CENTER for PRODUCE SAFETY

CPS 2018 RFP
FINAL PROJECT REPORT

Project Title
A systematic review of *Listeria* growth and survival on fruit and vegetable surfaces: responding to critical knowledge gap

Project Period
January 1, 2019 – December 31, 2019

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Objectives

1. *Conduct a systematic review to identify and characterize published data on the growth and survival of Listeria monocytogenes on intact fruit and vegetable surfaces.*
2. *Perform L. monocytogenes growth and survival experiments on intact fruit and vegetable commodities at selected conditions to fill missing data gaps.*
3. *Develop risk models for a sub-set of fruit and vegetable storage or handling conditions shown to display growth or enhanced survival of L. monocytogenes.*

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FINAL REPORT

Abstract

There are critical knowledge gaps regarding the risk of *Listeria monocytogenes* on intact fruit and vegetable surfaces. This is of particular concern as, within the last decade, *L. monocytogenes* has been associated with outbreaks linked to contaminated intact produce including cantaloupe, stone fruit, and caramel apples. While *L. monocytogenes* has been isolated from a wide variety of environments, including produce production, urban, natural, processing, and retail environments, nearly all (99%) listeriosis infections are attributed to contaminated food. Therefore, as food moves throughout the supply chain, controlling growth or survival conditions is essential for minimizing contamination events. This control is especially important for produce, which is often consumed raw or with minimal processing. Since it is widely accepted that *L. monocytogenes* may be present in produce production environments, data on *L. monocytogenes* behavior on whole produce when handled/stored at typical and abuse conditions over the typical shelf life is needed. Thus, the following objectives were investigated: 1. Conduct a systematic review to identify and characterize published data on the growth and survival of *L. monocytogenes* on intact fruit and vegetable surfaces; 2. Perform *L. monocytogenes* growth and survival experiments on intact fruit and vegetable commodities at selected conditions to fill missing data gaps; and 3. Develop risk models for a sub-set of fruit and vegetable storage or handling conditions shown to display growth or enhanced survival of *L. monocytogenes*. Overall, the project demonstrated that *L. monocytogenes* growth and/or survival on intact produce differed by commodity. Both the literature studies and laboratory experiments showed intact whole produce held at >20°C had the highest *L. monocytogenes* growth rates. *L. monocytogenes* growth was affected by produce surface roughness (↑), nutrient ability (↑), and competitive background microflora (↓). Additionally, microbial carrying capacity was crucial to characterizing growth and/or survival patterns. Of the ten studied whole, intact commodities (except carrot), *L. monocytogenes* growth was supported at 35, 22, and 12°C but not at 2°C. Whole, intact produce may be stored at lower temperatures to minimize *L. monocytogenes* growth potential, as growth rates were lower at 2°C than at 12, 22, and 35°C. Models showed inoculum concentration, produce microbial carrying capacity, and temperature impacted the estimated *L. monocytogenes* growth rate. Moreover, the ComBase model (assuming pH 5) was generally fail safe for all produce items (validated based on laboratory-generated data and confirmed with literature derived data), except for tomato stored at 35°C.

Background

The economic burden of foodborne illness in the United States is estimated to be nearly 78 billion dollars annually (USDA ERS 2014). Listeriosis is the leading cause of foodborne disease-related deaths from bacterial infections in the US. There are an estimated 1,600 cases of listeriosis in the US each year, with a mortality rate of about 20% (Scallan et al. 2011). The economic burden specific to listeriosis has been predicted to exceed 2.8 million yearly (USDA-ERS 2014). While *Listeria monocytogenes* has been isolated from a wide variety of environments, including produce production (Strawn et al. 2013), urban (Sauders et al. 2006), natural (Chapin et al. 2014), processing (Lappi et al. 2004) and retail environments (Simmons et al. 2014), nearly all (99%) listeriosis infections are attributed to contaminated food (Scallan et al. 2011). This means that as food moves throughout the supply chain, controlling the growth or enhanced survival conditions for pathogens is essential to minimize large-scale contamination

events (outbreaks). Such control is especially important for foods like produce, which is often consumed raw or with minimal processing. According to several government reports (US FDA/FSIS 2003, US FDA 2017) on ready-to-eat (RTE) foods, *L. monocytogenes* growth during storage is cited as one of the main factors associated with outbreaks. Historically, produce-borne *L. monocytogenes* outbreaks were associated with processed produce products, such as coleslaw or diced celery (Schlech et al. 1983, Gaul et al. 2013). Only within the last decade has *L. monocytogenes* been associated with contaminated whole produce, including cantaloupe, stone fruit, and caramel apples (CDC 2011, 2015, Jackson et al. 2015). A 2011 multistate outbreak of listeriosis was traced to whole cantaloupes produced by Jensen Farms in Colorado (CDC 2011). One hundred and forty-seven persons from 28 states were infected with any one of the five *L. monocytogenes* subtypes involved; the outbreak led to 33 deaths, making it the deadliest outbreak of foodborne illness to occur in the past 25 years. In 2014, a recall of stone fruit (whole peaches, nectarines, plums, and pluots) occurred due to possible *L. monocytogenes* contamination. When PFGE-types from the recalled stone fruit were uploaded to PulseNet, four listeriosis patients from the system had exact PFGE matches; two of these cases were linked to the recalled stone fruit (Jackson et al. 2015, Buchanan et al. 2017). Therefore, it is critical for the produce industry to understand *L. monocytogenes* growth/no growth conditions on intact whole fruits and vegetables to establish parameters (e.g., temperature) during handling and storage that can be applied to reduce *L. monocytogenes* proliferation or long-term survival.

It is well understood that fruits and vegetables are grown in environments where *L. monocytogenes* is present, albeit sporadically and in low numbers (Fenlon et al. 1996). It is unrealistic to assume that intact whole fruits and vegetables may not become contaminated. Sporadic, low levels of contamination on whole intact produce may be a regular part of the production environment. The produce production environment is not thought to promote the growth of pathogens, unless environmental factors and management practices support favorable conditions (Beuchat 2002, Park et al. 2013, 2014, Chapin et al. 2014). It is therefore important to consider how intact whole produce postharvest handling may amplify risk from these infrequent, sporadic, low levels of contamination. Whole fruits and vegetables are handled under a wide range of parameters. Some whole produce items may be refrigerated during storage and transport activities, and yet displayed and sold at ambient temperatures. Growth may be impacted by temperature, competitive microflora, humidity, water activity (moisture), pH, among other factors (Hoelzer et al. 2012a). *L. monocytogenes* growth has been observed on stored produce and this growth potential can vary by commodity and handling conditions (Berrang et al. 1989, Francis and Beirne 2001, Harris et al. 2003). Growth of *L. monocytogenes* has been observed on intact whole tomato stored at ambient temperatures, while no growth of *L. monocytogenes* was observed on intact whole strawberry stored at ambient temperatures (Flessa et al. 2005). Intact whole produce surfaces are different, and *L. monocytogenes* growth appears dependent on surface properties, including moisture and/or nutrient availability. Holding (or storage) conditions also play a significant role, and Flessa et al. (2005) observed greater pathogen survival when storage conditions were cooler (<10°C). *L. monocytogenes* can grow at refrigeration temperatures, especially if the product is kept at refrigeration for extended periods (Beuchat and Brackett 1990, Carlin et al. 1995), unlike other important pathogens including *Salmonella* or *Escherichia coli* O157:H7. Data are needed on *L. monocytogenes* behavior on intact whole fruits and vegetables to assist agencies or industry groups in managing risk. Directly after the *L. monocytogenes* outbreak in cantaloupe (2011), the US FDA risk assessment group (Hoelzer et al. 2012a, b) sought to build predictive growth models for produce and concluded the lack of available data on *L. monocytogenes* growth and survival was insufficient, stating “data were very scarce and further studies on are urgently needed”. This project answers the key question: “To what extent are *Listeria monocytogenes* growth and survival supported by certain intact whole fruit and vegetable commodities?”

Research Methods and Results

Objective 1: Conduct a systematic review to identify and characterize published data on the growth and survival of *Listeria monocytogenes* on intact fruit and vegetable surfaces.

The goal of this objective was to identify and characterize published data on the growth and/or survival of *L. monocytogenes* on the surfaces of intact, whole fruits and vegetables. Relevant studies were identified by searching seven electronic databases: AGRICOLA, CAB Abstracts, Center for Produce Safety funded research project final reports, FST Abstracts, Google Scholar, PubMed, and Web of Science. Searches were conducted using the following terms: *Listeria monocytogenes*, produce, growth, and survival. Search terms were also modified and "exploded" to find all related subheadings. Included studies had to be prospective, describe methodology (e.g., inoculation method), outline experimental parameters, and provide quantitative growth and/or survival data. Studies were not included if methods were unclear or inappropriate, or if produce was cut, processed, or otherwise treated.

Of 3,459 identified citations, 88 were reviewed in full and 29 studies met the inclusion criteria (**Figure 1**). Included studies represented 21 commodities, with the majority of studies focusing on melons, leafy greens, berries, or sprouts. Synthesis of the reviewed studies suggests *L. monocytogenes* growth and survival on intact produce surfaces differ substantially by commodity (**Table 1**). Parameters such as temperature and produce surface characteristics had a considerable effect on *L. monocytogenes* growth and survival dynamics. The systematic review provides an inventory of the current data on *L. monocytogenes* growth and/or survival on intact produce surfaces (see Appendix for publication citation). Identification of which intact produce commodities support *L. monocytogenes* growth and/or survival at various conditions observed along the supply chain assists in managing *L. monocytogenes* contamination risks.

Objective 2: Perform *L. monocytogenes* growth and survival experiments on intact fruit and vegetable commodities at selected conditions to fill missing data gaps.

The purpose of this objective was to examine the behavior (growth and/or survival) of *Listeria monocytogenes* on ten different commodities (cherry, mandarin orange, lemon, tomato, blueberry, raspberry, blackberry, broccoli, cauliflower, and carrot) stored under different post-harvest temperatures utilized along the supply chain. Samples (of each commodity) were inoculated with a five-strain *L. monocytogenes* cocktail at approximately 3 to 4 log CFU per g or piece and stored at temperatures 35±2, 22±2, 12±2, and 2±2°C for up to shelf life and beyond. Samples were enumerated following a rub (1 min), shake (1 min), rub (1 min) procedure. *L. monocytogenes* populations were determined from plating samples (0.1 mL) onto tryptic soy agar (TSA) and modified Oxford agar (MOX) supplemented with rifampicin after serial dilutions in 0.1% peptone in duplicate. To increase the limit of detection, 1 mL of the lowest dilution was plated onto four plates (0.25/mL) on each agar. Storage temperatures were selected to represent temperature abuse (35°C), ambient/room temperature (23°C), open-case display temperature (12°C), and refrigeration/cold storage (2°C). Quantitative *L. monocytogenes* population data was entered in Excel, and all statistical analyses were performed with R version 3.3.1. Data was imported in R using the *XLConnect* package. Differences between mean values of sampling time points (d) and storage temperatures (35, 22, 12, and 2°C) were analyzed by a multiple Tukey's adjusted analysis of variance (ANOVA) with the R package *agricolae*. Additionally, differences between media (TSA and MOX with rifampicin) and commodity (cherry, mandarin orange, lemon, tomato, blueberry, raspberry, blackberry, broccoli, cauliflower, and carrot) mean values were analyzed by a t-test. *P* values were considered significant if less than 0.05.

L. monocytogenes populations (log CFU/g or piece) by time point (up to 28 d) are displayed in **Figures 2–11**. Most of the commodities supported the growth of *L. monocytogenes* at 35, 22, 12 and 2°C, with higher growth rates observed at higher temperatures, except for carrot. In general, populations of *L. monocytogenes* on produce samples increased within 3 d at 35 and 22°C. No significant difference over time was observed in *L. monocytogenes* populations on several commodities held at refrigeration (however *L. monocytogenes* populations survived up to shelf life and beyond). Most *L. monocytogenes* growth maxed out at 6 log CFU/g or piece. Once the carrying capacity was reached (or max growth rate), *L. monocytogenes* populations declined over the shelf life. The data generated in objective 2 were directly used for objective 3 to validate models as well as being distributed in peer-reviewed literature (see Appendix).

Objective 3: Develop risk models for a sub-set of fruit and vegetable storage or handling conditions shown to display growth or enhanced survival of *L. monocytogenes*.

The primary objective was to develop risk models to describe the growth and or enhanced survival of *L. monocytogenes* for two types of data collected—literature (published studies) and the laboratory-derived data from objective 2—therefore two types of analyses were performed to develop models. Growth parameters were extracted directly from spreadsheet data using DMFit (both online and Excel versions) and simple linear regression in Excel and R. Secondary models for the temperature typically use a square-root model, relating the square-root of the bacterial growth rate and storage temperature. The Ratkowsky equation was used to model microbial growth. When possible, secondary polynomial models that combined the effect of temperature and relative humidity/inoculum/other factors were used. Results from the primary predictive models (created using DMFit) were entered into Microsoft Excel with other relevant descriptive variables. Multiple linear regression using R software created secondary predictive models for maximum growth rate and maximum cell concentration and these models were refined using stepwise regression. ANOVA models were also used to determine overall variable significance. Best subset models were created using the Akaike Information Criterion (AIC) in R.

(i) *Models for growth of L. monocytogenes on whole intact fresh produce from literature data* – We developed models for factors that influence the growth of *L. monocytogenes* on whole intact fresh produce using data extracted from the published literature. Published or final report datasets (n=29) characterizing the behavior of *L. monocytogenes* on 21 different types of whole intact fresh produce were found by searching seven databases. Growth models were fit to each data set to estimate growth rates using DMfit. Multiple linear stepwise regression models were developed using R software. Model factors included: incubation temperature, inoculation buffer, initial and final cell concentrations, inoculation method, container characteristics, and produce surface characteristics. Subset regression modeling was used to further refine the models. The olsrr package was used to create best subset models of the significant parameters. Parameters used in the reduced model were incubation temperature, inoculation buffer type, initial and final cell concentrations, container characteristics and produce surface characteristics.

The reduced multiple linear regression model for growth rate had an adjusted R^2 value of 0.51 with a p-value of <4.00e-15. ANOVA analysis showed that incubation temperature, initial cell concentration, final cell concentration, and produce surface characteristics all had significant ($P < 0.05$) effects on growth rate. The best regression model for growth rate had 3 parameters: incubation temperature, and initial and final cell concentrations. The model created using these parameters had an adjusted R^2 of 0.37 and a p-value of 3.33e-13.

(ii) *Validation of existing ComBase models for suitability in ten different types of whole, intact fresh produce commodities* – The ability of ComBase Predictor to model *L. monocytogenes* growth on ten different whole fresh produce commodities stored between 2 to 35°C was

assessed. Ten different produce types (blueberry, broccoli, carrot, cauliflower, cherry, mandarin orange, lemon, raspberry, tomato) were investigated. Five *L. monocytogenes* outbreak strains were made rifampicin resistant to facilitate recovery. A cocktail of the 5 strains in 0.1% peptone water was used to inoculate samples (~3.5 log CFU/sample), incubated at 2, 12, 22 and 35°C and enumerated over 28 days. Experiments were replicated six times for each temperature and produce combination. Growth rates were estimated with DMFit and "growth" was defined as an increase of >1 log CFU for at least two time points. Growth rates were compared with ComBase modeling predictions for *Listeria* at different pH values and temperatures at high water activities (similar to many produce commodities).

DMFit provided generally good fits to initial growth curves. Growth was not observed for any produce items stored at 2°C. Apparent growth was almost always observed at 12, 22 and 35°C for all produce types, with the exception of whole carrots, where no growth was observed under any conditions. In many cases, growth of *L. monocytogenes* up to a maximum of >6.0 log CFU/sample was followed by a decline for the remainder of the storage period.

Outcomes and Accomplishments

Systematic literature review:

The systematic literature review summarized many studies that investigated the growth and/or survival of *L. monocytogenes* on intact fruit and vegetable surfaces. Full details of the 29 selected documents are summarized in a peer-reviewed publication (Marik et al., 2020, *Journal of Food Protection* 83:108–128), including data on temperature, relative humidity, study duration, sample collection time points, storage, and reported *L. monocytogenes* population outcome(s). The studies included 21 unique fruit and vegetable commodities: apples var. Gala and Granny Smith (1); asparagus (1); Haas avocado (1); blueberries (1); canary melons (1); cantaloupe melons (4); celery (1); cranberries (1); cucumbers (2); jalapenos (1); kale (1); lettuce (1); mangoes var. Ataulfo, Kent, and 'Tommy Atkins' (2); mushrooms (*Agaricus bisporus*) (1); nectarine var. August Fire (1); peach var. Autumn Flame (1); persimmons (1); raspberries (1); spinach (3); sprouts (4); and strawberries (1). Generally, the outer surface of fruits and vegetables was not a favorable environment for *L. monocytogenes* growth; however, *L. monocytogenes* growth and/or enhanced survival was observed under some handling and storage conditions along the supply chain. The 21 intact produce commodities examined differed in their ability to support the growth of *L. monocytogenes*. Data compiled from the review reported herein suggest *L. monocytogenes* growth and/or enhanced survival on intact fruits and vegetables was dependent on surface characteristics, temperature, relative humidity, storage matrix (e.g., package, container), and starting inoculum concentration. Identification of these factors that influence the growth and/or enhanced survival of *L. monocytogenes* on intact produce will assist the industry in identifying *L. monocytogenes* contamination risk (by adopting best practices or implementing mitigations specific to the handling, transporting, storing, and displaying of their specific commodities). The review also emphasized that future studies describing experimental conditions, such as relative humidity, may have useful applications for risk modeling or comparison studies of *L. monocytogenes* on intact produce.

L. monocytogenes growth and survival experiments on intact fruits and vegetables:

Data was generated for ten commodities (broccoli, cauliflower, tomato, lemon, mandarin orange, cherry, blackberry, raspberry, blueberry, and carrot) at four different storage temperatures. Growth and survival data are shown in **Figures 2–11**. While there were some generalizations derived from models, *L. monocytogenes* growth and/or survival on the ten intact produce commodities differed. Produce commodities held at 35°C had the highest *L.*

monocytogenes growth rates. Studied whole, intact commodities, except carrot, supported *L. monocytogenes* growth at 35, 22, and 12°C but not at 2°C. Across all commodities, except carrot, *L. monocytogenes* growth rates increased as storage temperature increased (4 to 35°C). While L. monocytogenes populations can grow at refrigeration temperatures, we did not see significant growth over the shelf life of the produce commodities ($P \leq 0.05$). As *L. monocytogenes* populations reached the carrying capacity (approximately 6 log CFU/g or piece), populations started to decline rapidly. Findings suggest intact produce commodities should be held or stored at refrigeration temperatures to limit *L. monocytogenes* growth, which was interesting as several of the commodities are typically held at temperatures above 2°C.

Risk models for a sub-set of fruit and vegetable storage or handling conditions shown to display growth or enhanced survival of *L. monocytogenes*:
The developed models based on prior data and also laboratory-generated data displayed similar findings, as the lab-generated data were used to validate ComBase models. Findings show the importance of inoculum concentration and produce microbial carrying capacity on the estimated growth rate, as well as highlight the overall importance that storage temperature has on growth rate (**Figures 12–14**). These models can be used to guide future experimental design and in quantitative microbial risk assessments for *L. monocytogenes* on whole produce. Additionally, the ComBase model (assuming pH 5) was generally fail safe for all produce items, except for tomatoes stored at 35°C. These results demonstrate that the ComBase model is fail safe for *Listeria*, and industry can feel confident using the model. Interestingly, there is a research need to investigate factors causing apparent growth, especially for items not typically refrigerated. This may be due to an inoculation protocol standard (used by the majority of prior published peer-reviewed literature) that uses an aqueous medium (wet inoculation), compared to use of a non-aqueous medium (dry inoculum).

Summary of Findings and Recommendations

- *L. monocytogenes* growth and/or survival on intact produce differed by commodity.
- Produce surface conditions affected *L. monocytogenes* growth and/or survival. Specifically, increasing roughness and nutrient ability better supported *L. monocytogenes* growth/survival (↑), whereas increased competitive background microflora limited *L. monocytogenes* growth/survival (↓).
- Produce storage conditions affected *L. monocytogenes* growth and/or survival.
- Intact produce held at 22 and 35°C had the highest *L. monocytogenes* growth rates.
- *L. monocytogenes* growth rates increased as temperature increased (4 to 35°C).
- At cooler storage temperatures (≤12°C), relative humidity influenced growth/survival, where low RH limited survival.
- Large shifts in CO_2 and O_2 concentrations within storage containers may suppress the growth/survival of *L. monocytogenes* on produce surfaces.
- Microbial carrying capacity is crucial to characterizing growth and/or survival patterns.
- Studied whole, intact commodities, except carrot, supported *L. monocytogenes* growth at 35, 22, and 12°C but not at 2°C.
- Produce commodities held at refrigeration temperature (2°C) had little to no *L. monocytogenes* growth.
- Inoculum concentration, produce microbial carrying capacity, and temperature impact the estimated *L. monocytogenes* growth rate according to models.
- The ComBase model (assuming pH 5) was generally fail safe for all produce items (validated based on laboratory-generated data), except for tomatoes stored at 35°C.

APPENDICES

Publications

Marik, C.M., J. Zuchel, D.W. Schaffner, and L.K. Strawn. 2020. Growth and Survival of *Listeria monocytogenes* on Intact Fruit and Vegetable Surfaces during Postharvest Handling: A Systematic Literature Review. *J. Food Prot.* 83:108–128.

Pinton, S.P., C.A. Bardsley, C.M. Marik, R.R. Boyer, and L.K. Strawn. 2020. Fate of *Listeria monocytogenes* on Broccoli and Cauliflower at Different Storage Temperatures. *J. Food Prot.* 83:858–864.

Presentations

Strawn, L.K, D. Schaffner. 2019. "A systematic review of *Listeria* growth and survival on fruit and vegetable surfaces Progress Research Report – Lightning Round". CPS Research Symposium, Austin, TX, June 19.

Marik, C., J. Zuchel, D. Schaffner, L.K. Strawn. 2019. "Growth and Survival of *Listeria monocytogenes* on Intact Fruit and Vegetable Surfaces: A Systematic Review" – P2-148. International Association of Food Protection Annual Meeting, Louisville, KY, July 23.

Marik, C., J. Zuchel, D. Schaffner, L.K. Strawn. 2019. Growth and Survival of *Listeria monocytogenes* on Intact Fruit and Vegetable Surfaces: A Systematic Review. 7th Annual Virginia Tech FST department poster competition. Blacksburg, Virginia, April 23.

Submitted Presentations:

Igo, M.J., L.K. Strawn, C. Marik, C. Bardsley, J. Zuchel, D.W. Schaffner. "Models for Growth of *Listeria* on Whole Intact Fresh Produce from Literature Data". International Association for Food Protection Annual Meeting, Cleveland, OH, August 2020.

Girbal, M., L.K. Strawn, C. Marik, C. Bardsley, J. Zuchel, D.W. Schaffner. "Validation of Existing ComBase Models for Suitability in Ten Different Types of Whole, Uncut Fresh Produce". International Association for Food Protection Annual Meeting, Cleveland, OH, August 2020.

Budget Summary

Total funds awarded to this project were $186,523. Final expenditures were ~$168,717; the remaining balance was due to reduced travel funds, a changeover in employees and also our technician was awarded more state-funding.

Table and Figures (see below)

Table 1 and Figures 1–14

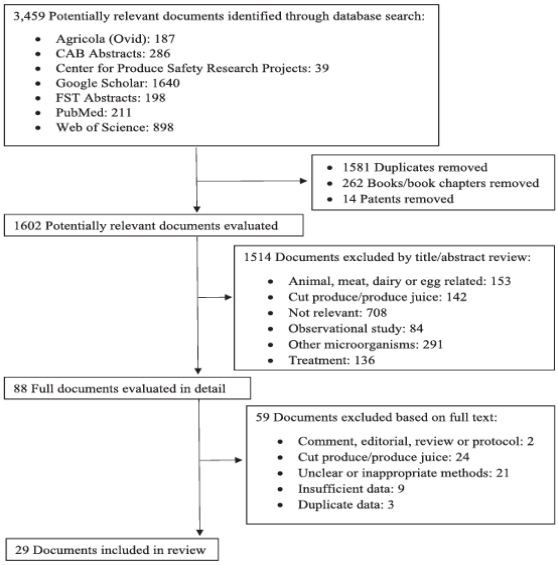

Figure 1. Schematic representation showing selection of studies through the process of the systematic literature review.

Table 1. Growth rate (log CFU/unit/day) and standard deviations for all reported produce commodities[a]

Commodity	Growth rate at refrigeration (4 ± 2°C)	Growth rate at display case (10 ± 2°C)	Growth rate at ambient (≥20°C)	Reference(s)
Apple	0.034	—[b]	0.043 ± 0.026	*83*
Asparagus	−0.372 ± 0.507	1.27 ± 0.496	1.86	*19*
Avocado	—	—	−0.332	*45*
Blueberries	−0.049	−0.136	—	*29*
Canary melon	0.460	—	8.43 ± 5.37	*90*
Cantaloupe	−2.16 ± 4.72	0.177 ± 0.341	0.244 ± 0.469	*66, 68, 71, 113*
Celery	−0.213 ± 0.023	0.119 ± 0.240	0.464 ± 0.115	*114*
Cranberries	−0.131	—	—	*49*
Cucumbers	0.222 ± 0.007	1.14 ± 1.52	1.35 ± 1.59	*8, 65*
Jalapenos	—	0.089	—	*55*
Kale	0.347	—	—	*67*
Lettuce	—	−0.113 ± 0.072	−0.397 ± 0.086	*65*
Mango	−0.115 ± 0.065	11.8	0.161 ± 0.520	*30, 82*
Mushroom	−0.058 ± 0.019	0.343 ± 0.487	—	*46*
Nectarine	—	—	−0.034 ± 0.264	*1*
Peaches	—	—	0.035 ± 0.158	*1*
Persimmons	—	0.492 ± 0.103	4.38 ± 0.642	*105*
Raspberries	−0.007	—	0.532	*70*
Spinach	0.121 ± 0.115	0.301 ± 0.060	6.53 ± 5.20	*36, 73, 74*
Sprouts	0.151 ± 0.441	0.397 ± 0.575	—	*5, 39, 100, 101*
Strawberries	−0.339 ± 0.084	—	−1.25 ± 0.303	*38*

[a] Growth rates for produce data at temperatures not included within the three ranges were excluded.
[b] Dashes indicate no data were available.

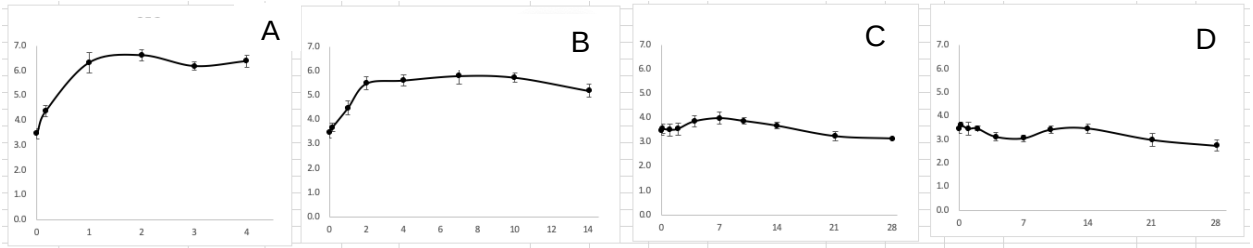

Figure 2. Average *L. monocytogenes* population ± standard error on the surface of fresh tomato during storage at 35±2°C (A), 22±2°C (B), 12±2°C (C), and 2±2°C (D). N=6

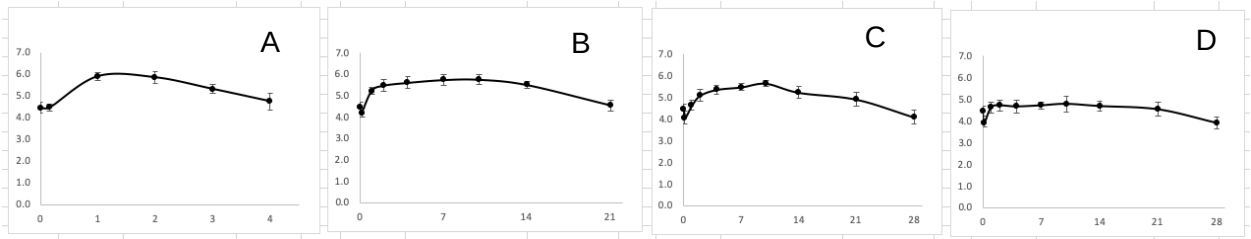

Figure 3. Average *L. monocytogenes* population ± standard error on the surface of fresh mandarin orange during storage at 35±2°C (A), 22±2°C (B), 12±2°C (C), and 2±2°C (D). N=6

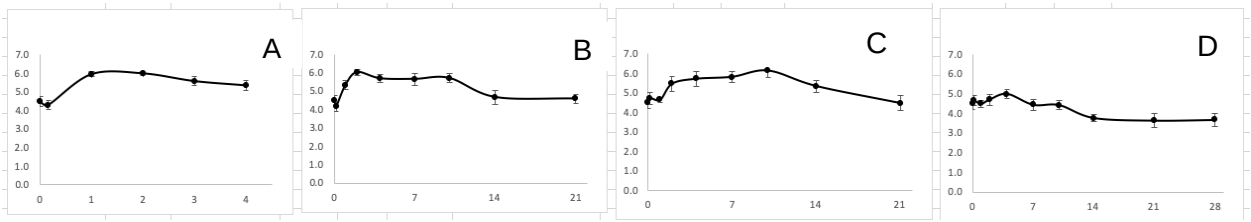

Figure 4. Average *L. monocytogenes* population ± standard error on the surface of fresh lemon during storage at 35±2°C (A), 22±2°C (B), 12±2°C (C), and 2±2°C (D). N=6

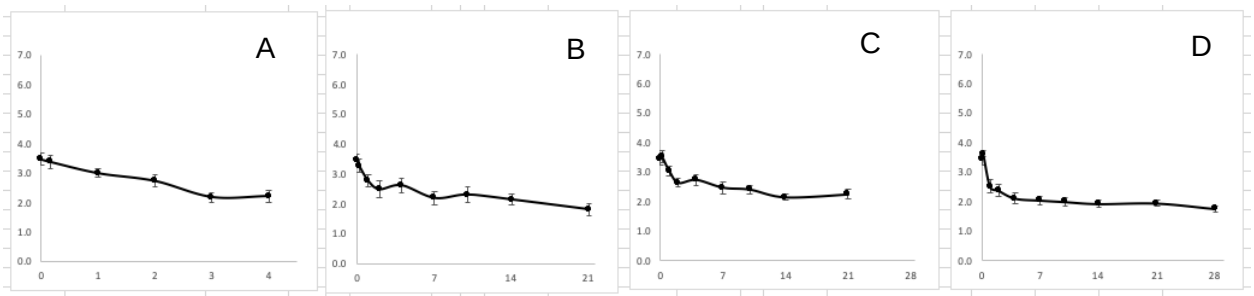

Figure 5. Average *L. monocytogenes* population ± standard error on the surface of fresh carrot during storage at 35±2°C (A), 22±2°C (B), 12±2°C (C), and 2±2°C (D). N=6

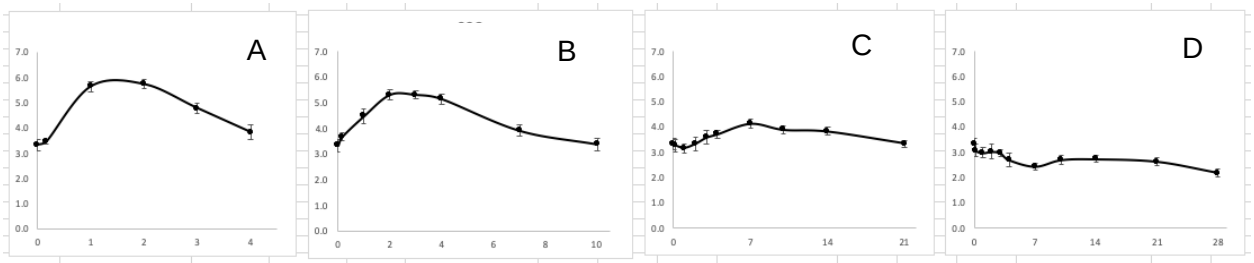

Figure 6. Average *L. monocytogenes* population ± standard error on the surface of fresh cherry during storage at 35±2°C (A), 22±2°C (B), 12±2°C (C), and 2±2°C (D). N=6

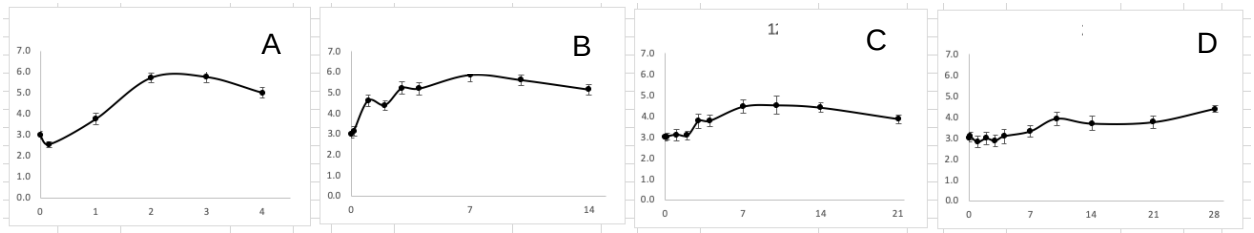

Figure 7. Average *L. monocytogenes* population ± standard error on the surface of fresh broccoli during storage at 35±2°C (A), 22±2°C (B), 12±2°C (C), and 2±2°C (D). N=6

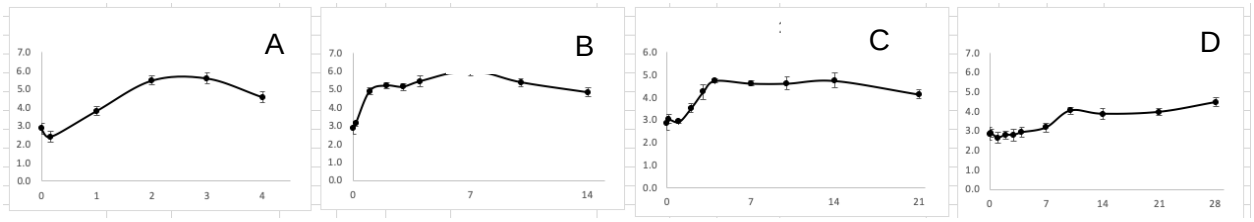

Figure 8. Average *L. monocytogenes* population ± standard error on the surface of fresh cauliflower during storage at 35±2°C (A), 22±2°C (B), 12±2°C (C), and 2±2°C (D). N=6

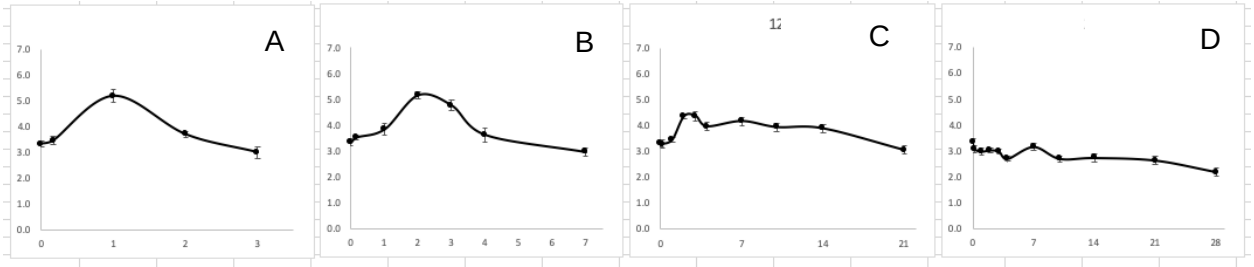

Figure 9. Average *L. monocytogenes* population ± standard error on the surface of fresh blackberry during storage at 35±2°C (A), 22±2°C (B), 12±2°C (C), and 2±2°C (D). N=6

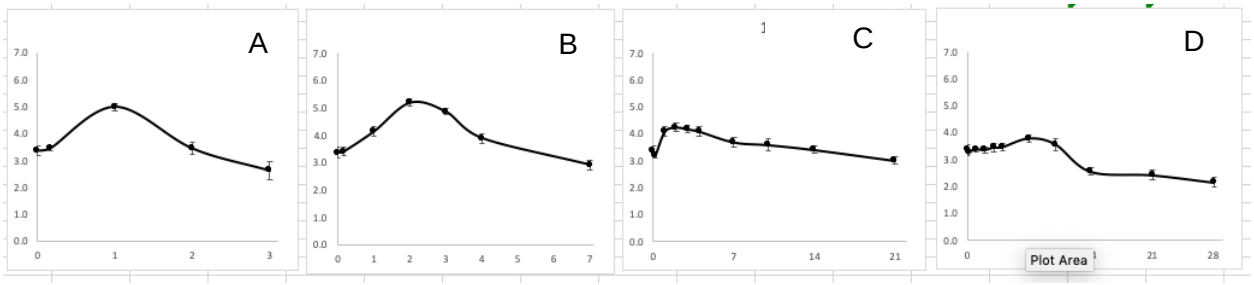

Figure 10. Average *L. monocytogenes* population ± standard error on the surface of fresh raspberry during storage at 35±2°C (A), 22±2°C (B), 12±2°C (C), and 2±2°C (D). N=6

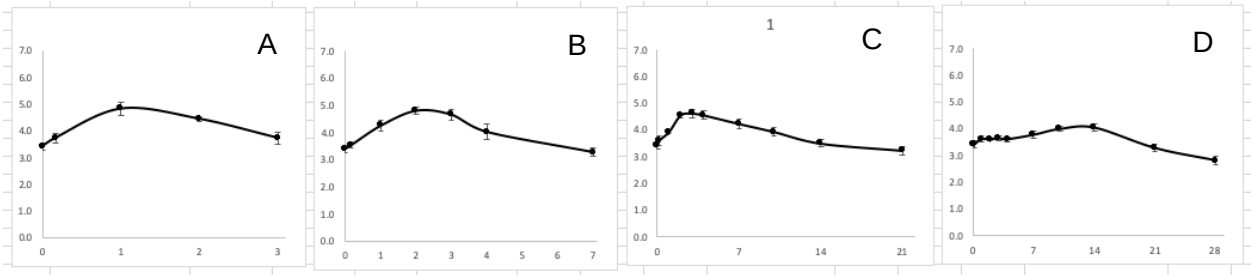

Figure 11. Average *L. monocytogenes* population ± standard error on the surface of fresh blueberry during storage at 35±2°C (A), 22±2°C (B), 12±2°C (C), and 2±2°C (D). N=6

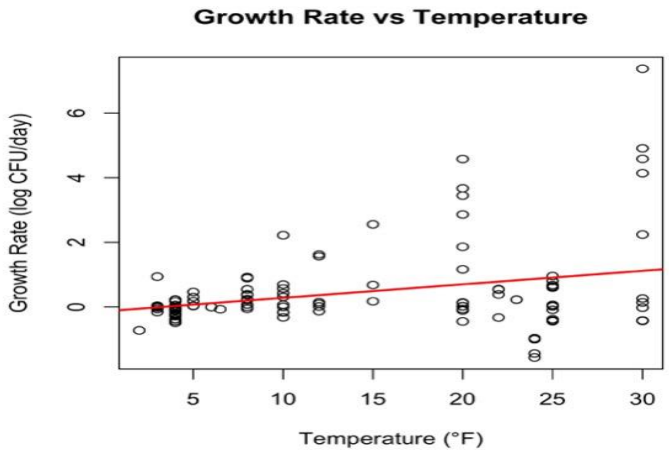

Figure 12. Relationship between *L. monocytogenes* growth rate and storage temperature.

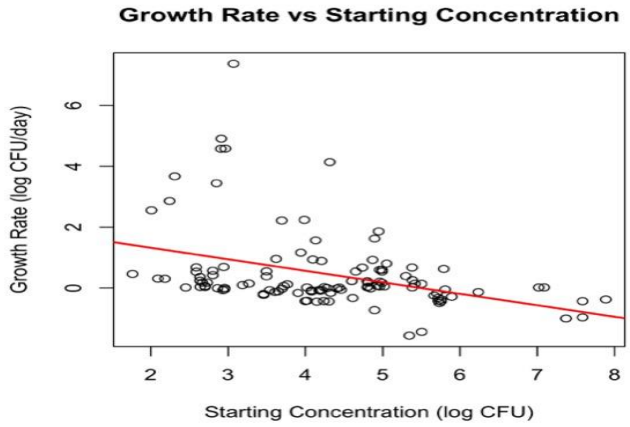

Figure 13. Relationship between *L. monocytogenes* growth rate and starting inoculum concentration.

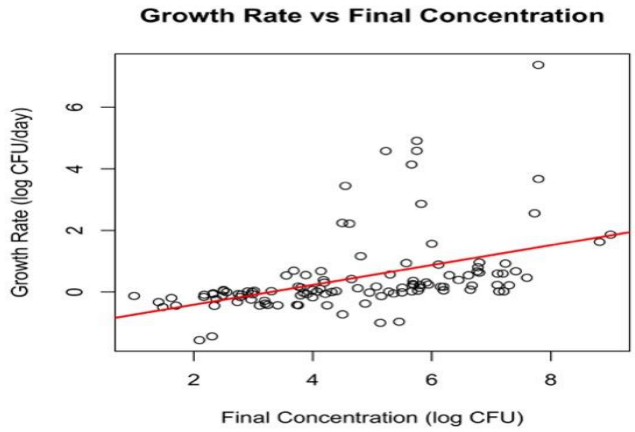

Figure 14. Relationship between *L. monocytogenes* growth rate and ending inoculum concentration.

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