Research Article

Development of Prediction Model for *Staphylococcus aureus* Enterotoxin Production Based on Temperature, pH and Water Activity Levels

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Abstract | *Staphylococcus aureus* (*S. aureus*) produces enterotoxins that cause food poisoning, a significant public health concern in Korea. Preventing contamination is challenging due to its multiple contamination pathways in food production and handling. To address this, a predictive model was developed to estimate *S. aureus* production based on key environmental factors, including temperature, pH, and water activity (Aw). The effects of temperature (10~50°C), pH (5.5~8.5), and Aw (0.70~0.80) on *S. aureus* growth and toxin production were analyzed. The bacteria grew actively at 30-40°C, with toxin production starting at 30°C after 40 hours and peaking at 100 hours. Optimal growth occurred at pH 6.0~7.0, while growth and toxin production were suppressed under extreme pH levels (5.5 and 8.5). At Aw 0.80, steady growth and toxin production were observed after 40 hours, but both were inhibited at Aw ≤ 0.77. A Modified Gompertz model was developed to predict *S. aureus* production under optimal conditions (30~40°C, pH 6.0~7.5, Aw 0.80) and showed high accuracy (R^2 ≥ 0.997). Foods like fruits, vegetables, meat, and bread with Aw ≥ 0.80 pose a high risk for *S. aureus* contamination, underscoring the need for further research to enhance food safety.

Keywords | *Staphylococcus aureus*, Enterotoxin, Toxin production, Predictive model

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INTRODUCTION

Globally, 1 in 10 people, approximately 600 million, contract foodborne illnesses after consuming contaminated food, leading to 420,000 deaths each year. Children under the age of 5 bear 40% of the burden of foodborne diseases, with 125,000 children dying annually (WHO, 2020). In Korea, between 2014 and 2023, there were a total of 3,142 reported food poisoning incidents, affecting 63,821 patients. Among them, the number of *S. aureus* cases has been steadily increasing, from 157 cases in 2022 to 377 cases in 2023, marking an increase of approximately 140% (MFDS, 2024). Food poisoning cases caused by *S. aureus* have been consistently reported in dairy products such as cream and cheese, as well as in processed meats, beef, and pork (Lee *et al.*, 2010; Al-Jaghifi and Khudhir, 2024). *S. aureus* is a gram-positive coccus that causes nosocomial and contact infections (Kluytmans *et al.*, 1997).

S. aureus carriers account for 25-50% of people, and 15-20% of these carriers are known to harbor enterotoxin-producing strains (Kerouanton *et al.*, 2007). *S. aureus* is commonly found on the skin, particularly in the nasal mucosa and hands, making improper food handling by workers a major source of contamination (Park *et al.*, 2013). *S. aureus* is expressed through three stages of contamination of food, proliferation of causative bacteria in contaminated food,

and production of pathogenic factors, and various exotoxins are produced as pathogenic factors (Pinchuk *et al*., 2010). Exotoxins include toxic shock syndrome toxin (TSST), which causes toxic shock syndrome, and enterotoxins, which lead to food poisoning (Fraser, 1989; Scholl *et al*., 1989). *S. aureus* enterotoxin (SE) has 23 species based on antigenicity, with SEA, SEB, SEC, and SED accounting for approximately 95% of food poisoning cases (Hu *et al*., 2018). Typical symptoms of food poisoning caused by SE in humans include vomiting, diarrhea, abdominal pain, and nausea after a short incubation period (within 2 to 6 hours) (Cenci-Goga *et al*., 2003). Symptoms generally improve within 8 to 24 hours of onset, and most toxins in the human body naturally degrade, so the fatality rate is low. However, it can be fatal for vulnerable groups such as children and the elderly (Murray, 2005; Schelin *et al*., 2017). These SEs are particularly resistant to heat compared to other food toxins, as they are not destroyed even by heating at 100°C for 30 minutes (Kim *et al*., 2017).

Predictive model studies of *S. aureus* primarily focus on predicting bacterial growth or contamination in foods such as egg, milk, cheese, flour, and processed foods (Cai *et al*., 2023; Cao *et al*., 2017; Ding *et al*., 2011; Fujikawa and Morozumi, 2006). While some studies have examined combined effects of temperature, pH, and water activity on *S. aureus* growth, most focus on growth prediction rather than enterotoxin production. However, bacterial growth does not always correlate with enterotoxin production, as toxin synthesis can occur under specific environmental conditions even when growth is limited. Among various contamination routes, dairy products are of particular concern as *S. aureus* from bovine mastitis can directly contaminate raw milk during milking, potentially introducing enterotoxins into the food supply chain. Given that mastitis is one of the most common diseases in dairy cattle and a primary source of *S. aureus* contamination in milk, this study utilized a single mastitis-derived strain to establish baseline enterotoxin production patterns under controlled environmental conditions. This approach allows for precise characterization of toxin production dynamics without the variability introduced by strain differences. Therefore, the objective of this study is to develop a predictive model specifically for enterotoxin production by a mastitis-derived *S. aureus* strain under various environmental conditions, including temperature (10-50°C), pH (5.5-8.5), and Aw (0.70-0.80). As a fundamental laboratory-scale study, this research aims to characterize the toxin production dynamics and growth patterns of this specific isolate in microbiological media. While bacterial growth is monitored to understand its relationship with toxin synthesis, the primary focus is on quantifying and predicting SE production levels. This experimental model is intended to provide baseline data that can be applied to assess contamination risks in real food systems and to establish effective control strategies for food safety management.

MATERIALS AND METHODS

Verification of enterotoxin productivity by *S. aureus*

The strain used in this study was *S. aureus* isolated in 2023 from a clinical mastitis case at a dairy cattle farm in Boryeong, Chungcheongnam-do, South Korea, using the method described by Neri *et al*. (2024). Strains stored in glycerol stocks at -80 °C were thawed at -20°C for 24 hours before use. On the day of the experiment, they were stored at 4 °C. To activate the bacteria, they were inoculated into tryptic soy broth (TSB; Difco, USA) supplemented with 10% NaCl and precultured three times for 24 hours at 36±1°C.

DNA extraction and PCR were performed to identify the enterotoxin-producing genes in this strain. DNA extraction was performed according to the manufacturer's instructions using a DNA extraction kit (TaKaRa, Korea). For the detection of enterotoxin SEA, SEB, SEC, and SED genes, PCR was conducted using a Q-Cycler (Quantabiotech, England), and oligonucleotide primers, as shown in Table 1, were synthesized by Bioneer (Korea). The PCR products were observed using the Gel Doc system (GDS-200D, MDM, Korea). PCR was denatured for 5 minutes at 94 °C, followed by 1min denaturation at 94°C, 1 min annealing at 55 °C, and 2 min extension at 72 °C for a total of 35 cycles, and extended for 10 minutes at 72°C.

Table 1: Oligonucleotide sequences used in PCR to identify SE-types toxic produced by *S. aureus*.

Primer name	Oligonucleotide sequence (5'→3')	Amplicon size (bp)
sea1	CCTTTGGAAACGGTTAAAACG	127
sea2	TCTGAACCTTCCCATCAAAAAC	
seb1	TCGCATCAAACTGACAAACG	477
seb2	GCAGGTACTCTATAAGTGCCTGC	
sec1	CTCAAGAACTAGACATAAAAGCTAGG	271
sec2	TCAAAATCGGATTAACATTATCC	
sed1	CTAGTTTGGTAATATCTCCTTTAAACG	319
sed2	TTAATGCTATATCTTATAGGGTAAACATC	

Measurement of growth and SE production of *S. aureus*

Media at pH 5.5, 6.0, 6.5, 7.0, 7.5, 8.0, and 8.5 were prepared by adding 1 N HCl (Difco, USA) to tryptic soy broth containing 10% NaCl. The Aw levels of the media were adjusted to 0.70, 0.74, 0.77 and 0.80 by adding glycerol (Daejung Chemicals and Metals Co., Ltd., Siheung, Korea). The final Aw values were verified and precisely calibrated using a portable water activity meter (WA-160A, Amittari, Guangzhou, China). The incubation temperature was set at 10°C, 20°C, 30°C, 40°C, and 50°C, with control media set to pH 7.0 and Aw 0.80. The pH- and Aw-adjusted media were inoculated with 2% (0.2 mL) of the precultured medium and incubated at 37°C. For growth measurement by temperature, 10 mL of TSB medium with 10% NaCl was placed in a test tube, inoculated with 2% (0.2 mL each) culture, and incubated at 10°C, 20°C, 30°C, 40°C, and 50°C. All experiments were conducted in three replicates. *S. aureus* growth was measured by collecting 0.2 mL from each test tube at 5, 10, 20, 40, 60, 80, and 100 hours of incubation. The samples were placed in 96-well plates (SPL, Korea), and absorbance at 595 nm was measured using a microplate reader. Toxin production was quantified using the RIDASCREEN® SET Total kit (*S. aureus* enterotoxins A, B, C, D, E; R-Biopharm, Germany) by comparison with the standard toxin in the kit.

Development of predictuin model

The predictive model was developed by measuring toxin production over time under constant environmental conditions (temperature, pH, Aw) after inoculation of the medium. Nonlinear regression was conducted using the Modified Gompertz model (Zwietering *et al.*, 1990) in GraphPad Prism 10.1.0 (GraphPad Software, USA). In this study, environmental conditions where toxin concentrations fell below the analytical sensitivity (limit of detection) of the kit were excluded from the analysis. The cutoff value was set at 0.310 ng/mL, as it was not possible to calculate significant kinetic parameters for samples below this threshold. The model equation is:

$$Y = A \cdot exp\left\{-exp\left[\left(\frac{\mu_m \cdot e}{A}\right) \cdot (\lambda - X) + 1\right]\right\} \quad \ldots(1)$$

Y: Cumulative toxin production (ng/mL), T: Incubation time (hour), A: Toxin production potential (ng/mL), μ_m: Maximum toxin production rate (ng/mL/hour), λ: Duration of lag phase (hour), X: Incubation time (hour).

Statistical analysis

Statistical analyses of *S. aureus* growth and SE production under each experimental condition were performed using analysis of variance (ANOVA) with SPSS 25.0 (IBM Corp., Armonk, NY, USA). Significant differences between the means were determined using Duncan's multiple range test at a significance level of $P < 0.05$.

RESULTS AND DISCUSSION

Confirmation of SE production by *S. aureus*

DNA from *S. aureus* was extracted, subjected to PCR, and loaded onto an agarose gel. PCR analysis was conducted for SEA, SEB, SEC, and SED, which are the major enterotoxins responsible for most *S. aureus* food poisoning cases. SEE was excluded from this study due to its significantly lower epidemiological relevance. The presence of enterotoxin genes was confirmed by comparing the PCR amplicons with a 100 bp DNA ladder. As shown in Figure 1, the target genes were identified by their specific molecular sizes: SEC (271 bp) and SED (319 bp) in panel (a), SEB (477 bp) and SEA (127 bp) in panel (b), and the consistent detection of SED (319 bp) across multiple samples in panel (c). The observed band sizes for SEA (127 bp), SEB (477 bp), SEC (271 bp), and SED (319 bp) were in exact agreement with the expected sizes of the oligonucleotide primers, confirming the identity of the mastitis-derived *S. aureus* isolate. Since Betley and Mekalanos (1985) first identified SEA, a type of enterotoxin, in *S. aureus*, enterotoxins with more than 25 genetic forms have been identified. However, these diverse enterotoxins can be divided into the SEA, SEB, SEI, and

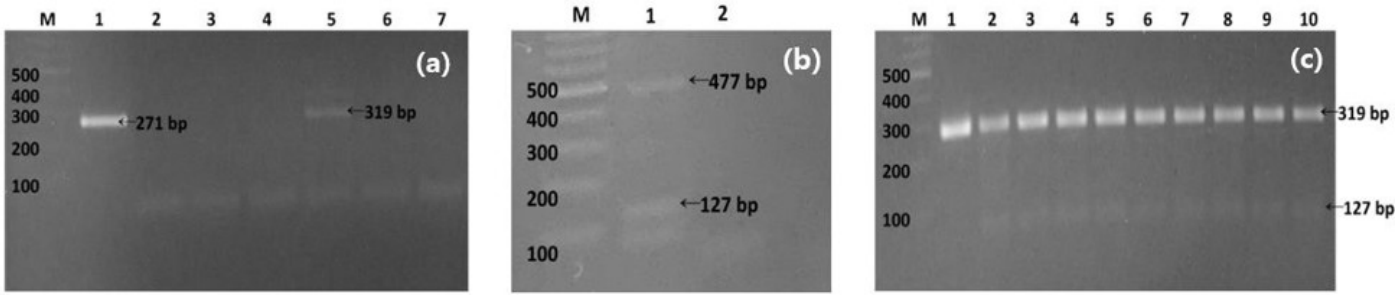

Figure 1: Detection of staphylococcal enterotoxin (SE) genes in *S. aureus* using the Gel Doc system.
(a) SE gene profiles of *S. aureus*; M: 100 bp DNA ladder, Lanes 1–7: *S. aureus* isolates. (b) SE gene profiles of *S. aureus*; M: 100 bp DNA ladder, Lanes 1–2: *S. aureus* isolates. (c) SE gene profiles of *S. aureus*; M: 100 bp DNA ladder, Lanes 1–10: *S. aureus* isolates.

SE/X groups based on their nucleotide and amino acid sequences (Ono *et al*., 2015). The detection and results of enterotoxins (SEA, SEB, SEC, SED) confirmed through this study were identical to those of various enterotoxin studies conducted using *S. aureus* (Malachowa and DeLeo, 2010; Ono *et al*., 2015; Umeda *et al*., 2017; Thomas *et al*., 2006).

Measurement of growth and se production of *S. aureus*

To determine the growth of S. aureus according to temperature, Aw, and pH levels, the OD value of the culture was measured at 595 nm. Regarding the effect of temperature (Figure 2a), the growth of *S. aureus* began to increase significantly (P<0.05) at 30 °C and 40 °C from 20 hours after incubation, steadily increasing until 100 hours at 30°C and 80 hours at 40°C. At 50°C, while growth increased significantly compared to 10°C and 20°C starting from 20 hours, it was inhibited after 80 hours and remained significantly lower than at 30°C and 40°C. No significant growth was observed at 10°C and 20°C throughout the incubation period. Although *S. aureus* can generally grow between 6.7-48.5°C with an optimum of 37°C (Balaban and Rasooly, 2000; Sutherland *et al*., 1994), our study showed no clear growth at 20°C. This is likely because the Aw of the medium was 0.80. Medveďová *et al*. (2019) previously reported that *S. aureus* does not grow at 18°C when Aw is 0.893 or less. Regarding the effect of Aw (Figure 2b), *S. aureus* exhibited significant and active growth only at Aw 0.80, with OD values increasing steadily from 20 hours (P<0.05). At Aw levels of 0.77, 0.74, and 0.70, only minimal increases in OD were observed after 10-20 hours. These increases were significantly lower than at Aw 0.80 and likely represent limited survival or metabolic maintenance rather than active cell division (Mira *et al*., 2022). While *S. aureus* is halophilic and can grow at Aw as low as 0.83-0.86 (Sutherland *et al*., 1994), our results indicate that active growth is severely restricted below Aw 0.80. This inhibition may have been further enhanced by the use of glycerol as an osmotic agent (Stewart *et al*., 2002). The growth of *S. aureus* according to pH levels (Figure 2c) began to significantly increase after 10 hours at pH 7.0, 40 hours at pH 6.5, 60 hours at pH 6.0, and 100 hours at pH 7.5 (P<0.05). Notably, growth at pH 7.0 was significantly higher than at other pH levels (5.5, 6.0, 6.5, and 8.5) from the 10 hour mark and continued to increase steadily until 100 hours. Growth at pH 5.5 and 8.5 did not change significantly over time, supporting the finding that extreme pH values strongly inhibit proliferation (Arvidson and Holme, 1971; Lanciotti *et al*., 2001).

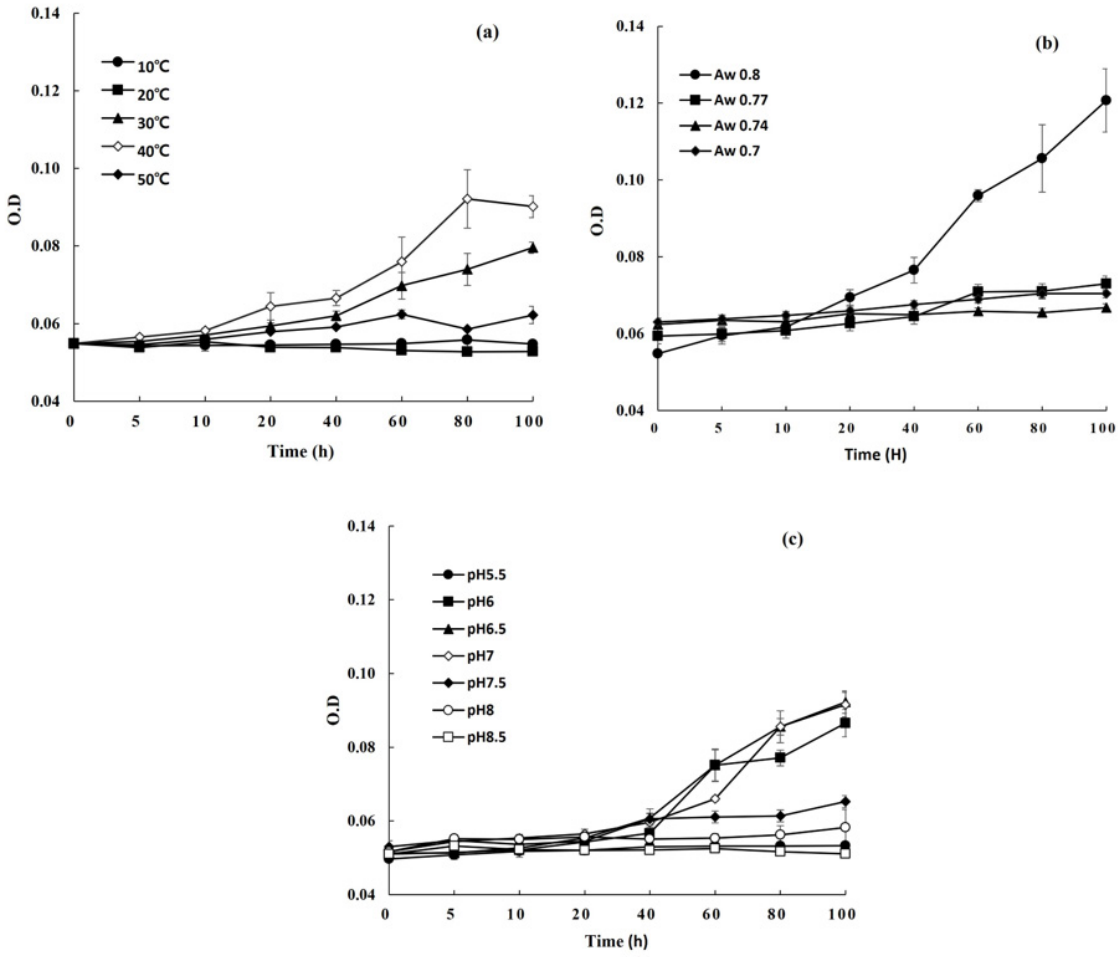

Figure 2: Growth of *S. aureus* under different environmental conditions: (a) temperature, (b) Aw, and (c) pH.

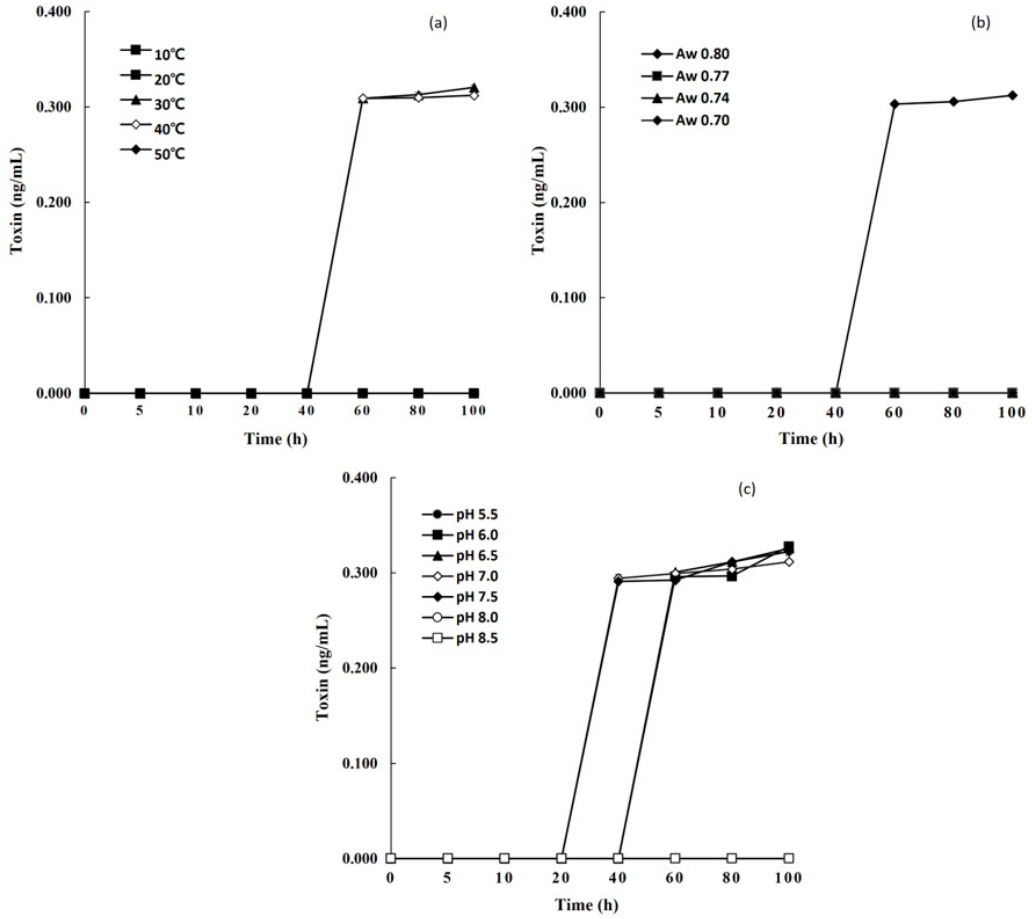

Figure 3: SE production under various environmental conditions: (a) temperature, (b) Aw, and (c) pH.

The standard toxin (positive control) included in the RIDASCREEN® SET Total kit was measured by absorbance at 450 nm and a trend line was derived using the standard curve. The R^2 of the standard curve trend line was 0.989, which quantified the amount of SE produced according to temperature, pH, and Aw levels and expressed it as ng/mL. The results of quantifying the toxin in the culture broth of *S. aureus* by measuring the OD value at 450 nm are shown in Figure 3. As for temperature (Figure 3a), SE significantly ($P<0.05$) increased to 0.3091 ng/mL after 60 hours of incubation at 30°C, and reached 0.3206 ng/mL after 100 hours. Similarly, at 40°C, toxin production significantly ($P<0.05$) increased to 0.3091 ng/mL after 60 hours and to 0.3123 ng/mL after 100 hours. Depending on pH levels (Figure 3b), SE production began to increase significantly ($P<0.05$) after 40 hours of incubation at pH 7.0 (0.2943 ng/mL) and pH 7.5 (0.2911 ng/mL). At pH 6.0 and 6.5, significant production was observed after 60 hours, reaching 0.2962 ng/mL and 0.3007 ng/mL, respectively. After 100 hours of incubation, the highest toxin concentration was recorded at pH 6.0 (0.3277 ng/mL). As for Aw (Figure 3c), SE production was detected only at Aw 0.80, where it significantly ($P<0.05$) increased over time, reaching 0.3033 ng/mL after 60 hours and 0.3123 ng/mL after 100 hours. In contrast, SE production was not detected or remained below the detection limit at 10°C, 20°C, 50°C, pH 5.5, 8.0, 8.5, and Aw levels of 0.77, 0.74, and 0.70, where *S. aureus* growth was limited or indistinct. SE production occurs between 10-46°C, with the optimum production temperature ranging from 40~45°C (Medved'ová *et al.*, 2017). Depending on pH, *S. aureus* grows over a wide range of pH levels, from 4.5~9.3, with the optimum pH being 7.0~7.5, while optimum SE production occurs at pH 6~7 (Balaban and Rasooly, 2000; Medved'ová *et al.*, 2017).

Development of toxin production prediction model

The prediction model was developed to measure the toxin production of *S. aureus* over time under specific environmental conditions after medium inoculation. Data were analyzed using a nonlinear regression curve based on the Modified Gompertz model (Zwietering *et al.*, 1990), with toxin production as the dependent variable and incubation time as the independent variable. According to the toxin production results, treatment groups with toxin levels exceeding the detection limit (cutoff value 0.310 ng/mL) were selected for the modeling process. Kinetic data obtained at 30°C and 40°C, pH 6.0-7.5, and Aw 0.80 were used to develop the predictive models, consisting of individual primary models for each environmental condition.

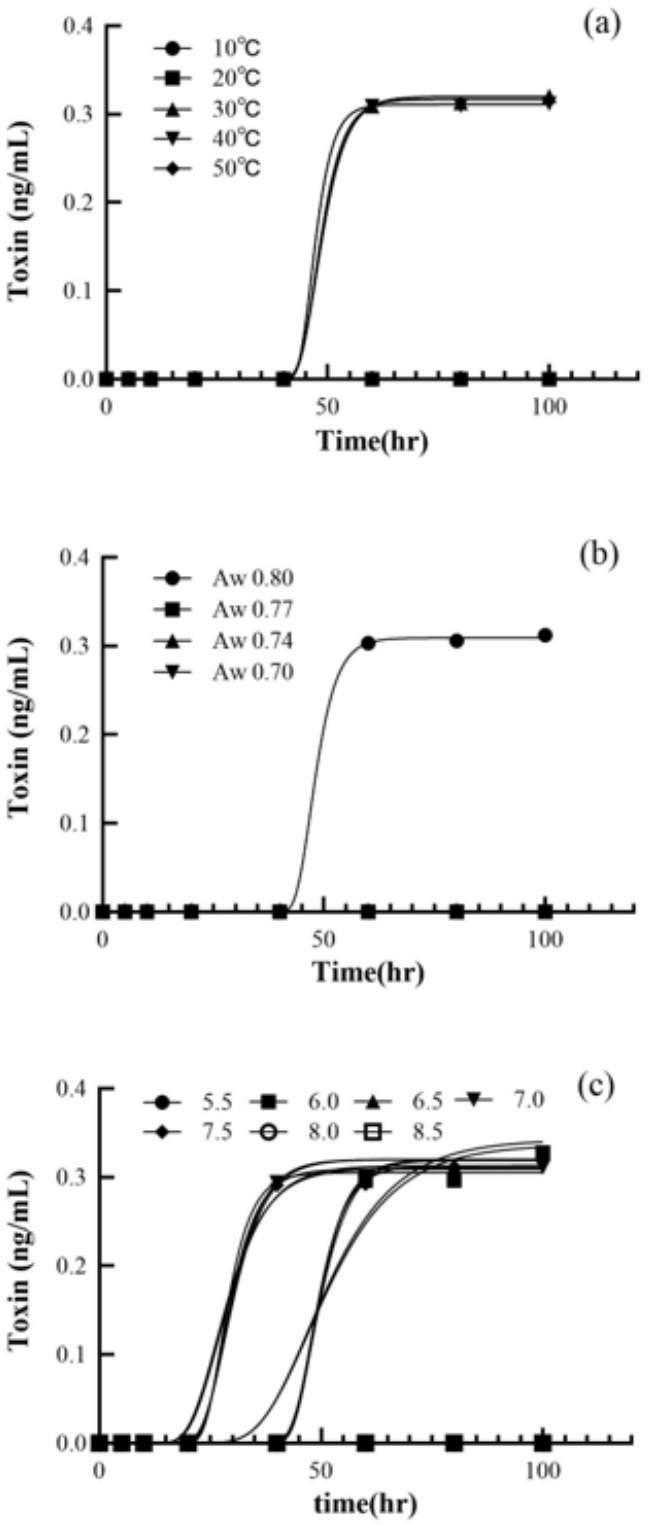

Figure 4: Toxin production kinetics of S. aureus fitted with the Modified Gompertz model under various (a) temperature, (b) Aw, and (c) pH conditions. Symbols represent the observed experimental data, while solid lines represent the model predictions.

The kinetic parameters for toxin production under various temperature, Aw, and pH conditions were analyzed using the Modified Gompertz model, and the resulting primary models and calculated parameters are summarized in Table 2 and illustrated in Figure 4. Across all experimental conditions, the coefficients of determination (R^2) exceeded 0.997, confirming that the model was highly suitable for describing the toxin production curves (Table 2). As the temperature increased from 30°C to 40°C, the maximum toxin production rate (μ_m) rose from 0.0336 to 0.0423 ng/mL/h, while the lag phase (λ) showed a slight decrease. This suggests that 40°C, being more proximal to the optimal growth temperature range for *S. aureus* (35-37°C), enhanced metabolic activity and accelerated toxin biosynthesis. Under the Aw 0.80 condition, the kinetic parameters were determined to be 0.0346 ng/mL/h for μ_m and 43.69 h for λ. Furthermore, the analysis of pH levels revealed that the highest μ_m (0.0298 ng/mL/h) was achieved at pH 7.0, within the neutral range. Notably, the lag phase (λ) was nearly doubled under acidic conditions (pH 6.0 and 6.5) compared to the durations observed at pH 7.0 (23.72 h) and 7.5 (23.49 h), indicating that an acidic environment acts as a critical inhibitory factor that delays the initiation of toxin production. These findings highlight that *S. aureus* can produce toxins even under challenging conditions, supporting the fact that it is frequently found in various foods due to its strong environmental adaptability. *S. aureus* is not only widespread in nature but also has numerous routes for contaminating food, it is essentially impossible to completely prevent *S. aureus* contamination of food. Therefore, to prevent food poisoning caused by SE, it is most important to inhibit the proliferation of *S. aureus* during the production, storage, and distribution process of food. Predictive microbiology, the study that predicts the growth and toxin production of pathogenic microorganisms, is being emphasized to ensure food safety from such foodborne bacteria (Kapperud *et al*., 1995). Among its branches, predictive food microbiology uses mathematical models to determine the between external factors (temperature, time, etc.) and internal factors (pH, Aw, etc.) that affect the growth and toxin production of pathogenic microorganisms (Kumar *et al*., 2024).

Table 2: Kinetic parameters of Modified Gompertz model for toxin production under various environmental conditions.

Condition		Model parameters			
		A (ng/mL)	μ_m (ng/mL/h)	λ (h)	R^2
Temperature	30°C	0.3168	0.0336	43.73	0.9998
	40°C	0.3110	0.0423	43.55	1.0000
Aw	0.80	0.3091	0.0346	43.69	0.9999
pH	6.0	0.3124	0.0273	43.51	0.9973
	6.5	0.3189	0.0277	43.78	0.9995
	7.0	0.3050	0.0298	23.72	0.9996
	7.5	0.3090	0.0261	23.49	0.9975

CONCLUSION

S. aureus produces enterotoxins that cause food poisoning, which continues to occur steadily in Korea. Completely preventing contamination is challenging because *S. aureus* can contaminate food through various routes. Therefore, for the prevention of food poisoning, it is important to suppress the growth of *S. aureus* in the production, storage, and distribution of food, so a model was developed to predict the SE production of *S. aureus* under conditions of temperature, pH, and Aw, which are key factors affecting microbial proliferation. To investigate the effects of temperature, pH, and Aw on the proliferation and toxin production of *S. aureus*, changes in growth and SE production were compared under various culture conditions, including temperatures (10, 20, 30, 40, 50°C), pH (5.5-8.5), and Aw (0.70-0.80). *S. aureus* proliferated actively at 30-40°C but was inhibited at other temperatures (10, 20, and 50°C). Toxin production began after 40 hours at 30°C and 60 hours at 40°C, reaching its peak at 30°C after 100 hours. While stable growth of *S. aureus* was observed at pH 6.5-7.0, both proliferation and toxin production were suppressed at pH 5.5 and 8.5. Under Aw conditions, *S. aureus* proliferated steadily at Aw 0.80, with toxin production starting after 40 hours. Both proliferation and toxin production were suppressed at Aw 0.77 or lower. A Modified Gompertz model was developed to predict toxin production under temperature (30°C, 40°C), pH (6.0, 6.5, 7.0, 7.5), and Aw (0.80) conditions. The model followed a microbial growth curve pattern, with R^2 values of 0.997 or higher, indicating high accuracy and reliability. In addition to knowing the factors that limit the growth and SE production of *S. aureus*, it is also important to identify the characteristics under optimal conditions to optimize risk assessment. Foods such as fruits, vegetables, fresh meat, milk, and bread, which have water activity values of 0.80 or higher, can support *S. aureus* growth and pose a risk of food poisoning, emphasizing the need for further research.

ACKNOWLEDGEMENT

Not applicable.

NOVELTY STATEMENT

This novelty of our study lies in developing a model for the SE production capacity of S. aureus under various growth environments, including temperature, pH, and Aw. Only few studies have been reported on the development of predictive models for SE production capacity of S. aureus under various growth environments. The results of this study are expected to provide important data for food safety management and ultimately contribute to public health in the food sector.

AUTHOR'S CONTRIBUTION

Su Jin Kang and A Jin Lee take responsibility of collecting and analysing the data to drive the results of this study. Dr. Seung Hee Back and Dr. In Sik Nam conducted research design, advised on entire experimental process, and prepared the manuscript to submit the JAHP.

Generative AI and AI assisted technology statement

The authors declare that no generative AI and AI assisted technology was used in the creation of this manuscript.

Conflict of interest

The authors have declared no conflict of interest.

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