Food Microbiology 77 (2019) 21–25

Contents lists available at ScienceDirect

Food Microbiology

journal homepage: www.elsevier.com/locate/fm

Modelling the effect of oxygen concentration on bacterial growth rates

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ARTICLE INFO

Keywords:
Modified atmosphere packaging
MAP
Predictive microbiology
Food safety
Listeria monocytogenes
Pseudomonas fluorescens
Clostridium perfringens
Clostridium sporogenes
Bacillus weihenstephanensis

ABSTRACT

Predicting the microbial safety of food products stored in modified atmosphere packaging implies taking into account the effect of oxygen reduction on microbial growth. According to their respiratory-type, the microorganisms are not impacted similarly by the oxygen concentration. The aim of this article was to quantify and model the oxygen effect on the growth rates of 5 bacterial species: *Listeria monocytogenes* and *Bacillus weihenstephanensis* (facultative anaerobic), *Pseudomonas fluorescens* (strict aerobic), *Clostridium perfringens* and *Clostridium sporogenes* (strict anaerobic). The results showed the oxygen concentration doesn't modify the behavior of both facultative anaerobic strains. The growth rate of *P. fluorescens* decreased with the oxygen concentration, but the effect is only noticeable when the oxygen concentration fell below 3% in the gaseous phase. Conversely, the oxygen acted as a growth inhibitor for both *Clostridium* species. But total inhibition is reached only for 3.26% and 6.61% respectively for *C. sporogenes* and *C. perfringens*. Two models have been fitted for both respiratory-types, the first is the Monod model considering oxygen as a substrate for growth, and the second is the classic inhibitory model based on minimal inhibitory concentration.

1. Introduction

The interest in the use of the modified atmosphere packaging (MAP) relies on the increase of carbon dioxide concentration, and the reduction of oxygen level (except for fresh meat, where it is held at higher oxygen levels in order to maintain the red meat colour). The packaging processes don't allow the total elimination of the oxygen. Commonly, some percent of oxygen remains in MAP, and will impact the behavior of the microflora contaminating the food product.

The respiratory-type is a main character for the classification of bacteria in several groups. Strict aerobic bacteria can only grow in the presence of oxygen, used to re-oxide coenzymes reduced during the energy metabolism. For this group, the oxygen can be considered as an essential substrate and a lack of oxygen leads to growth inhibition. Anaerobic bacteria can grow in the absence of oxygen, because they can use other electron acceptors than oxygen. While the majority of species can grow indifferently in the presence or absence of oxygen, strict anaerobic bacteria don't have the enzyme make-up to neutralize oxygen derived toxic compounds such as peroxides. For this group, the oxygen can be considered as a growth inhibitor which may lead to total inhibition or bacterial death.

Despite its importance in food safety, the impact of oxygen on microbial growth remains unsatisfactorily described. For example, oxygen inhibits the growth of anaerobes, however the minimal inhibitory concentration (MIC) is not available in the literature. Predictive microbiology can quantify the impact of most of physical-chemical factors, such as temperature, pH, salt, organic acid, and many inhibitors, but little information is available concerning the gaseous environment, despite the fact that oxygen concentration is unavoidable in many microbiological reactions. The aim of this paper is to explore the effect of oxygen on the growth rates of five bacterial species of interest in food microbiology: *Pseudomonas fluorescens* (strict aerobic), *Listeria monocytogenes* and *Bacillus weihenstephanensis* (facultative anaerobic), *Clostridium perfringens* and *Clostridium sporogenes* (strict anaerobic).

2. Material and methods

2.1. Bacterial strains

Listeria monocytogenes strain ADQP105 isolated from seafood product and *Pseudomonas fluorescens* strain J2 isolated from ham were provided from the Sym'Previus collection (www.symprevius.eu).

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https://doi.org/10.1016/j.fm.2018.08.005
Received 1 February 2018; Received in revised form 18 July 2018; Accepted 10 August 2018
Available online 14 August 2018
0740-0020/

Bacillus weihenstephanensis KBAB4 isolated from forest soil, was provided from INRA (Avignon, France). *Clostridium perfringens* Ad 1137 isolated from meat product (pork) was provide from IFIP Collection. *Clostridium sporogenes* 80 L *were isolated from dairy product (milk) and belong to Adria's collection.*

The culture media used in all experiments was Brain Heat Infusion (BHI, Biokar Diagnostics, Beauvais, France) supplemented with yeast extract at 2 g.L^{-1} and glucose at 3 g.L^{-1} (BHIYG) for *Listeria monocytogenes*, *Bacillus weihenstephanensis* and *Pseudomonas fluorescens*. The pH was adjusted to 7.4. Both *Clostridium* species were cultivated in Reinforced Clostridium Medium (RCM, Biokar Diagnostics, Beauvais, France) supplemented with yeast extract at 2 g.L^{-1} and glucose at 3 g.L^{-1} (RCMYG).

The strains were cultivated and frozen (−18 °C) as 1 mL aliquots in culture medium diluted in 50% glycerol (v/v). For all experiments, a first pre-culture obtained from 1 mL of frozen aliquots was performed. This culture was carried out in BHI for *L. monocytogenes*, *B. weihenstephanensis*, *P. fluorescens*, and in RCM for *C. perfringens* and *C. sporogenes*. A second pre-culture was carried out in the same conditions by inoculation with the first preculture. The precultures were incubated for 24 h at 37 °C, 30 °C, 25 °C, 37 °C and 37 °C respectively for *L. monocytogenes*, *B. weihenstephanensis*, *P. fluorescens*, *C. perfringens* and *C. sporogenes*.

2.2. Growth rate acquisition

To evaluate the influence of the oxygen level on the growth rate, strains were inoculated on the surface of agar medium (previously described media supplemented with agar at 1.5%). Agar plates were inoculated with 100 μL of the previous subculture, spread out with sterile inoculators, and incubated in a hypoxic chamber (SCI-TIVE NN Station Hypoxie, AWEL International) where the temperature was maintained at 25 °C. For each enumeration, a petri dish content was transferred to a stomacher bag and a 1/5 dilution was done with tryptone salt broth (BM 11408, Biokar Diagnostics, Beauvais, France). The sample was homogenized with a stomacher (Bag Mixer 400, Interscience Saint Nom) for 1 min. Serial decimal dilutions were prepared in Tryptone salt broth, 1 mL of appropriate dilutions was plated and incubated at 25 °C anaerobically for both *Clostridium* spp strains and aerobically for the three other strains. After about 48 h-72 h, when the number of colony did not change anymore, colony counting was performed and the growth kinetics were plotted.

2.3. Modelling

2.3.1. Estimation of specific growth rate

To evaluate the maximum specific growth rates, the growth kinetics were fitted by the logistic with a delay growth model (Rosso et al., 1996): In

$$N = \begin{cases} \ln N_0 & t \le lag \\ In\ \ N_{\max} - \ln\left(1 + \frac{N_{\max}}{N_0} - 1\right)\exp(-\mu\ \max(t\text{–}log)) & t > lag \end{cases} \quad (1)$$

where lag (h) is the lag time, $\mu_{\max}$ (h^{-1}) is the maximum growth rate, N_0 (CFU/mL) is the initial population size and $N_{\max}$ (CFU/mL) is the maximum population size.

2.3.2. Secondary model for strict aerobic strain

Maximum growth rates were fitted by the well-known Monod's model (Monod, 1942), written as:

$$\mu_{max} = \mu_{opt}\frac{\%O_2}{K_S + \%O_2} \quad (2)$$

where $\mu_{\max}$ (h^{-1}) is the maximum growth rate, μ_{opt} (h^{-1}) is the maximum growth rate in optimal conditions (non-limiting oxygen concentration), $\%O_2$ denotes the substrate concentration (oxygen percentage in the gaseous phase), and K_S is the so-called Michaelis-Menten constant. Here K_S represents the oxygen percentage for which the growth rate is divided by 2.

2.3.3. Secondary model for strict anaerobic strains

Maximum growth rates were fitted by the inhibitory function used by Coroller et al. (2005), written as:

$$\mu_{\max} = \begin{cases} \mu_{opt}\cdot\left(1 - \left(\frac{\%O_2}{MIC}\right)^{\alpha}\right), & \%O_2 < MIC \\ 0, & \%O_2 \ge MIC \end{cases} \quad (3)$$

where $\mu_{\max}$ (h^{-1}) is the maximum growth rate, μ_{opt} (h^{-1}) is the maximum growth rate in optimal conditions (in absence of oxygen, 0%), % O_2 denotes the inhibitor concentration (oxygen percentage in the gaseous phase), MIC is the Minimal Inhibitory Concentration of oxygen expressed as percentage in the gaseous phase from which growth is inhibited, and α reflects the curve shape.

2.4. Model performances and statistical analysis

A non-linear fitting function (lsqcurvefit function, Optimization Toolbox, MATLAB R2013b, The MathWorks, Natick, USA) was used to estimate model parameters. The 95% confidence intervals were estimated using the Matlab Statistics Toolbox function nlparci (Statistical Toolbox, MATLAB R2013b, The MathWorks, Natick, USA).

The goodness of fit was evaluated by the determination coefficient (R^2). A value close to one indicates a best fitting.

The likelihood ratio test was performed to assess whether the difference between growth rates is significant when they are obtained in different oxygen concentrations. The likelihood ratio test (SL) was calculated (Equation 4) to compare the two models: the first without constraints and the second with imposed parameters (Huet et al., 2003).

$$S_L = n.\ ln\left(\frac{SSE_u}{SSE_w}\right) \quad (4)$$

where n is the number of experimental data, SSE_W is the sum of squares due to error obtained from fitting the model without constraints and SSE_U is the sum of squares due to error obtained from fitting the model under constraints. The null hypothesis corresponded to a non-significant difference between the two models and it was rejected when the S_L value was higher than the Chi-squared distribution for $\alpha = 5\%$. The degree of freedom corresponded to the parameter number difference between the two models (without and under constraint).

3. Results

Primary model (equation (1)) was fitted for each growth kinetic, and growth rates were estimated (Table 1). Some growth curves are presented in Fig. 1. The behavior of the studied strains greatly depends on the respiratory-type.

3.1. Pseudomonas fluorescens, strict aerobic species

The growth of *P. fluorescens* was monitored at various oxygen percentages in the gaseous phase, ranged from total anaerobic (0%) to air (21%). Not surprisingly, no growth was observed in the absence of oxygen. However, very low oxygen concentration allowed growth, since at the lower concentration tested (0.1%), the observed growth rate was 0.41 h^{-1}. Above 3%, the growth rate reached the optimal value recorded under air atmosphere. Equation (2) was fitted (Fig. 2), given an optimal growth rate estimated at 0.632 h^{-1}, and a K_S value estimated at 0.118% that means the growth rate is reduced by a factor of two when the oxygen concentration is decreased to 0.118% (Table 2).

Table 1
Growth rates (± 95% confidence intervals) at various oxygen concentrations at 25 °C for the 5 strains. R^2 is the determination coefficient.

% O_2	μ_{max}	R^2
P. fluorescens		
0.1	0.341 ± 0.050	0.983
0.41	0.455 ± 0.059	0.979
0.69	0.510 ± 0.032	0.990
1.5	0.528 ± 0.078	0.984
2.2	0.588 ± 0.060	0.988
3.1	0.615 ± 0.089	0.981
5	0.687 ± 0.091	0.986
21	0.650 ± 0.091	0.986
B. weihenstephanensis		
0.1	0.946 ± 0.388	0.989
0.3	0.620 ± 0.116	0.977
0.41	0.862 ± 0.256	0.980
0.5	0.811 ± 0.126	0.990
0.69	1.407 ± 0.248	0.996
0.7	0.816 ± 0.111	0.990
1.1	0.846 ± 0.173	0.986
2.2	0.889 ± 0.106	0.993
3.1	0.989 ± 0.294	0.990
L. monocytogenes		
0.1	0.538 ± 0.086	0.982
0.14	0.720 ± 0.328	0.958
0.3	0.565 ± 0.081	0.977
0.41	0.570 ± 0.073	0.972
0.5	0.586 ± 0.051	0.987
0.7	0.542 ± 0.073	0.974
1.1	0.587 ± 0.031	0.985
21	0.611 ± 0.106	0.979
C. perfringens		
0.1	0.610 ± 0.187	0.978
0.2	0.223 ± 0.038	0.977
0.2	0.206 ± 0.034	0.975
0.2	0.256 ± 0.033	0.985
0.5	0.294 ± 0.055	0.965
0.5	0.322 ± 0.096	0.946
0.5	0.308 ± 0.106	0.927
0.69	0.348 ± 0.171	0.935
1	0.367 ± 0.048	0.981
1	0.333 ± 0.058	0.978
1	0.241 ± 0.105	0.904
1.5	0.335 ± 0.125	0.963
1.5	0.190 ± 0.033	0.959
1.5	0.221 ± 0.070	0.935
3.1	0.160 ± 0.322	0.950
3.1	0.131 ± 0.123	0.938
3.1	0.141 ± 0.136	0.919
4	0.123 ± 0.114	0.940
4	0.105 ± 0.094	0.891
4	0.172 ± 0.203	0.875
5	0.038 ± 0.018	0.897
5	0.119 ± 0.118	0.869
5	0.038 ± 0.020	0.892
6	No Growth[a]	
6	No Growth[a]	
6	No Growth[a]	
Clostridium sporogenes		
0.2	0.680 ± 0.164	0.978
0.2	0.596 ± 0.114	0.990
0.2	0.568 ± 0.135	0.985
1	0.703 ± 0.123	0.981
1	0.694 ± 0.095	0.986
1	0.644 ± 0.081	0.986
1.5	0.689 ± 0.223	0.982
1.5	0.717 ± 0.169	0.989
1.5	0.614 ± 0.149	0.982
1.5	0.789 ± 0.158	0.975
1.5	0.667 ± 0.201	0.957
1.5	0.600 ± 0.235	0.943
2	0.353 ± 0.168	0.947
2	0.357 ± 0.113	0.951
2	0.349 ± 0.109	0.953
2.6	0.606 ± 0.279	0.978
2.6	0.352 ± 0.060	0.963
2.6	0.234 ± 0.107	0.915
3	0.135 ± 0.036	0.974
3	0.136 ± 0.032	0.979
3	0.137 ± 0.024	0.984
4	No Growth[a]	
4	No Growth[a]	
4	No Growth[a]	

[a] No growth: inactivation was observed.

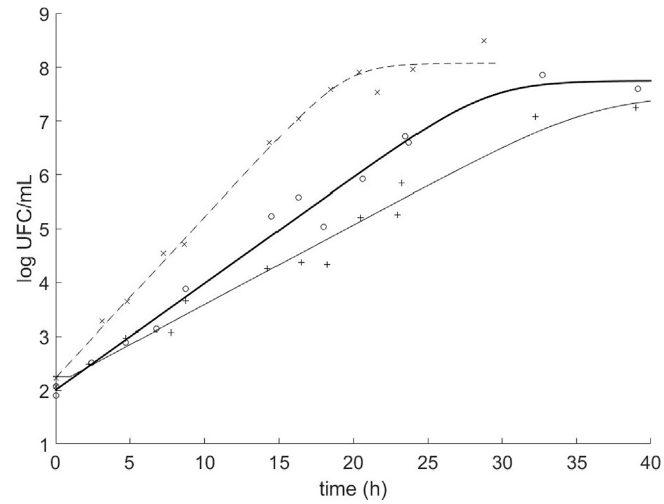

Fig. 1. Growth kinetics of *P. fluorescens* J2 in various oxygen concentration in the gas phase. Squares: 5%; Circles: 0.41%; diamonds: 0.1%.

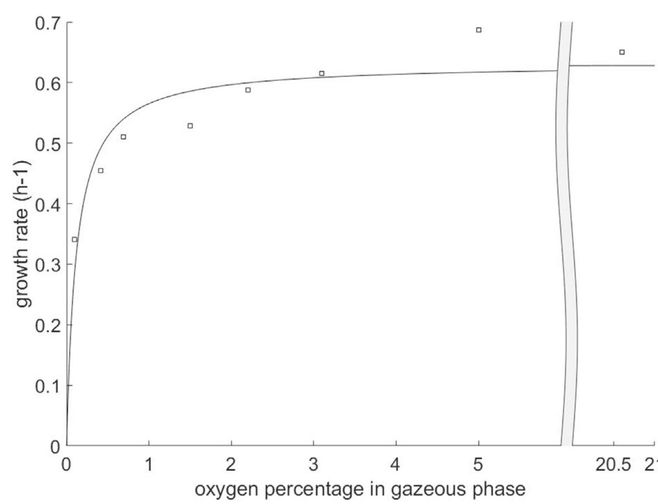

Fig. 2. Growth rate of *P. fluorescens* J2 as a function of oxygen concentration in the gas phase at 25 °C. Solid line represents the fitted model.

3.2. Listeria monocytogenes, and Bacillus weihenstephanensis, facultative anaerobic species

The growth rates of *L. monocytogenes* were estimated at various oxygen percentages in the gaseous phase, and ranged from 0.1% to air 21% for *L. monocytogenes*, and from 0.1% to 3.1% for *B. weihenstephanensis*. No significant difference was noticed when oxygen concentration was modified (Table 1, Figs. 3 and 4). *L. monocytogenes* and *B. weihenstephanensis* growth is unaffected by the absence of oxygen. According to the likelihood ratio test (SL) (Equation 4), the null hypothesis, by which there is no difference between the fitting without

Table 2
Secondary parameters (± 95% confidence intervals) from Monod's model (equation (2)) and inhibitory model (equation (3)). R^2 is the determination coefficient.

	μ_{opt}	Ks	MIC	α	R^2
P. fluorescens (Monod's model)	0.632 ± 0.060	0.118 ± 0.081			0.948
C. perfringens (Inhibitory model)	0.368 ± 0.153		6.61 ± 3.75	0.764 ± 1.04	0.835
C. sporogenes (Inhibitory model)	0.674 ± 0.111		3.26 ± 0.39	2.983 ± 2.32	0.885

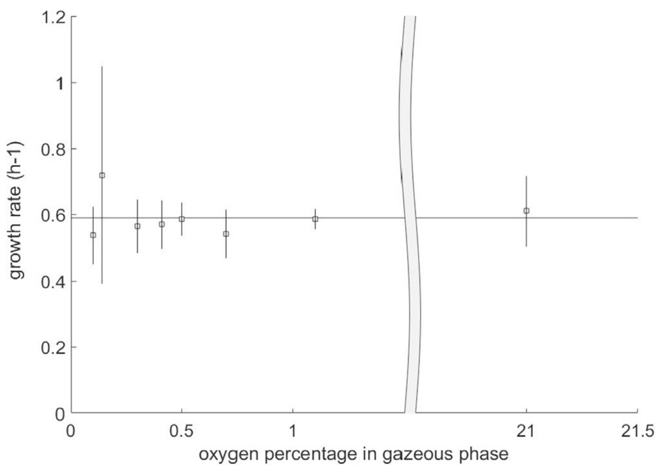

Fig. 3. Growth rate of *L. monocytogenes* ADQP 105 as a function of oxygen concentration in the gas phase at 25 °C. Solid lines represent the fitted inhibitory model.

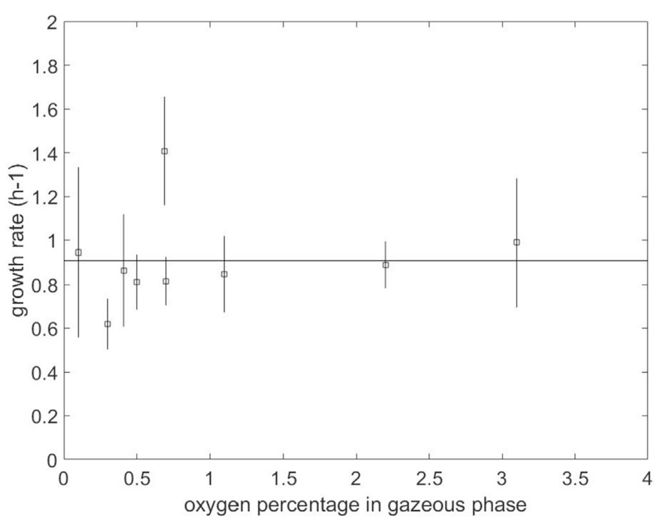

Fig. 4. Growth rate of *B. weihenstephanensis* KBAB4 as a function of oxygen concentration in the gas phase at 25 °C. Solid lines represent the fitted inhibitory model.

constraints (one growth rate value for each kinetic) and with constraints (a single growth rate value for all kinetics was accepted).

3.3. *Clostridium perfringens and Clostridium sporogenes, strict anaerobic species*

The growth of two *Clostridium* species was studied at various oxygen percentages from 0.1 to 6% in the gaseous phase. The results showed a relative tolerance to oxygen for both species. The optimal growth rate was monitored in lower oxygen levels, but the growth was observed until 3% and 5% respectively for *C. sporogenes* and *C. perfringens*. The inhibitory model (equation (3)) was fitted and MIC was estimated at 3.26% and 6.61% respectively for *C. sporogenes* and *C. perfringens* (see Table 2). Fig. 5 represents both fittings.

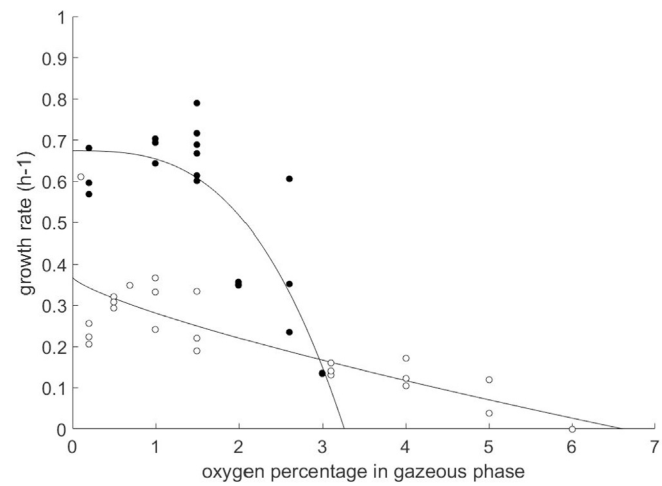

Fig. 5. Growth rate of *C. perfringens* Ad1131 (open circles) and *C. sporogenes* 80 L (closed circles) as a function of oxygen concentration in the gas phase at 25 °C. Solid lines represent the fitted inhibitory model.

4. Discussion

Oxygen can either be indispensable, facultative, or toxic for microbial growth. Except for anaerobes, it is generally recognized that the reduction of oxygen level causes metabolic modification and reduction of growth rate. It could be thought that the oxygen concentration in air is optimal for growth, and a reduction below 21% would cause slower growth. Alexeeva et al. (2002) showed the respiration catabolism of *Escherichia coli* (facultative anaerobe) was gradually replaced by fermentative catabolism by decreasing the oxygen supply: the production rate of fermentation product was directly correlated to oxygen transfer from gas phase to the culture. In our studies, oxygen transfer was modulated by changing the oxygen rate in the gas phase. The catabolism type was not examined, but it seems plausible the microorganism adapted it according to the oxygen availability. However, growth rate is not modified for both facultative anaerobic strains when oxygen concentration decreases, and the inhibitory effect on strict aerobic *P. fluorescens* is observed only when oxygen concentration becomes very low. In contrast to the general characteristics of the genus *Pseudomonas* (strictly aerobic), it cannot be expected that removing oxygen from a food package will easily avoid spoilage by *Pseudomonas* species (Stoops et al., 2012).

Conversely, oxygen is toxic for strict anaerobic bacteria. However, both studied strains present a substantial resistance since growth is totally inhibited for oxygen concentration over 3.2% for one strain, and over 6.6% for the other. Whereas *C. perfringens* is considered as strictly anaerobic, it is an aerotolerant anaerobe that is capable of surviving in soil or arterial blood. It was shown that *C. perfringens* can escape from the phagosomes of macrophages in both aerobic and anaerobic conditions (Briolat and Reysset, 2002). This bacteria owns a system to response to reactive oxygen species. *C. perfringens* possesses specialized genes that might be involved in this adaptive process, such as those encoding superoxide dismutase (SOD), superoxide reductase and alkyl hydroperoxide reductase, but their contribution to the oxidative stress response and their control mechanisms are unknown (Jean et al., 2004).

Modified Atmosphere Packaging (MAP) relies on the replacement of air in the packaging atmosphere by a mixture of different gases (mainly composed of O_2, CO_2 and N_2) in order to prevent food degradation during storage. Except in particular cases, the targeted oxygen concentration should be as low as possible, but the conditioning material and the high-speed conditioning lines cannot allow to achieve a strict anaerobic. Typical values of residual oxygen could be from a few percent to a fraction of a percent (Cocola et al., 2017). According to the results above, residual oxygen in MAP neutralizes the intended effects regarding *P. fluorescens* without preventing the growth of strict anaerobic species as both *Clostridium* studied above. The interest of MAP should also be due to the carbon dioxide concentration which acts as an important inhibitor (Couvert et al., 2017), while a decrease of the oxygen level should influence mainly oxidative reactions. These results are supported by Samapundo et al. (2011) who showed no effect of oxygen ranged between 0 and 21% on *B. weihenstephanensis* growth. Inversely, Geysen et al. (2005) studied high concentrations of oxygen, up to 100%, and showed no effect on the growth rate of *Listeria innocua*.

The residual oxygen levels in MAP products can increase due to factors such as gas permeability of the packaging material, gas trapping ability of enclosed food, compromised packaging, inefficient gas flushing, accidental damage during packaging, handling or transportation (Banerjee et al., 2016).

In general, when MAP is filled with a mixture of N_2 and CO_2, the residual O_2 content tends to decrease with time. The respiration of the naturally present microflora cannot be neglected in most cases, and could, in the particular case of aerobic microbes, contribute to limiting growth by removing all residual O_2 in the package (Guillard et al., 2016). However, the consumption of this residual O_2 needs some time and as long as oxygen remains in the food pack, aerobic growth continue. So the main objective of MAP, which is to prevent the growth of spoilage and/or foodborne pathogens, is not immediately achieved.

Finally, it is necessary to bear in mind that this article focused on the effect of oxygen, independently of others factors as temperature, pH, redox potential, or the presence of growth inhibitor (carbon dioxide, organic acids, etc.). Experiments were lead in conditions very favorable for growth. However, it seems obvious some interaction could appear and impact adversely the growth rate if the conditions turn less favorable.

To conclude, the results highlight the importance of residual O_2 in modified atmosphere packaging regards to microbial behavior. Conditioning under a modified atmosphere reduces the oxygen level, from 21% (air) to a few percent or a fraction of a percent. Reducing oxygen concentration promotes the growth of strict anaerobic bacteria, and sparingly reduces the strict aerobic ones. Whereas a benefit is certainly obtained for chemical and oxidative reaction, the impact on microflora growth, whatever its respiratory-type, remains heavily dependent on the exact residual oxygen concentration.

Acknowledgments

This work was supported by a grant from the Agence Nationale de la Recherche (ANR) (France) as part of the ANR-10-ALIA-0002 *Map'Opt* contract "Equilibrium gas composition in modified atmosphere packaging and food quality".

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