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Desiccation: An environmental and food industry stress that bacteria commonly face

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ABSTRACT

Water is essential for all living organisms, for animals as well as for plants and micro-organisms. For these latter, the presence of water or a humid environment with a high air relative humidity (RH) is necessary for their survival and growth. Thus, variations in the availability of water or in the air relative humidity constitute widespread environmental stresses which challenge microorganisms, and especially bacteria. Indeed, in their direct environment, bacteria are often faced with conditions that remove cell-bound water through air-drying of the atmosphere. Bacterial cells are subject to daily or seasonal environmental variations, sometimes going through periods of severe desiccation. This is also the case in the food industry, where air dehumidification treatments are applied after the daily cleaning-disinfection procedures. In plants producing low-water activity products, it is also usual to significantly reduce or eliminate water usage. Periodic desiccation exposure affects bacteria viability and so they require strategies to persist. Negative effects of desiccation are wide ranging and include direct cellular damage but also changes in the biochemical and biophysical properties of cells for which planktonic cells are more exposed than cells in biofilm. Understanding the mechanisms of desiccation adaptation and tolerance has a biological and biotechnological interest. This review gives an overview of the factors influencing desiccation tolerance and the biological mechanisms involved in this stress response.

Contents

1. Introduction

In terrestrial habitats, bacteria habitually live as multicellular aggregates adhering to biotic or abiotic surfaces and/or to each other (sessile cells) rather than in free suspension in liquid medium (planktonic cells). In this lifestyle, a.k.a. biofilm, cells are often

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involved in highly complex communities that enable efficient resource use in hostile environments (Bogino et al., 2013; Vogeleer et al., 2014). Hence, about 99% of the world's bacterial population is seen in the form of biofilms at various stages of growth (Costerton et al., 1987). Water availability is of particular importance in all environmental habitats since bacteria are submitted to daily (including nycthemeral rhythms) and seasonal variations of air relative humidity (RH) due to rain, drought periods or to drainage. Variations in air RH also occur in food processing plants due to cleaning and disinfection procedures followed by air dehumidification.

Microorganisms are settled in a wide range of environments, their genetic and physiological adaptability enables them to withstand numerous harsh and sometimes combined environmental factors (Moissl-Eichinger et al., 2016). This ability to adapt and persist in harsh environments lies in how cells are able to sense and respond to environmental changes. The switch between planktonic and sessile mode of growth, as well as the adaption to physicochemical variations surrounding the cells, require profound physiological changes which occur through the regulation of gene expression in response to various signals (Renier et al., 2011). Furthermore, it has been reported that bacterial cells growing in biofilm have significantly higher survival rate to stress conditions (Giaouris et al., 2014). The biofilms present in food industry plants may be of major concern when containing pathogen and/or spoilage bacteria, since they can produce significant public health and economic consequences (Carpentier and Cerf, 1993). Moreover, bacterial cells in biofilms are embedded in extracellular polymeric substances that are able to give protection against stresses (Lequette et al., 2010). In spite of the relevance of biofilm, the physiological and molecular responses of bacteria to desiccation stress remains poorly known. Furthermore, most of the desiccation tolerance data comes from planktonic cell reports, as evidenced by the data summarized in Table 1. Thus, this review intends to clearly define the meaning of water stress and then give an updated state of the art regarding cellular mechanisms of adaptation and bacterial strategies to overcome desiccation.

2. Water relevance for bacteria

Before analyzing the effects of desiccation stress on bacterial cells, it is important to shed light on the different phenomena related to water. Thus, it is first indispensable to outline some definitions.

Water activity (a_W) is the ratio between water vapour pressure in a material (p) and the vapour pressure of pure water (po) at the same temperature. A_W is suitable to predict the growth of microorganisms because they can only use "available" water. The a_W value for each bacterium is generally the minimum a_W which can lead to growth. Growth is minimal at the minimum a_W, increasing as a_W increases. At a_W values below the minimum required for growth, bacteria do not necessarily die. Some bacteria, such as *Deinococcus radiodurans* (Blasius et al., 2008) and *Mycobacterium* (Harland et al., 2008), are extremely resistant to prolonged desiccation times while others, such as *Neisseria gonorrhoeae* (Tzeng et al., 2014), can survive only short periods of desiccation.

The relative humidity (RH) of air is the ratio between vapour pressure of air and its vapour pressure saturation. When vapour and temperature levels are stable, the a_W of the sample matches the RH of the air surrounding the sample in a sealed measurement chamber. The percentage of the relative humidity equilibrium (ERH) can be obtained by multiplying a_W by 100.

$$a_W = p/po = ERH\ (\%)\ /\ 100$$

As described by the above equation, a_W is the ratio between vapour pressures and therefore it has no units. It ranges from 0.0a_W (bone dry) to 1.0a_W (pure water).

Microorganisms that are able to grow in low a_W conditions are qualified as xerophilous (Madigan et al., 2006). A xerophile is an organism that can grow and multiply in an environment with an extremely low water availability. They can often survive in situations with a_W below 0.8, as is the case with arid desert soil environments. Among this class of organisms is *Chloroflexus aurantiacus*, a well-known isolated from hot springs.

Desiccation leads to the exit of water from a body and this phenomenon can be natural or forced. Several mechanisms can be used to dry an atmosphere or a specific biological entity, such as a bacterial cell. Removing air from water by the use of physical means is a way to reach desiccation; drying, usually by exposure to dry air, is a special case of desiccation.

Desiccation tolerance is the ability to undergo nearly absolute dehydration through air drying without being killed (Billi and Potts, 2002). A desiccated cell is characterized by its singular lack of water, with contents as low as 0.02 g of H_2O (dry weight)$^{-1}$. Low water potential is considered the biggest life threatening abiotic stress and it negatively affects all biological functions (Krisko et al., 2010). Drying is often associated with osmotic stress but in fact, they are two different stresses. In drying air, dried cells are surrounded by an atmosphere, while under osmotic stress they are immersed in an

Table 1
Examples of bacterial adaptive responses to desiccation stress.

Bacteria	Cell state	Mechanism of resistance to desiccation	Reference
Cyanobacteria	Planktonic	Trehalose and sucrose accumulation	(Hershkovitz et al., 1991)
Pseudomonas spp.	Planktonic	Hygroscopic secreted polysaccharides and fatty acid *trans*-configuration to maintain membrane fluidity	(Roberson and Firestone, 1992)
Escherichia coli	Planktonic	Trehalose synthesis	(Welsh and Herbert, 1999)
Salmonella enteritidis and *S. Typhimurium*	Planktonic	Filament formations	(Mattick et al., 2000)
Listeria monocytogenes	Planktonic	Osmolytes uptake	(Bayles and Wilkinson, 2000)
Enterobacteriaceae	Planktonic	Production of extracellular cellulose, EPS, fimbriae, changes to membrane permeability	(Ramos et al., 2001)
Chroococcidiopsis spp.	Planktonic	Development of thick multilayered envelopes rich in polysaccharides, lipids and proteins	(Billi and Potts, 2002)
Shewanella baltica	Planktonic	Expression of a proteinaceous osmotic shock response	(Leblanc et al., 2003)
Salmonella spp.	Planktonic	Fimbriae and cellulose protection	(Gibson et al., 2006)
Listeria monocytogenes	Biofilm	Increase in extrapolymeric substances (EPS)	(Chae et al., 2006)
Staphylococcus aureus	Planktonic	SigB activity via oxidative stress	(Chaibenjawong and Foster, 2011)
Pseudomonas spp.	Planktonic	Upregulation of alginate synthesis and flagellar genes	(Gulez et al., 2012)
Salmonella spp.	Biofilm	RpoS and OtsB	(Aviles et al., 2013)
Deinococcus radiodurans	Planktonic	Increased levels of Mn(II)	(Anderson et al., 2015)