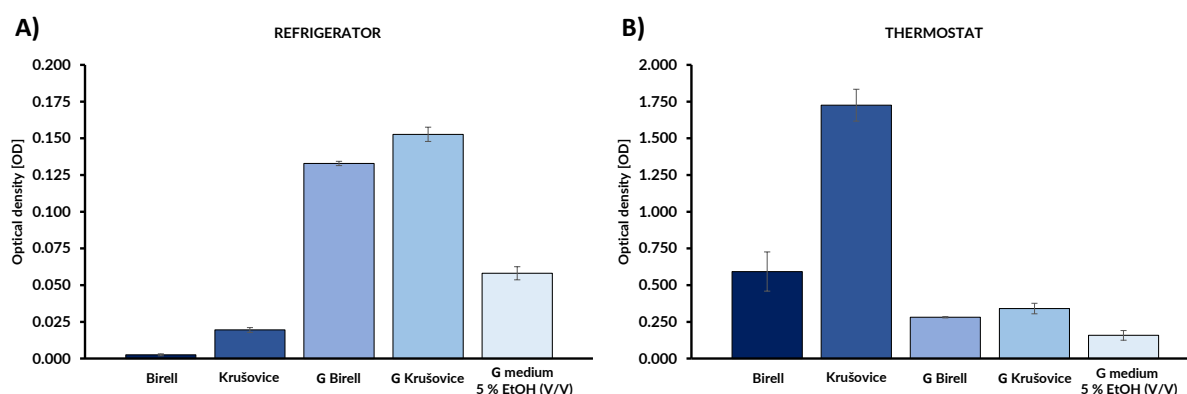


Figure 4 Growth in selected non-alcoholic beers and in modified culture media designed to mimic the beer environment the refrigerator at 7 °C (A) and in the thermostat at 30 °C (B)

ously demonstrated utilization of amino acids as carbon sources (Hasek et al., 2025) and was in line with the observations published for *E. coli* in LB medium (Sezonov et al., 2007). Excess nitrogen, remaining after the carbon skeleton of the amino acid has been utilized, is released into the culture medium in the form of ammonium ions, leading to alkalization of the environment. The use of amino acids instead of carbohydrates would also explain the poorer growth in simulated media supplemented with glucose. Controlled alkalization of the environment may also be one of the strategies by which Gram-negative bacteria cope with acid stress, a process known as ammonia buffering, which involves the production of ammonia through the deamination of amino acids (without their utilization as carbon sources) and the subsequent reaction of ammonia with hydrogen protons inside the cells, leading to the formation of ammonium ions (Lund et al., 2020).

to growth inhibition. However, none of these factors, including the usual acidic beer pH, seem to be able to completely prevent contamination of non-alcoholic beers. In addition, the contaminants in beer have so far been considered to be primarily Gram-positive bacteria (Roselli et al., 2024), such as various lactic acid bacteria, rather than Gram-negative bacteria.

4 Conclusion

The answer to the question in the article's title is: under normal storage conditions, the bacteria naturally present on hops do not cause beer spoilage. The observed growth, ranging within an optical density interval of 0.01–0.11, does not pose any problem, and this is the case for alcoholic beers cultured under any conditions and non-alcoholic beers cultured in the refrigerator. The only

Table 2 Comparison of final pH in different beer brands and culture media after 144 h culture in refrigerator – R or thermostat – T

	Svijany 10	Svijany 11	Svijany 12	Gambrinus 10°	LB	LB 4.0 %	LB 4.8 %	LB 5.0 %
R	4.98±0.00	4.80±0.00	4.91±0.00	4.88±0.01	4.78±0.01	4.89±0.02	4.87±0.02	4.90±0.07
T	4.97±0.00	4.77±0.00	4.88±0.01	4.89±0.01	5.62±0.02	5.48±0.36	5.10±0.05	5.09±0.02
	Birell	Krušovice	G	G Gambrinus 10°	G Birell	G Krušovice		
R	5.03±0.02	5.49±0.03	4.75±0.00	4.82±0.00	7.09±0.11	7.30±0.08		
T	7.39±0.03	7.39±0.04	7.12±0.04	4.93±0.01	6.81±0.07	6.92±0.11		

It appears that in all cases, low initial pH is a key factor influencing the growth of *P. agglomerans*. The optimal pH for the growth of *P. agglomerans* is around 7.0 (Sharma et al., 2024); however, this bacterium is capable of growing within a wide pH range from 5 to 8.6 and in some cases even as low as 4.5 (Costa et al., 2002). A low pH in beer is therefore close to the threshold below which growth is not possible, and if another stress factor is present, growth is ruled out. This may be due to a general mechanism whereby, at acidic pH, weak organic acids such as lactic acid, commonly found in beer (Choi et al., 2020), are undissociated and can diffuse into cells with water. However, at neutral pH inside the cells, the acids dissociate. The splitting of the hydrogen proton leads to the need for active pumping of H⁺ ions out of the cells to maintain the stable intracellular pH, which depletes ATP reserves and stops growth (Guan and Liu, 2020). This phenomenon, combined with other factors – such as suboptimal temperature, ethanol concentration, lack of oxygen, low/no carbohydrates, and probably also the presence of hop substances – leads

potential issue was with non-alcoholic beers cultured in a thermostat at 30 °C, where the optical density after 5 days of cultivation reached OD 0.5 for Birell beer and 1.75 for Krušovice non-alcoholic beer. Even so, this finding should not be overestimated; few people store beer at 30 °C, and moreover, the beer was intentionally inoculated with bacteria. The endophytic bacterium *P. agglomerans*, which colonizes the above-ground parts of the hop plant, can thus enter the beer during dry hopping and may even survive in it; nevertheless, the conditions in beer – particularly the low pH, alcohol content, and lack of oxygen – present significant barriers that quite effectively prevent beer contamination.

5 Acknowledgement

The research was co-funded by the grant of Specific university research grant No. A2_FPBT_2026_036 awarded by the Ministry of Education, Youth and Sports (MEYS) of the Czech Republic.

6 References

- Andersen A.Z., Carvalho A.L., Neves A.R., Santos H., Kummer U., Olsen L.F. (2009). The metabolic pH response in *Lactococcus lactis*: An integrative experimental and modelling approach. *Computational Biology and Chemistry*, 33, 71–83. <https://doi.org/10.1016/j.compbiolchem.2008.08.001>
- Bocquet L., Sahpaz S., Rivière C. (2018). An Overview of the Antimicrobial Properties of Hop. In: Mérillon J.-M., Riviere C. (Eds.) *Natural Antimicrobial Agents*. Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-67045-4_2
- Bogdanova K., Kolar M., Langova K., Dusek M., Mikyska A., Bostikova V., Bostik P., Olsovska J. (2018). Inhibitory effect of hop fractions against Gram-positive multi-resistant bacteria. A pilot study. *Biomedical Papers*, 162, 276–283. <https://doi.org/10.5507/bp.2018.026>
- Costa E., Usall J., Teixidó N., Delgado J., Viñas I. (2002). Water activity, temperature, and pH effects on growth of the biocontrol agent *Pantoea agglomerans* CPA-2. *Canadian Journal of Microbiology*, 48(12), 1082–1088. <https://doi.org/10.1139/w03-001>
- Dutkiewicz J., Mackiewicz B., Lemieszek M.K., Golec M., Milanowski J. (2016). *Pantoea agglomerans*: a mysterious bacterium of evil and good. Part IV. Beneficial effects. *Annals of Agricultural and Environmental Medicine*, 23(2), 197–205. <https://doi.org/10.5604/12321966.1203878>
- Guan N., Liu L. (2020). Microbial response to acid stress: mechanisms and applications. *Applied Microbiology and Biotechnology*, 104, 51–65. <https://doi.org/10.1007/s00253-019-10226-1>
- Hasek T., Kastanek F., Smirnova T.A., Solcova O., Kuckova S., Branska B., Melzoch K., Patakova P. (2025). Ammonia release from hydrolysed animal and food waste by the hop endophyte, *Pantoea agglomerans*. *World Journal of Microbiology and Biotechnology*, 41, 494. <https://doi.org/10.1007/s11274-025-04720-0>
- Hrabia O., Ditrych M., Ciosek A., Fulara K., Andersen M.L., Poreda A. (2022). Effect of dry hopping on the oxidative stability of beer: Food Chemistry, 394, 133480. <https://doi.org/10.1016/j.foodchem.2022.133480>
- Choi E.-J., Park J.-W., Kim J. H., Kim W. J. (2020). Biological acidification and beer quality: addition of lactic acid bacteria isolated from malt. *Journal of The Institute of Brewing*, 126, 176–183. <https://doi.org/10.1002/jib.601>
- Jelinek L., Mullerova J., Karabin M., Dostalek P. (2018). The secret of dry hopped beers – review. *Kvasny Prumysl*, 64(6), 287–296. <https://doi.org/10.18832/kp201836>
- Jones T.H., Vail K.M., McMullen L.M. (2013). Filament formation by food-borne bacteria under sublethal stress. *International Journal of Food Microbiology*, 165(2), 97–110. <https://doi.org/10.1016/j.ijfoodmicro.2013.05.001>
- Kolek J., Patakova P., Junkova P., Krofta K., Hynek R., Dostalek P. (2021). Isolation and identification of *Pantoea agglomerans* from the inflated bag with dried hop pellets stored under a modified atmosphere. *Journal of Applied Microbiology*, 131, 281–287. <https://doi.org/10.1111/jam.14970>
- Krofta K., Mravcova L., Kolek D., Patakova P., Patzak J., Henychova A., Dostalek P. (2021) Microbial community of hop (*Humulus lupulus* L.) and its impact on the quality of hop products. *Acta Horticulturae*, 1328, 109–114. <https://doi.org/10.17660/ActaHortic.2021.1328.15>
- Lund P. A., De Biase D., Liran O., Scheler O., Mira N.P., Cetecioglu Z., Fernández E.N., Bover-Cid S., Hall R., Sauer M., O'byrne C. (2020). Understanding How Microorganisms Respond to Acid pH Is Central to Their Control and Successful Exploitation. *Frontiers in Microbiology*, 11, 556140. <https://doi.org/10.3389/fmicb.2020.556140>
- Manzano M., Iacumin L., Vendrames M., Cecchini F., Comi G., Buiatti S. (2011). Craft Beer Microflora Identification Before and After a Cleaning Process. *Journal of The Institute of Brewing*, 117, 343–351. <https://doi.org/10.1002/j.2050-0416.2011.tb00478.x>
- Patakova P., Vasylikivska M., Sedlar K., Jureckova K., Bezdicek M., Lovecka P., Branska B., Kastanek P., Krofta K. (2024). Whole genome sequencing and characterization of *Pantoea agglomerans* DBM 3797, endophyte, isolated from fresh hop (*Humulus lupulus* L.). *Frontiers in Microbiology*, 15, 1305338. <https://doi.org/10.3389/fmicb.2024.1305338>
- Riccioni C., Belfiori B., Cenci M., Rubini A. (2025). Exploring Endophytic Fungi from *Humulus lupulus* L. for Biocontrol of Phytopathogenic Fungi. *Diversity*, 17(2), 94. <https://doi.org/10.3390/d17020094>
- Roselli G.E., Kerruish D.W.M., Crow M., Smart K.A., Powell C.D. (2024). The two faces of microorganisms in traditional brewing and the implications for no- and low-alcohol beers. *Frontiers in Microbiology*, 15, 1346724. <https://doi.org/10.3389/fmicb.2024.1346724>
- Sezonov G., Joseleau-Petit D., D'Ari R. (2007). *Escherichia coli* Physiology in Luria-Bertani Broth. *Journal of Bacteriology*, 189(23), 8746–8749. <https://doi.org/10.1128/jb.01368-07>
- Sharma P., Pandey R., Chauhan N.S. (2024). Unveiling wheat growth promotion potential of phosphate solubilizing *Pantoea agglomerans* PS1 and PS2 through genomic, physiological, and metagenomic characterizations. *Frontiers in Microbiology*, 15, 1467082. <https://doi.org/10.3389/fmicb.2024.1467082>
- Sood S., Singhal R., Bhat S., Kumar A. (2011). 2.13 – Inoculum Preparation. In: Moo-Young M. (Ed.) *Comprehensive Biotechnology* (Second Edition). Burlington: Academic Press, 151–164. <https://doi.org/10.1016/B978-0-08-088504-9.00090-8>
- Takahashi M., Aoyagi H. (2018). Monitoring of CO₂ and O₂ concentrations in the headspace of Sakaguchi flasks during liquid culture of microorganism. *Applied Microbiology and Biotechnology*, 102, 6637–6645. <https://doi.org/10.1007/s00253-018-9076-4>
- Young J., Oakley W.R.M., Fox G. (2023). *Humulus lupulus* and microbes: Exploring biotic causes for hop creep. *Food Microbiology*, 114, 104298. <https://doi.org/10.1016/j.fm.2023.104298>