Effects of two Weissella viridescens strains on Listeria monocytogenes growth at different initial inoculum proportions

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ABSTRACT
This study analyzed the effect of initial inoculum proportions on Listeria monocytogenes growth when cocultured with two different Weissella viridescens strains. W. viridescens C1 had a strong antimicrobial effect on L. monocytogenes which may be due to the acid, H$_2$O$_2$ and proteinaceous nature of its antimicrobial compounds. W. viridescens C2 had no antimicrobial properties. In liquid coculture, W. viridescens C1 inhibited L. monocytogenes growth, while W. viridescens C2 did not. Thus, L. monocytogenes showed the same growth in the W. viridescens C2 coculture as in the monoculture. Coculturing with W. viridescens at different initial inoculum proportions in laboratory media had no effect on L. monocytogenes growth. This study may help to characterize the interactions between L. monocytogenes and W. viridescens.

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Introduction
Predicting bacterial growth to summarize microbial kinetics is very important in microbial risk assessment (Dong et al., 2015). The typical experimental system for bacterial growth measures growth under actual food conditions. However, the true potential of application of food microbial predictive models is often unknown because most models do not consider microbial interactions in food. Therefore, predictive models for the pathogen of interest must consider the presence of organisms that can spoil food to more accurately describe the bacteria of interest (Brul, Gerwen, & Zwietering, 2007; Malakar, Barker, Zwietering, & Van’t Riet, 2003). Therefore, the microbial interaction between the background microorganism and the pathogen need to be first studied to confirm whether the background microorganism had the effect on the growth of the pathogen. Listeria monocytogenes threatens the food industry and is a concern to public health (Oxaran et al., 2017). Risk assessment is important for controlling L. monocytogenes in food, and bacterial growth predictions must accurately estimate L. monocytogenes concentrations in food at the time of consumption (McMeekin et al., 2008).

Lactic acid bacteria (LAB) are naturally found in food and dominate the microbiota of many foods, such as meat and meat products (Castellano, Holzapfel, & Vignolo, 2004; Chenoll, Macián & Eliazuquivel, 2007; Han et al., 2011; Jiang et al., 2010; Samelis, Kakour & Rementzis, 2000; Yost & Nattress, 2000). In recent years, LAB have received attention for their ability to inhibit foodborne pathogens through various antimicrobial compounds, such as lactic acid, hydrogen peroxide, and bacteriocins. Data in the literature have described some Weissella species, including Weissella viridescens, Weissella halotolerans, and Weissella hellenica, which are reported to be predominant microbiota in meat and meat products (Han et al., 2011; Hu, Zhou, Xu, Li, & Han, 2009; Santos et al., 2005). Some authors have studied predictive models of these predominant microbiota (Gimenez & Dalgaard, 2004; Le Marc, Valik & Medvedová, 2009; Liu, Guo, Li, 2006; Möller et al., 2013). Cornu, Billoir, Bergis, Beaufort, and Zuliani (2011) studied the microbial competition models of L. monocytogenes behavior and LAB in pork meat products.
However, different strains and their different environments may affect the growth of the pathogenic bacteria of interest. Mellefont, McMeekein, and Ross (2008) studied the effect of relative inoculum concentrations on the growth kinetics of L. monocytogenes in coculture, and found that the Jameson effect is often seen in food, particularly those in which LAB dominate. In another case, Coleman, Tamplin, Phillips, and Marmer (2003) showed that the effects of agitation, initial density, pH, and strain were significant for growth kinetics near the boundaries of the growth/no growth interface for E. coli O157:H7. In predictive microbiology, typical experimental systems for growth studies measure the growth of the microorganism of interest under specific conditions, including initial inoculum, background microbiota, and bacterial strains. In this study, two W. viridescens strains with different bacteriocinogenic characteristics were isolated from meat and meat products, and coculture experiments of L. monocytogenes and W. viridescens in liquid media were designed to address two factors that may bias microbial predictive models for L. monocytogenes growth: strains and initial inoculum proportions.

Materials and methods

Bacterial strains

Bacterial strains used in this study were either obtained from the culture collection center or isolated from meat products. The two W. viridescens strains labeled as C1 and C2, were originally isolated from meat products. In the subsequent section of this experiment, it was shown that the W. viridescens C1 strain was bacteriocinogenic, whereas the W. viridescens C2 strain was non-bacteriocinogenic. L. monocytogenes ATCC 19115 was a standard strain purchased from the China Center of Industrial Culture Collection (Beijing, China).

Inoculum preparation

All strains were stored at −80°C in a frozen storage medium with glycerol. Before inoculation, strains were activated and purified. The cultures of W. viridescens were incubated at 37°C for 15 h in MRS broth (de Man, Rogosa and Sharpe, OXOID, London, UK). The indicator strain L. monocytogenes was cultivated in TSB-YE Broth (Trypticase soy-yeast extract broth, Luqiao Co., Beijing, China) at 37°C for 15 h. The final concentrations were approximately 10^6–10^9 CFU/mL per strain, subsequently diluted to give the desired cell numbers before use.

Antilisterial activity of W. viridescens

The antilisterial activity of W. viridescens was analyzed by the agar disk diffusion assay (Ribeiro et al., 2014; Zeng et al., 2014). The L. monocytogenes ATCC 19115 suspensions used as the indicator strains were diluted to 0.1 OD, then plated by spreading them onto BHI agar (Brain-Heart Infusion agar, Luqiao Co., Beijing, China). The cell-free supernatants (CFS) of W. viridescens were obtained by centrifugation at 8000 g for 20 min, then filtered through a 0.22 μm membrane filter. In total, 200 μL of the CFS was added to four wells (6 mm diameter), then added to the plate containing L. monocytogenes. The plates were incubated at 4°C for 4 h for diffusion, then incubated at 37°C for at least 24 h to give a well-defined inhibition zone. Inhibition zone diameters were measured by Vernier calipers. The results represented the average of three trials.

Screening of bacteriocin-producing features

To validate W. viridescens inhibition, the inhibition effect under different conditions was performed as follows. (1) The CFS fluid was adjusted to pH 6.5 with 0.1 mol·L⁻¹ NaOH to suppress the acid’s effect. (2) The above CFS fluid was then treated with 1 mg·mL⁻¹ catalase (Solarbio, Beijing, China) and placed at 37°C for 4 h in a water-bath to suppress the effect of H₂O₂. (3) Then the CFS fluid was treated with 2 mg·mL⁻¹ pepsin (Solarbio, Beijing, China) and 2 mg·mL⁻¹ trypsin (Solarbio, Beijing, China) and placed in the water-bath. The CFS fluid pH was adjusted to the initial pH to suppress the bacteriocin effect. All the above treated CFS fluids were used for the antibacterial activity experiments. All measurements were conducted in duplicate.

Growth characteristics and acid-producing abilities

The growth characteristics and acid-producing ability of two W. viridescens strains were tested. W. viridescens strain C1 was shown to be bacteriocinogenic, while strain C2 was non-bacteriocinogenic. Each W. viridescens strain was incubated at 37°C for 24 h in MRS broth and detected once an hour to obtain the OD600 value by spectrophotometer. The culture pH was monitored every two hours. Non-inoculated W. viridescens in MRS broth was the control.

Mixed culture of W. viridescens with L. monocytogenes

The two W. viridescens strains and the L. monocytogenes strains at different concentrations were prepared for the coculture experiment. In total, 200 mL of Lysogeny Broth medium (Luqiao Co., Beijing, China) was divided into three groups to prepare for the monoculture and coculture experiments as follows: (1) inoculated with both L. monocytogenes strain (final concentration of approximately 10^3 CFU·mL⁻¹) and the W. viridescens strain (concentration of approximately 10^6 CFU·mL⁻¹), (2) inoculated with L. monocytogenes (final concentration of approximately 10^3 CFU·mL⁻¹), and (3) inoculated with the W. viridescens strain (final concentration of approximately 10^6 CFU·mL⁻¹). The flasks were incubated at 4°C, and monitored daily. Each experiment was conducted in triplicate.

Experimental designs based on different initial inoculum proportions

The experimental design assessed the effect of initial inoculum proportions of L. monocytogenes and W. viridescens on bacterial growth in the cocultures. Three combinations of initial inoculum proportions were assessed including a high concentration group (final concentration of approximately 10^3 CFU·mL⁻¹) and a low concentration group (final concentration of approximately 10^3 CFU·mL⁻¹). All coculture experiments had either L. monocytogenes at a high concentration, L. monocytogenes at a low concentration or had equal concentrations of L. monocytogenes and W. viridescens. The monoculture of each species was the control. All flasks
with Lysogeny Broth medium (Luqiao Co., Beijing, China) were incubated at 4°C. Each trial was repeated three times.

**Microbiological analysis and pH measurement**

The cultures at different time intervals were serially diluted, then plated on PALCAM agar (Luqiao, Beijing, China) for *L. monocytogenes* counts and on MRS agar (Oxoid, Basingstoke, UK) for *W. viridescens* counts. The average CFU·mL$^{-1}$ of two plates was recorded. Simultaneously, 4 mL aliquots were removed from the inoculated test samples daily to determine the pH value, using a pH meter (METTLER TOLEDO, Switzerland).

**Statistical analyses**

The data were analyzed in Microsoft Excel (Version 2013). Analysis of variance (ANOVA) tests were applied to determine the differences at a 95% confidence level ($\alpha = 0.05$) by SPSS 18.0.

**Results**

**Characterization of antimicrobial activity of *W. viridescens***

Effects of pH and enzyme treatment on CFS antimicrobial activity of the two *W. viridescens* strains on *L. monocytogenes* are summarized in Table 1. The original *W. viridescens* C1 CFS at room temperature exhibited a strong antimicrobial activity on *L. monocytogenes* (the inhibition zone diameter was $17.97 \pm 1.03$ mm). The NaOH treatment (adjusted to pH 6.5) and treatment with catalase and pepsin reduced the CFS antimicrobial activity, where the inhibition decreased significantly in each treated CFS ($P < 0.05$). However, the CFS after all antimicrobial activity treatments remained within detectable levels.

**Growth characteristics and acid-producing ability of two *W. viridescens* strains**

Studies on bacterial growth and acid production can provide a basis for their inhibitory effects. Therefore, the growth and acid production of two *W. viridescens* strains were monitored at 37°C over a 24 h culture period. Figure 1 shows that both *W. viridescens* strains had high growth abilities, and each bacteria grew quickly after a three hour lag period, then entered the stationary phase after 14 h. Figure 1 also shows pH changes in the culture medium of each strain during the 24 h growth. After 4 h in the culture, the pH rapidly decreased from 6 to below 4.5, indicating that both *W. viridescens* strains could produce acid after the lag, thus inhibiting the other microorganism in the coculture. Compared with the results of

![Figure 1. Growth curves and acid production of two *W. viridescens* isolates at 37°C within 24 h. W. C1-OD600: the OD600 value in *W. viridescens* C1 culture; W. C2-OD600: the OD600 value in *W. viridescens* C2 culture; W. C1-pH: the pH value in *W. viridescens* C1 culture; W. C2-pH: the pH value in *W. viridescens* C2 culture.](image)

![Figure 1. Curvas de crecimiento y producción de ácido de dos aislados de *W. viridescens* a 37°C en un lapso menor a 24 h. W. C1-OD600: el valor OD600 en el cultivo de *W. viridescens* C1; W. C2-OD600: el valor OD600 en el cultivo de *W. viridescens* C2; W. C1-pH: el valor de pH en el cultivo de *W. viridescens* C1; W. C2-pH: el valor de pH en el cultivo de *W. viridescens* C2.](image)
two *W. viridescens* strains, there were no obvious differences in the growth and acid production abilities in the monoculture.

**Characterization of antimicrobial activity of *W. viridescens***

To further understand the inhibitory effect of the two *W. viridescens* strains on *L. monocytogenes* growth, coculture experiments were performed, and the results are shown in Figure 2. In the monoculture, *W. viridescens* C1 inhibited *L. monocytogenes* growth, where *L. monocytogenes* was always in the initial numbers during the entire coculture period. However, *L. monocytogenes* in the coculture with *W. viridescens* C2 showed the same growth as that of the monoculture, and *W. viridescens* C2 was inhibited from Day 2 to Day 9.

**Effect of different relative inoculum proportions on *L. monocytogenes* growth when cocultured with two *W. viridescens* strains**

Three groups, including the high concentration group (final concentration of approximately 10^6 CFU·mL^-1 of *L. monocytogenes* and final concentration of approximately 10^3 CFU·mL^-1 of *W. viridescens*), equal concentration group (final concentration of approximately 10^3 CFU·mL^-1 in both *L. monocytogenes* and *W. viridescens*) and low concentration group (final concentration of approximately 10^3 CFU·mL^-1 of *L. monocytogenes* and final concentration of approximately 10^2 CFU·mL^-1 of *W. viridescens*) were prepared to study the effect of different relative inoculum proportions on *L. monocytogenes* growth in cocultures with two *W. viridescens* strains. As shown in Figure 3, *W. viridescens* C1 suppressed *L. monocytogenes* growth in each concentration group, particularly
when \textit{W. viridescens} C1 began growing. Regardless of the relative inoculum proportions of \textit{L. monocytogenes} and \textit{W. viridescens} C2 (Figure 4), it was evident that \textit{W. viridescens} C2 did not affect \textit{L. monocytogenes} growth, as it had the same growth process as that in its monoculture. This indicated that the relative inoculum proportion did not inhibit \textit{L. monocytogenes} when cocultured with \textit{W. viridescens}.

**Discussion**

In this study, two \textit{W. viridescens} strains were evaluated for their effect on \textit{L. monocytogenes} growth. In previous studies, several LAB metabolites, such as acid, hydrogen peroxide and bacteriocins, were considered as factors affecting antimicrobial activity (Hadji-Sfaxi et al., 2011). Inhibition zones of the different treated CFS in this study suggested that acid, H\textsubscript{2}O\textsubscript{2} and the proteinaceous nature of antimicrobial compounds are involved in the antimicrobial activity of \textit{W. viridescens} C1 on \textit{L. monocytogenes}. For \textit{W. viridescens} C2, no antimicrobial properties were detected in its CFS. Therefore, two \textit{W. viridescens} with different characteristics, C1 and C2, were used for follow-up tests. Bacterial characteristics of the two \textit{W. viridescens} strains indicated that acid was not a factor on \textit{W. viridescens} C1 inhibiting \textit{L. monocytogenes}. Several studies previously found that other factors, such as bacteriocin-like substances, quorum-sensing signaling molecules and competition for nutrients, may contribute to this inhibition (Cruz, Graham, Gagliano, Lorenz, & Garsin, 2013; Huang, Ye, Yu, Wang, & Zhou, 2016; Park et al., 2014). For example, Benkerroum et al. (2002) and Han, Lee, Choi, and Paik (2013) showed that LAB could produce various metabolic products, such as bacteriocin, during the stationary period. Stratakis et al. (2016) found that the protective culture of \textit{W. viridescens} in lower pH was able to gradually reduce the \textit{L. monocytogenes} counts during storage. Therefore, it is important to understand their growth characteristics to analyze their metabolic production.

Coculture experiments had similar findings to the experiments on their antimicrobial activity. LAB dominate the spoilage bacterial population in meat and meat products, and \textit{W. viridescens} is one of the species in this group (Comi & Lacumin, 2012; Hu et al., 2009; Samelis, Kakouriot & Rementzis, 2000). When meat and meat products were contaminated with \textit{L. monocytogenes}, both species interacted and affected microbial growth predictions. This result was also seen in strains selected for bio-protective cultures. This study found that bacteriocinogenic \textit{W. viridescens} C1 affected \textit{L. monocytogenes} growth in coculture, while non-bacteriocinogenic \textit{W. viridescens} C2 did not. Previous studies demonstrated that the bacteriocin-producing LAB strains isolated from foods significantly inhibited pathogen growth. In this study, different strains of \textit{W. viridescens} had different effects on \textit{L. monocytogenes} growth. Figure 5 shows that the pH did not change in either coculture. However, \textit{W. viridescens} C2 had a strong acid-producing ability at lower temperatures in the monoculture, but not in the coculture. This may be due to the interaction between \textit{L. monocytogenes} and \textit{W. viridescens}. \textit{W. viridescens} strains with different characteristics had different inhibitory actions on \textit{L. monocytogenes} growth. This differed from the results of Coleman et al. (2003) and Mellefont et al. (2008), where \textit{L. monocytogenes} was suppressed by all other strains when its inoculum level was lower. Conversely, when \textit{L. monocytogenes} was initially present at a higher concentration, other bacterial growth was suppressed. These inconsistent results may be due to the different inhibitory mechanisms of different bacteria. Therefore, this study evaluated their effect on \textit{L.
monocytogenes growth, to obtain an accurate growth prediction for L. monocytogenes in coculture.

In conclusion, this study indicates that W. viridescens C1 exhibited strong antimicrobial activity against L. monocytogenes, while W. viridescens C2 had no antimicrobial properties. H$_2$O$_2$ and the proteinaceous nature of antimicrobial compounds play a part in the antimicrobial activity of W. viridescens C1 on L. monocytogenes. Effects of initial inoculum proportions for L. monocytogenes and W. viridescens were similar for the growth/no growth of L. monocytogenes when cocultured with W. viridescens C1/C2 in laboratory media. This study may provide microbial interaction information for interspecific predictive models. Furthermore, validating predictive microbiological models generated in food matrices should consider background microorganisms for microbial foodborne hazards.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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