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Survival of *Listeria monocytogenes*, *Bacillus cereus* and *Salmonella* Typhimurium on sliced mushrooms during drying in a household food dehydrator

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ABSTRACT

The historic view on low-moisture foods (LMFs) as safe due to the lack of microbial growth in these foods is challenged by an increasing number of reports of outbreaks and recalls caused by LMFs contaminated with foodborne pathogens. The objective of this study was to determine the survival of *Salmonella* Typhimurium, *Bacillus cereus* and *Listeria monocytogenes* on sliced Portobello mushrooms (*Agaricus bisporus* variant Portobello) during hot-air drying (mushroom internal temperature below 45 °C) for 8 h (h) in a small household food dehydrator (250 W) and subsequent storage of the vacuum-packed dried product for 2 months at room temperature. Hot-air drying reduced the water activity (a_w) of the mushrooms to 0.17 ± 0.03 well below the limit for microbial growth. *S.* Typhimurium and L. *monocytogenes* displayed total log CFU reductions of 2.5 ± 0.4 and 2.6 ± 0.8, respectively, while *B. cereus* exhibited significantly ($p < 0.05$) lower log reductions of 1.2 ± 0.1. Storage of vacuum-packed dried mushrooms further reduced *L. monocytogenes* by 2 log CFU, while numbers of viable *S.* Typhimurium and *B. cereus* were not further reduced. The higher stability of *S.* Typhimurium and *B. cereus* were reflected in the number of reports in the European Rapid Alert System for Food and Feed system of the presence of these organisms in dried mushrooms. All three organisms regrew to high concentrations when dried mushrooms were soaked overnight at room temperature, simulating a scenario where mushrooms are improperly rehydrated. Combining results from hot-air drying and subsequent storage underlines that hot-air drying and prolonged storage at low a_w cannot be relied on alone to reduce the microbial and pathogen load on Portobello mushroom.

1. Introduction

In recent years there has been an increase in outbreaks or recalls of low-moisture foods (LMFs) contaminated with foodborne pathogens (Beuchat et al., 2013; Sánchez-Maldonado et al., 2018). LMFs are defined as foods that are naturally low in moisture or have been through a drying process to lower the water activity (a_w) below 0.85 to inhibit growth and toxin production of foodborne pathogens (Young et al., 2015). Examples of LMF products include cereals, herbs, spices, honey, milk powder, pasta, peanut butter and dried meat, fruit and vegetables that are all considered less vulnerable to growth of foodborne pathogens and spoilage due to the low a_w (Podolak et al., 2010).

Drying of mushrooms is attractive due to the short shelf-life of fresh mushrooms, which can be as low as 1–3 days at ambient temperatures (Fernandes et al., 2012) and up to 8–14 days at 2–3 °C if packaged in modified or controlled atmosphere (Singh et al., 2010). Industrial drying of fruits and vegetables is mostly by convective air drying in tunnels or trays with internal product temperatures rarely exceeding 35–45 °C (Chitrakar et al., 2019; Ngamwonglumlert & Devahastin, 2018; Nijhuis et al., 1998), but several other industrial techniques such as vacuum, freeze, infrared or microwave drying are used depending on product characteristics, e.g., type, cost and size (Saravacos & Kostaropoulos, 2002). In order to minimize loss of organoleptic properties the temperature during drying is kept relatively low (40–80 °C) with shorter drying times at higher temperatures, which restricts the inactivation of the microbial load present in the food (Bourdoux et al., 2016).

Several studies have investigated the prevalence of foodborne pathogens and total microbial counts in fresh mushrooms with

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Samadpour et al. (2006) detecting *Salmonella* spp. and *L. monocytogenes* in 5% and 1%, respectively, of 100 samples of (uncategorised) mushrooms. Venturini et al. (2011) tested 402 samples representing 22 different species of fresh mushrooms and found a high microbial load (6–8 log CFU/g) in both wild and cultivated mushrooms with no pathogenic bacteria detected in the cultivated mushrooms, while 26 samples (6.5%) of wild mushrooms were positive for *L. monocytogenes*. In contrast, none of the samples tested positive for *Salmonella* spp. In line with these findings, 18.8% of 255 environmental samples obtained in a commercial fresh mushroom slicing and packing environment were positive for *L. monocytogenes* (Murugesan et al., 2015). Presence of L. *monocytogenes* was detected in 141 (21%) of 665 samples of mushrooms from Chinese markets (Chen et al., 2018). Taken together, these studies indicate that *L. monocytogenes* is commonly associated with production of fresh mushrooms.

The prevalence of foodborne pathogens in fresh vegetables destined for drying is problematic if drying conditions fail to lower the a_w to below 0.85 to reduce numbers and prevent their growth and hence risk of disease when consumed (Gurthler et al., 2014). Additionally, the routine of rehydrating dried mushrooms at ambient temperatures before use may induce microbial growth leading to an unsafe food product, if not cooked properly before consumption (Ajis et al., 2017). Furthermore it has repeatedly been shown how several foodborne pathogens including *L. monocytogenes* (Taylor et al., 2018), *Salmonella* spp. (Forghani et al., 2019; Lambertini et al., 2016) and *Bacillus cereus* (Dinh Thanh et al., 2018) show a high level of stability during storage of LMFs surviving for months as well as an increased heat resistance during subsequent food preparations. Consequently there has been many outbreaks caused by LMFs contaminated with especially *Salmonella* spp. and *B. cereus* (Chitrakar et al., 2019; Finn et al., 2013; Sánchez-Maldonado et al., 2018) causing an increase in surveillance and recalls of LMFs due to detection of these pathogens (Bourdoux et al., 2016). There is limited evidence of LMFs contaminated with *L. monocytogenes* causing outbreaks, but in 2016 the U.S. and Canada alone experienced 196 recalls due to detection of *L. monocytogenes* in products such as sunflower seeds, trail mixes and protein, energy and granola bars (Maberry, 2017). These recalls may be related to the increased surveillance and focus on *L. monocytogenes* leading to voluntary recalls, causing considerable economic loss and food waste (Sánchez-Maldonado et al., 2018). These observations were supported through an analysis of 1999–2020 microbial and pathogen contaminant notification data from the European Rapid Alert System for Food and Feed system (RASFF) for mushrooms, showing that *Salmonella* spp., *B. cereus*, *L. monocytogenes* and *Clostridium* spp. made up 76% of the 72 notifications (Table S1). All 11 notifications for *L. monocytogenes* were related to fresh mushrooms, with contamination levels ranging from 0.9 to 4 log CFU/g. In contrast, nearly all cases with *B. cereus* (n = 15/17) and *Salmonella* spp. (n = 21/23) involved dried mushrooms. Levels of *B. cereus* were >5 log CFU/g in all cases, whereas detection of *Salmonella* spp. was qualitative (presence in 25 g).

Given the prevalence of foodborne pathogenic bacteria including *L. monocytogenes*, *Bacillus cereus* and *Salmonella* spp. in fresh and dried mushrooms, the objective of this study was to investigate the survival of these foodborne pathogens on sliced mushrooms (*Agaricus bisporus* var. Portobello) during an 8-h hot-air drying process and subsequent storage of the vacuum-packed product for two months, including testing the ability of the survivors to regrow during rehydration.

2. Materials and methods

2.1. Bacterial strain and culture conditions

Mushrooms were inoculated with cocktails comprised of three strains of each organism: *Listeria monocytogenes* (EGD-e, 568 and 08–5578), *Salmonella enterica* serovar Typhimurium: (R 91, R 29 and Colindale 2003–17) or *Bacillus cereus* (MS 11128, MS 10329 and ATCC 13061). Long-term stock cultures were stored at −80 °C in a 20% (v/v) glycerol peptone medium (TS/80, Technical Service Consultants Ltd, Heywood, UK). Routine culturing were done at 37 °C on Tryptic Soy Agar plates (TSA), composed of 30 g/L TSB (Merck, Darmstadt, Germany) and 15 g/L agar (Sigma-Aldrich, St. Louis, MO, USA) for *L. monocytogenes* and *B. cereus*, respectively, while TSA plates with 5% (v/v) calf blood (Statens Serum Institut, Copenhagen, Denmark) were used for *S.* Typhimurium.

Precultures for challenge tests were grown in 10-mL Tryptic Soy Broth with 1% (w/v) glucose (Fischer Scientific, Loughborough, UK) (TSB-glu). Precultures of L. *monocytogenes* were incubated for 72 h at 15 °C, while *B. cereus* and *S.* Typhimurium were incubated for 18 h at 37 °C.

2.2. Slicing of Portobello mushrooms

Fresh mushrooms (Organic Portobello [*Agaricus bisporos* variant Portobello], Levevis, Bilka Denmark) packaged in a wooden box covered with plastic were bought in local supermarkets and transported (less than 1 h) to the laboratory, where slicing and cutting of mushrooms were done aseptically prior to inoculation on the same day. The mushrooms were sliced using a slicer (Model 836, Berkel A/S, Denmark) to obtain a uniform thickness of 4 mm before slices were cut with a sterile disposable scalpel into smaller pieces of approximately 4 cm^2. Aliquots of 10 g sliced and cut mushrooms were placed in 450 mL twist-seal sterile LDPE bags (VWR International, USA) and stored at 5 °C.

2.3. Inoculation of mushrooms using standardized strain cocktails

Bacterial cells from precultures were harvested by centrifugation at 2300×*g* for 5 min and resuspended in sterile peptone saline (PS, 1 g/L bacteriological peptone (Oxoid, Hampshire, UK) and 8.5 g/L NaCl (Merck)) to a final absorbance at 600 nm of 1 (NP80 NanoPhotometer, Implen, Westlake Village, CA, USA). For each test organism, a mixed strain cocktail of 6 mL were obtained by combining aliquots of 2 mL standardized cell suspensions from each of the three strains of the respective bacterium; *L. monocytogenes, B. cereus* or *S.* Typhimurium. Each bag of mushrooms (10 g) was then inoculated with 100 μL of the strain cocktail to a final concentration of 1% (w/v). The inoculum was gently distributed by hand massaging the bags to ensure uniform distribution without damaging mushrooms. Bags with inoculated mushrooms were stored at 5 °C overnight (~16 h) until commencement of the hot-air drying process. Control samples to examine survival of the endogenous bacteria present on the mushrooms were prepared with 100 μL PS. Concentrations (CFU/mL) in the mixed strain cocktails were determined by spot plating (60 μL) suitable tenfold dilutions on TSA followed by enumeration after incubation for 24 h at 37 °C. Presence of spores in the *B. cereus* strain cocktail was tested by heating the *B. cereus* strain cocktail to 80 °C for 12 min before cooling, spot plating on TSA and enumeration after incubation for 24 h at 37 °C (Frank & Yousef, 2004).

2.4. Hot-air drying of artificially contaminated sliced mushrooms

Dehydration of the sliced mushrooms was done using a KitchPRO food dehydrator (Coolstuff AB, Copenhagen, Denmark), which is a small household unit (26 × 28 × 28, 250 W) with five trays. Two identical units were used with the air temperature set at the instrument's 55 °C setting (target dry bulb temperature) and the dehydrator heated up prior to the commencement of the hot-air drying experiments. The core temperature of the mushrooms (wet bulb temperature) was logged during the dehydration process using a data logger with probe (Tinytag 2 Plus TGP 4020, Metric Industrial A/S, Denmark). The actual dry bulb temperature was also measured during three independent drying experiments by placing a probe between the two drying racks.

Each challenge test used ten aliquots of 10 g of mushrooms prepared

as described in sections 2.2 and 2.3. Bacterial numbers in two aliquots were enumerated immediately (time 0 h, no drying control). The remaining eight aliquots were placed on two of the food dehydrator's five racks and subjected to hot-air drying with sampling every second hour (See Fig. S1 for a schematic drawing of the set-up and Table S2 for the number of samples). Preliminary tests showed that drying and survival kinetics were not significantly different ($p > 0.05$) for samples placed on the second and third rack counting from the top.

At each sampling point (0, 2, 4, 6, 8 h of drying, except for *B. cereus* where samples were only taken after 0 and 8 h of drying), two aliquots (n = 2) of the originally 10-g portions of contaminated mushrooms were placed in sterile bags, weighed to determine the loss of mass, mixed in a 1:10 proportion with PS and homogenized in a stomacher followed by tenfold dilutions in PS. For enumeration of survivors, appropriate dilutions were spot plated (three drops of 20 μL from each suitable dilution) on TSA (*L. monocytogenes* and *B. cereus*) or TSA with 5% (w/v) calf blood (*S.* Typhimurium) as well as on the appropriate selective media: *L. monocytogenes* (Palcam plates, Palcam Selective Agar, Sigma Aldrich, USA), *B. cereus* (MYP plates, Mannitol Egg Yolk Polymyxin Agar, Thermo Fisher, USA), *S.* Typhimurium (XLD plates, Xylose Lysine Deoxycholate Agar (Thermo Fisher, England). Colonies were enumerated after incubation for 24–48 h at 37 °C. Counts of *B. cereus* were total counts that included both vegetative cells and spores. Survivors were expressed as log CFU per 10-g aliquot of wet mushroom to allow for the comparison of the absolute number of survivors. Reporting of log CFU/g would skew the results due to the decrease in weight caused by the drying induced loss of water.

Survival of each microorganism was tested separately in three independent biological experiments with duplicates (n = 6). Non-inoculated control mushrooms (endogenous microbiota) were tested separately in two independent biological experiments (n = 4). A total of 11 experiments were conducted to study the survival of the different organisms as none of the tests were conducted simultaneously in the dehydrator. An overview of sampling points can be seen in the Supplementary Material (Table S2).

2.5. Changes in water activity and weight loss during drying of mushrooms

Sliced mushroom were prepared as described in section 2.2. The 10-g aliquots of mushrooms in bags were inoculated with 100 μL PS and stored at 5 °C overnight before commencement of dehydration. Mushrooms were hot-air dried as described in section 2.4 with duplicate samples pulled after 0, 2, 4, 6 and 8 h to determine water activity (a_w) and weight of the mushrooms. Water activity was measured using a water activity meter (Aqualab model CX-2, Meter Food, Pullman, WA, USA). Water activity and weight loss were measured in four independent hot-air drying experiments with four different batches of Portobello mushrooms.

2.6. Evaluation of long term survival in vacuum-packed dried mushrooms and regrowth potential of pathogenic bacteria

Inoculated mushrooms were prepared and dried for 8 h as described in sections 2.2-2.4 before being vacuum-packed to evaluate the long-term survival of the foodborne pathogenic bacteria (*L. monocytogenes, B. cereus* or *S.* Typhimurium) on the dried mushrooms. Mushrooms were sampled before (0 h) and immediately after hot-air drying (8 h) before the remaining samples were vacuum-packed in sterile bags (PA/PE 130 MV, <60 cm^3/m^2 for O_2, <190 cm^3/m^2 for CO_2, PM PACK A/S, Denmark). Vacuum-packed mushrooms were stored at 25 °C with samples drawn in triplicates every second week over an 8-week period in two independent biological experiments. Weighing and enumeration of survivors were done as described in section 2.4. The dried mushroom were left to rehydrate in PS (10^{-1} dilution) overnight at room temperature before ten-fold dilutions were prepared and spot plated to evaluate the regrowth potential of the desiccation stressed bacteria.

2.7. Modelling of the bacterial inactivation using a modified Weibull model

Log transformed survivor counts from selective agars were used to model the inactivation of the foodborne pathogens during hot-air drying. The survival data from hot-air drying experiments were fitted to the Weibull + Tail model using GInaFiT Version 1.6 (Geeraerd et al., 2005) for each replicate to generate estimates for the parameters to allow statistical analysis. The Weibull + Tail model as proposed by (Albert & Mafart, 2005) is parameterized as follows:

$$\log(N_t) = \log\left(\left(N_0 - N_{res}\right) \times 10^{\left(-\left(\frac{t}{delta}\right)^p\right)} + N_{res}\right)$$

where N_t is the cell concentration at the time t and delta is the time until the first log reduction of N_o (initial cell concentration) is reached. The shape of the survival curve is described by p ($p < 1$ leads to upward concave curves, while downward concave curves are seen when $p > 1$). N_{res} is the residual population representing the tail.

2.8. Statistical analysis

The results from the hot-air drying and storage experiments were log transformed (log(CFU)) and corrected for change in the weight of the sliced mushroom during drying to represent the cell concentration in each sample originally derived from the inoculum in 10-g aliquots of fresh mushrooms. This calculation of the absolute number cells per 10-g portion of fresh mushrooms was done to ensure that a reduction in cell concentration per g would not be masked by reduction in the weight of the mushroom. Cell counts prior to and after hot-air drying as well as before and after storage were used to calculate log CFU reductions during hot-air drying and storage. The log CFU reductions and Weibull parameters from the different models were compared with one-way ANOVA with the Tukey post hoc test at a significance level of $p < 0.05$ to compare means.

3. Results

3.1. Effect of hot-air drying on water activity and weight of Portobello mushrooms

Freshly cut Portobello mushrooms had an initial a_w of 0.994 ± 0.02. This a_w remained stable during the initial 2 h of hot-air drying, after which it continuously dropped with marked variation among samples from experimental runs after four and 6 h until reaching a final a_w of 0.17 ± 0.03 with no variation among independent batches of mushrooms (Fig. 1a).

The weight of each aliquot of sliced mushrooms (10.18 ± 0.10 g) began to decrease without initial delay, however, decreases varied after 2 h (5.95 ± 1.72 g) (Fig. 1a). Final weights of 0.77 ± 0.11 g were obtained in all independent experiments.

The logged recordings of the internal mushroom temperature during hot-drying showed a steady increase from 25 to 30 °C to reach a plateau after two to 4 h, where the temperature stabilized around 43 ± 2 °C in the core of the mushrooms. Measurements of air temperature revealed that the highest dry bulb temperature in the food hydrator was 46.6 °C.

3.2. Inactivation of pathogenic bacteria during hot-drying of mushrooms

Hot-air drying of sliced Portobello mushrooms reduced the initial load of *S.* Typhimurium, *L. monocytogenes* and *B. cereus* (Table 1). It should be noted that none of the foodborne pathogens were detected in uninoculated mushroom samples at levels above the detection limit (1.70 log CFU/g).

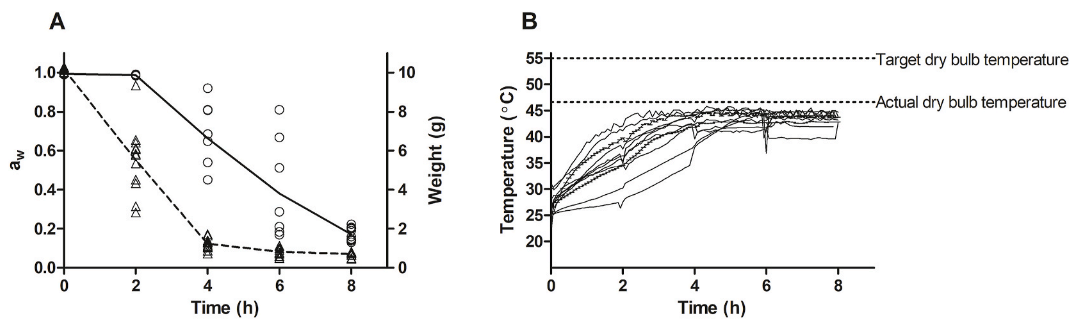

Fig. 1. Changes in water activity (a_w,○), weight (▲) **(A)** and temperature **(B)** in Portobello mushrooms during 8 h of hot-air drying in a household food dehydrator. Figure legend: **A)**. Lines denote the mean a_w (whole) and weight (dashed) calculated based on four biological independent experiments with duplicate samples (n = 8). **B)** Continuous (wet bulb) temperature profiles in the core of Portobello mushrooms from each of the 11 independent hot-air drying inactivation experiments.

Table 1
Survivor counts and inactivation kinetics of endogenous and spiked foodborne bacterial pathogens during hot-air drying of mushrooms. Inoculated mushrooms were enumerated using appropriate selective agars (SA) and TSA for total aerobic cell counts. Cell counts were expressed as total log CFU in each original 10-g aliquot of mushrooms to correct for weight loss of mushrooms during drying. Weibull analysis were done using counts from selective agars, except for endogenous, where TSA counts were used.

	Pre-drying (Log CFU)		*Post-drying (Log CFU)*		*Change during drying (ΔLog CFU)*		*Weibull parameters*		Model fit	
	SA	TSA	SA	TSA	SA	TSA	Delta (h)	p	R^2	MSE
S. Typhimurium	7.5 ± 0.1[a*]	7.6 ± 0.1[a]	4.9 ± 0.4[a]	5.1 ± 0.3[a]	−2.6 ± 0.4[a]	−2.5 ± 0.3[a]	4.58 ± 0.4[a]	3.12 ± 0.8[a]	0.90	0.15
L. monocytogenes	7.2 ± 0.6[a]	7.9 ± 0.4[a]	4.7 ± 0.3[a]	5.9 ± 0.9[a]	−2.5 ± 0.8[a]	−2.0 ± 0.6[a]	5.07 ± 0.2[a]	3.66 ± 0.5[a]	0.79	0.36
B. cereus	4.5 ± 0.3[b]	5.6 ± 0.6[b]	3.3 ± 0.2[b]	3.6 ± 0.3[b]	−1.2 ± 0.1[b]	−2.0 ± 0.4[a]	ND	ND	ND	ND
Endogenous	–	7.0 ± 0.5[a]	–	4.7 ± 0.7[a]	–	−2.3 ± 0.3[a]	3.99 ± 0.4[a]	2.63 ± 1.1[a]	0.91	0.11

SA: *L. monocytogenes*, Palcam agar; *B. cereus*, MYP agar; *S.* Typhimurium, XLD agar.
*Different letters in same column indicates differences at the 5% significance level.
ND: Not determined.

After 8 h of hot-air drying *S.* Typhimurium and L. *monocytogenes* displayed total reductions of 2.5 ± 0.4 log CFU and 2.6 ± 0.8 log CFU, respectively, with no significant ($p > 0.05$) difference among the bacteria (Table 1). The endogenous microbiota had a similar total reduction of 2.3 ± 0.3 log CFU, whereas *B. cereus* displayed a significantly ($p < 0.05$) lower reduction of 1.2 ± 0.1 log CFU. Initial *B. cereus* numbers were lower at the onset of hot-air drying, which coincided with significantly ($p < 0.05$) lower total aerobic counts of 4.6 log CFU/g obtained

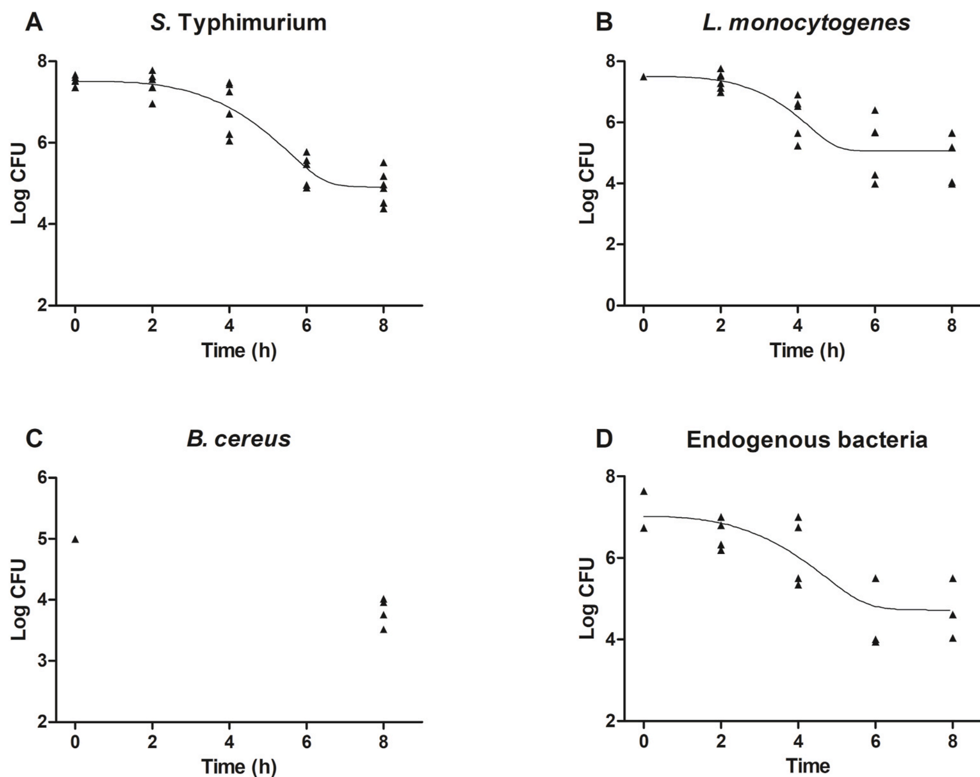

Fig. 2. Inactivation of endogenous and foodborne pathogenic bacteria on Portobello mushrooms during 8 h of hot-air drying (45 °C). Survivor counts were expressed as total Log CFU in each aliquot of 10-g mushrooms to correct for weight loss of mushrooms during drying. For every strain cocktail and non-inoculated mushrooms at least two biological independent experiments were conducted with total number of biological replicates as shown below: A) S. Typhimurium (n = 6), B) L. monocytogenes (n = 6), C) B. cereus (n = 6) and D) endogenous bacteria (n = 4). Enumeration was done using appropriate selective media or TSA for endogenous bacteria (see section 2.4).

in t = 0 h samples in experiments with *B. cereus*. Of the initial inoculum of 3.6 log CFU/g *B. cereus* heat resistant spores constituted 2 log CFU/g as determined by enumeration of spores. The log reduction of total aerobic counts was not significantly ($p > 0.05$) different from *S.* Typhimurium or L. *monocytogenes* with reductions ranging from 2.0 to 2.5 log CFU in all mushrooms with or without spiked foodborne pathogens (Table 1).

Fitting of the modified Weibull + Tail model (Albert & Mafart, 2005) to the inactivation data for *S.* Typhimurium, *L. monocytogenes* and the endogenous bacteria showed that the survival curves exhibited a delayed onset of inactivation (shoulder effect) and a surviving subpopulation (tail) (Fig. 2). As with the log reductions there were no significant differences ($p > 0.05$) between the model parameters obtained for the inactivation of *S.* Typhimurium, *L. monocytogenes* and the endogenous microbiota during hot-air drying (Table 1). The delta value, corresponding to the time until the first log reduction, varied from four to 5 h, which matched the slow increase of the internal temperature of the mushrooms and the delayed drop in a_w in the mushroom during drying (Fig. 1). The model fitting parameters (Table 1) were acceptable and it was possible to detect a tailing effect (N_{res} of ~4.5–5 log CFU) in each model where the inactivation rate decreased (Fig. 2).

3.3. Long term survival of desiccation stressed bacteria in low-moisture foods

Storage for up to 2 months at room temperature of the vacuum-packed dried mushrooms caused an increase in a_w from 0.17 to a maximum level of 0.5 (Fig. 3).

Numbers of *S.* Typhimurium and *B. cereus* were stable during storage of the low-moisture mushrooms with total reductions after 8 weeks of 0.7 ± 0.6 and 0.3 ± 0.3 log CFU, respectively. These numbers were thus not significantly ($p > 0.05$) different from cell concentrations enumerated just after drying (Table 2). In contrast, *L. monocytogenes* levels varied during storage but ended with a total reduction of 2.3 ± 0.4 log CFU after 8 weeks, which was significantly ($p < 0.05$) lower than *S.* Typhimurium and *B. cereus* (Fig. 3). The reduction in total aerobic counts on TSA plates ranged between 0.3 and 0.7 log CFU and was, as in the 8-h hot-air drying study, not different from the decreases observed for *B. cereus* and *S.* Typhimurium.

After storage for eight weeks, the dried mushrooms were soaked overnight to simulate a scenario where a consumer rehydrates the mushrooms prior to consumption as proposed on the packing, but leaves them too long and at room temperature. All bacteria regrew to concentrations of 10^7–10^8 CFU/g indicating that the surviving cells suffered no loss in regrowth potential after hot-air drying and subsequent storage of the vacuum-packed dried mushrooms.

4. Discussion

4.1. Changes in water activity and microbial load during hot-air drying of mushrooms

The maximum temperature reached internally in the mushrooms after 3–4 h of hot-air drying hovered around 40–43 °C never reaching the recorded air temperature of 46 °C. Furthermore the recorded dry bulb temperature never reached the targeted 55 °C revealing inaccurate calibration of the household dehydrator. This temperature profile is similar to profiles reported for conventional drying of vegetables (Chitrakar et al., 2019). The Portobello mushrooms' initial a_w of 0.99, which was similar to white button mushrooms (Salazar et al., 2017), dropped after 2 h below the critical food safety limit of 0.85, where growth and toxin production of the most xerophilic foodborne bacterial pathogen, *Staphylococcus aureus*, is inhibited (Doyle & Beuchat, 2007). In the present study, inactivation of the microbial load on the mushrooms peaked after ~4 h before tailing to a total reduction of 2–2.5 log CFU, a reduction which appeared mainly to be related to the decrease in a_w (Figs. 1 and 2). This decrease in a_w places an osmotic stress (matric stress) on bacterial cells. To overcome this, cells will elicit a stress response, which includes accumulating osmoprotectants to keep the turgor pressure intact (Finn et al., 2013). The low a_w will inevitable halt

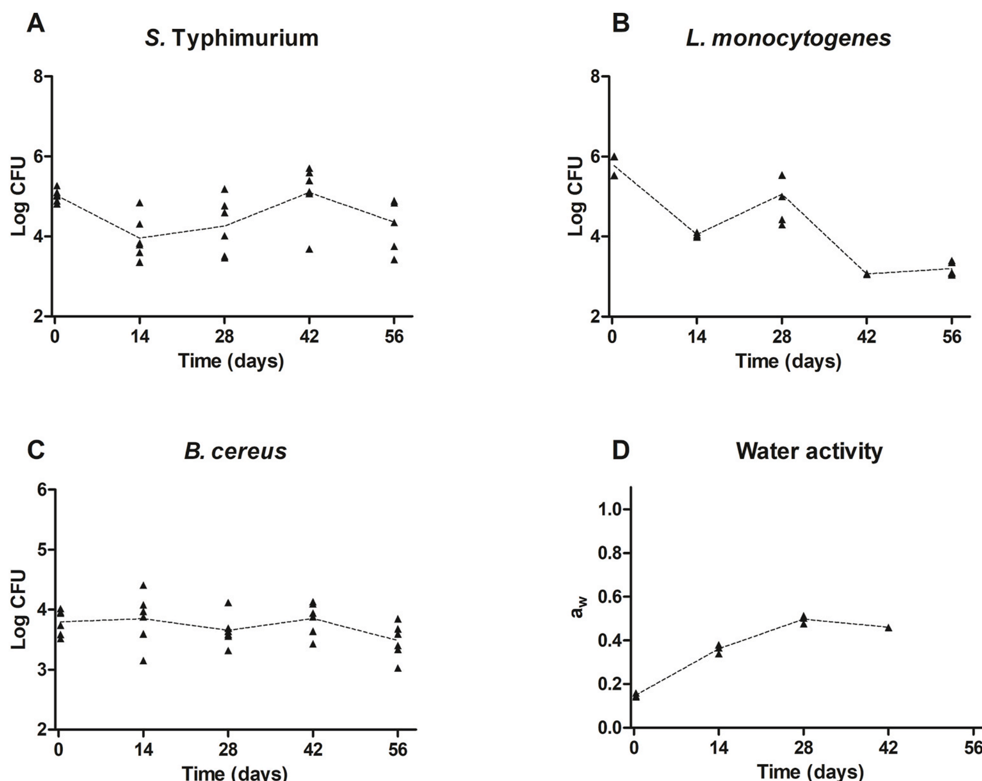

Fig. 3. Survival of A) S. Typhimurium, B) L. monocytogenes or C) B. cereus and D) change in aw during storage of vacuum-packed dried mushrooms at room temperature (25 °C). Survivor counts were enumerated on the appropriate selective agars (XLD, Palcam, and MYP agar, respectively) and expressed as total log CFU in each aliquot of 10-g mushrooms to correct for weight loss of mushrooms during drying. For every species and change in aw at least two biological independent experiments were conducted with triplicate samples (n = 6). Dashed lines represent the average survivor count (A, B, C) or water activity (D).

Table 2
Survivor counts of spiked foodborne bacterial pathogens on mushrooms after 8 h of hot-air drying and 8 weeks of storage of vacuum-packed mushrooms. Survivors were enumerated using appropriate Selective Agar (SA) and TSA for total aerobic cell counts. Cell concentrations were expressed as total log CFU in each aliquot of 10-g mushrooms to correct for weight loss of mushrooms during drying.

	Post-drying (Log CFU)		*End of storage (8 weeks) (Log CFU)*		*Change during storage (Log CFU)*		*Regrowth potential*	
	SA	TSA	SA	TSA	SA	TSA	SA	TSA
S. Typhimurium	4.9 ± 0.3	5.4 ± 0.2	4.2 ± 0.7	4.6 ± 0.5	−0.7 ± 0.6[a][a]	−0.7 ± 0.4[a]	+[b]	+
L. monocytogenes	5.8 ± 0.3	5.6 ± 0.1	3.2 ± 0.2	4.9 ± 0.9	−2.3 ± 0.4[b]	−0.7 ± 0.9[a]	+	+
B. cereus	3.3 ± 0.2	3.5 ± 0.2	3.0 ± 0.5	3.2 ± 0.5	−0.3 ± 0.3[a]	−0.3 ± 0.4[a]	+	+

SA: *L. monocytogenes*, Palcam agar; *B. cereus*, MYP agar; *S.* Typhimurium, XLD agar.
[a] Different letters in same column indicates differences at the 5% significance level.
[b] Growth to levels of 10^{7-8} CFU/mL in the mushrooms soaked in PS (1:10) for 24 h at room temperature (20–22 °C).

the metabolism and inactivate the majority of the cells because of water deficit and shrinkage of the cells. For organisms that are desiccation tolerant a subpopulation of 10–0.1% of the original population will remain viable depending on the drying kinetics (Burgess et al., 2016; Zoz et al., 2017). This corresponds to a 1–3 log reduction for desiccation tolerant organisms.

The present study showed the endogenous microbiota was reduced by 2.3 log CFU. Similar reductions of 2–2.5 log CFU were seen for *S.* Typhimurium and L. *monocytogenes* indicating a similar resistance to hot-air drying (Table 1). In contrast, *B. cereus* presented a significantly higher resistance to hot-air drying with reductions of 1.2 log CFU after the 8-h drying process. It should, however, be noted that the initial load of *B. cereus* (and of the endogenous bacteria in these trials) at the start of the hot-air drying was lower with 3.5 log CFU/g compared to 6.5 log CFU/g for the other strains. Also, the inoculum level used in the present study may not reflect the typical contamination level and could have affected the inactivation. Lievense and Riet (1994) proposed higher cell concentrations would yield a shielding effect due to release of intracellular components. On the other hand (Hingston et al., 2013) showed how different concentrations of cells on stainless steel had no effect on the survival kinetics of *L. monocytogenes* during desiccation. Thus it is unlikely that *B. cereus* or the other bacteria would exhibit a different desiccation resistance at higher or lower contamination levels.

The lower initial contamination level of *B. cereus* may be due to competition with the endogenous microbiota. *Pseudomonas* spp. are naturally occurring in mushrooms with reported levels of up to 8 log CFU/g (Venturini et al., 2011) and have been shown to inhibit *B. cereus* growth in co-cultures (Chakraborty et al., 2016). This could have caused the levels of *B. cereus* to decrease during the overnight storage before commencing the hot-air drying in the present study. Moreover, mushrooms contain bioactive compounds including some antimicrobials. Bach et al. (2019) showed that *B. cereus* was significantly more sensitive to phenols extracted from Portobello mushroom than *Salmonella enterica* subsp. *enterica* serovar Enteritidis, *Staphylococcus aureus* and *Escherichia coli*. Future studies should characterize these bioactive compounds and the endogenous microflora on mushrooms and possible roles in inhibition of *B. cereus*.

Even though several studies have been conducted on pathogen survival during dehydration of foods there is still uncertainty regarding the inactivation effect of solar drying and convective air drying (Bourdoux et al., 2016). Keller et al. (2018) reported 4 log CFU/g reductions for *S.* Typhimurium on pumpkin or sunflower seeds after 6 h of drying at 51 °C, while only 1 log CFU/g reduction was observed for chia seeds. Similarly (DiPersio et al., 2003) obtained 2.7–4.2 log CFU/g reductions on apple slices after 6 h at 60 °C, while only 1.3–2.0 log CFU/g reductions were seen on sliced carrots (DiPersio et al., 2005). Hence, the 2.5 log CFU reduction (corresponding to 1.5 log CFU/g reduction) of *S.* Typhimurium obtained in the present study was similar to that observed for sliced carrots. Collectively, the results highlight that the different food matrices need to be considered in predictions of the inactivation of *Salmonella* spp. during drying.

L. monocytogenes inactivation during hot-air drying of fruit or vegetables is not well documented, but recalls of sunflower seeds, trail mixes and various snack bars contaminated with *L. monocytogenes* in the USA in 2016 shows the ability of the bacterium to either survive drying or cross-contaminate these products during post-drying handling and packaging (Maberry, 2017). In the present study, the absolute number of *L. monocytogenes* was reduced by 2.0–2.5 log during drying of mushrooms, which corresponded to initial levels of 6.2 log CFU/g on fresh mushrooms decreasing to 4.8 log CFU/g dried mushrooms. *L. monocytogenes* on peach slices were reduced by 3.2–3.4 log CFU/g after drying for 6 h at 60 °C (DiPersio et al., 2004), while (Calicioglu et al., 2002) obtained reductions of 3 log CFU/cm^2 during drying of beef slices for 7 h at 60 °C.

B. cereus produces spores, which are relatively resistant to heat and other inactivation treatments (Griffiths & Schraft, 2017; Setlow, 2006). Studies on *B. cereus* inactivation in LMFs have mostly focused on foods, where drying processes at higher temperatures are possible e.g., rice dried at 90–120 °C (Houska et al., 2007). We saw levels of reduction during drying at 40–43 °C for 8 h, which largely corresponded to inactivation of vegetative cells and survival of the spores in the inoculum. Our results were comparable to the findings of (Kim et al., 2017), who reported no significant reductions in the viability of *B. cereus* spore suspensions on red chili peppers being hot-air dried for 48 h at 55 °C.

The quality of dried mushrooms depends on the rehydration ratio as well as taste, aroma, texture, and colour before and after rehydration. These quality parameters are affected by the drying method, temperature and duration of the drying (Politowicz et al., 2018). To improve the food safety, an increase in the temperature would be beneficial, but this could decrease the quality in terms of colour, rehydration ratio and lightness as noted by Nour et al. (2011) who compared drying of white button mushrooms (*A. bisporus*) at 50 °C and 70 °C. In contrast (Politowicz et al., 2018), obtained better results when drying oyster mushrooms at 60 °C and 70 °C as compared to 50 °C. Blanching of white button mushrooms prior to drying negatively impacted the rehydration ratio, whereas pre-treatments with a combination of 0.5% (v/v) citric acid and 0.5% (v/v) ascorbic acid before drying at 50 °C for 8 h resulted in superior quality dried mushrooms compared to mushrooms receiving no pretreatment (DiPersio et al., 2004). To improve inactivation of *L. monocytogenes* Calicioglu et al. (2002) dipped beef slices in 5% (v/v) acetic acid shorty before drying at 60 °C. This pre-treatment lowered the D-value from 2.2 to 1.8 h, while in comparison the D-values in the present study were 4–5 h.

In conclusion, drying of Portobello mushrooms at 45 °C results in the order of 1–2.5 log reductions and cannot be relied on to eliminate contamination with *S.* Typhimurium, *L. monocytogenes* or *B. cereus*. Future studies should focus on the application of additional pre- or post-drying treatments to inactivate the microbial load including *B. cereus* spores.

4.2. Stability of pathogens during storage of vacuum-packed dried mushrooms

Two months of post-drying storage of dried mushrooms caused no further reductions in the levels of endogenous microbiota, *S.* Typhimurium or *B. cereus* (Fig. 3). In contrast, levels of *L. monocytogenes* were reduced by up to 2 log CFU/g. Survivors were unaffected by the desiccation stress and regrew during rehydration of mushrooms. This demonstrated that up to 4 log CFU of *L. monocytogenes* were inactivated by drying and subsequent storage before retail, while reductions were limited to around 1 and 2.5 log CFU for *B. cereus* and *S.* Typhimurium, respectively. The lower survival rate of *L. monocytogenes* in dried mushrooms is perhaps reflected in the RASFF notifications (Table S1), where all the notifications regarding *L. monocytogenes* pertained to fresh mushrooms. *L. monocytogenes* is not growing well in whole white button mushrooms (Leong et al., 2015) while 1–2 log CFU/g increases were observed in sliced mushrooms (Salazar et al., 2017).

Considering the prevalence of *L. monocytogenes* reported in some species of fresh (especially wild) mushrooms (Chen et al., 2018; Murugesan et al., 2015; Venturini et al., 2011) and its ability to grow in sliced mushrooms, absence of *L. monocytogenes* in dried mushroom recalls and outbreaks as well as the inactivation observed in the present study, it appears that *L. monocytogenes* is a foodborne pathogen of less concern in dried mushrooms in comparison to *Salmonella* and *B. cereus.* It should, however, not be neglected that *L. monocytogenes* can survive in a desiccated state for months on stainless steel surfaces (Vogel et al., 2010) and has been isolated from a variety of LMFs after storage for up to a year (Brar et al., 2015; Kimber et al., 2012; Taylor et al., 2018), demonstrating how manufacturers of LMFs still need to pay attention to *L. monocytogenes*.

Salmonella spp. and *B. cereus* have repeatedly been involved in both recalls and outbreaks due to contaminated dried foods (Bourdoux et al., 2016; Chitrakar et al., 2019; Finn et al., 2013). This is reflected in the high frequency of *B. cereus* and *Salmonella* spp. in dried mushrooms in the RASFF notifications (Table S1). This concern is enhanced by the observed stability of the bacteria during storage of the dried mushrooms (Fig. 3). Additional concern is caused by the ability of *B. cereus* to produce heat and desiccation resistant spores (Kim et al., 2017) as well as heat-stable toxins (Griffiths & Schraft, 2017), although it should be noted that the bacterium has to grow to high levels in order to elicit illness in the consumer. The low infective dose of some *Salmonella* spp. makes their survival in fatty and low-water activity foods such as chocolate challenging (Doyle & Beuchat, 2007; Wiertzema et al., 2019). However, for non-typhoidal *Salmonella* and *B. cereus* the infective dose is more often >5 log CFU/g (Gurthler et al., 2014; McHugh et al., 2017). The presence of >5 log CFU/g *B. cereus* in some of the recalled lots of dried mushrooms (Table S1) underlines the stability of this pathogen in dried mushrooms also observed in the present study. The stability of *Salmonella* in LMFs is well documented with reports of viable cells being detected in pet food (Lambertini et al., 2016) and almonds (Limcharoenchat et al., 2019) after 19 and 24 months, respectively, with both foods having an a_w of 0.5. The long term stability (≥2 months) of these organisms in dried mushrooms has not previously been reported. However, this finding and the many outbreaks and recalls related to both *B. cereus* and *Salmonella* highlight why effective inactivation techniques are needed to avoid regrowth during rehydration of the mushrooms, especially if the soaking time and temperature are not controlled, e.g., a two log increase of coliforms was seen after rehydration of dried mushroom in sterile water for 4 h at room temperature (Limcharoenchat et al., 2019). As mentioned previously, pre-treatments with 0.5% (v/v) citric acid and 0.5% (v/v) ascorbic acid (DiPersio et al., 2003, 2004) or 5% (v/v) acetic acid (Calicioglu et al., 2002) should be investigated to see if these treatments can improve inactivation without affecting the sensory quality. Other treatments such as UV-C proved ineffective as inactivation of *B. cereus* spores required doses that negatively affected the edible quality (Lee et al., 2019).

5. Conclusion

Hot-air drying and subsequent storage for 2 months caused combined reductions of ~2 log CFU for *B. cereus* and *S.* Typhimurium*,* while *L. monocytogenes* was more sensitive with a combined 4 log reduction. This means that dried Portobello mushrooms with initial pre-drying contamination levels >10^2 CFU/g of *B. cereus* and *S.* Typhimurium and 10^2–10^4 CFU/g *L. monocytogenes* would still be contaminated and could lead to foodborne illnesses if not properly handled. The practice of rehydrating the dried mushrooms at room temperature for several h before cooking constitutes a risk of pathogen regrowth to unsafe levels. Moreover, cooking of the rehydrated mushrooms would not be sufficient to mitigate a potential presence of heat stable B. cereus toxins. Manufacturers of dried mushrooms should not rely on drying as their primary critical control point for attaining food safety, but rather implementation of additional pre- and/or post-drying treatments to secure better elimination of the microbial load is recommended.

CRediT authorship contribution statement

Martin Laage Kragh: Conceptualization, Formal analysis, Writing – original draft, Data curation, conception of the study, analysis of data and writing of manuscript. **Louisa Obari:** Formal analysis, Data curation, conducted the experiments and analysis of data. **Alyssa Marie Caindec:** Formal analysis, Data curation, conducted experiments and analysis of data. **Hanne Aarslev Jensen:** Formal analysis, Data curation, conducted experiments and analysis of data. **Lisbeth Truelstrup Hansen:** Funding acquisition, Conceptualization, Formal analysis, Data curation, Writing – original draft, funding and resource acquisition, conception of the study, analysis of data and writing of manuscript. All authors edited and approved the final manuscript.

Declaration of competing interest

The authors declare no financial or professional conflict of interest to the research conducted and described in this manuscript.

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Appendix A. Supplementary data

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