

To be or not to be a compatible solute: Bioversatility of mannosylglycerate and glucosylglycerate

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Abstract

Mannosylglycerate (MG) is an intracellular organic solute found in some red algae, and several thermophilic bacteria and hyperthermophilic archaea. Glucosylglycerate (GG) was identified at the reducing end of a polysaccharide from mycobacteria and in a free form in a very few mesophilic bacteria and halophilic archaea. MG has a genuine role in the osmoadaptation and possibly in thermal protection of many hyper/thermophilic bacteria and archaea, but its role in red algae, where it was identified long before hyperthermophiles were even known to exist, remains to be clarified. The GG-containing polysaccharide was initially detected in *Mycobacterium phlei* and found to regulate fatty acid synthesis. More recently, GG has been found to be a major compatible solute under salt stress and nitrogen starvation in a few microorganisms. This review summarizes the occurrence and physiology of MG accumulation, as well as the distribution of GG, as a free solute or associated with larger macromolecules. We also focus on the recently identified pathways for the synthesis of both molecules, which were elucidated by studying hyper/thermophilic MG-accumulating organisms. The blooming era of genomics has now allowed the detection of these genes in fungi and mosses, opening a research avenue that spans the three domains of life, into the role of these two sugar derivatives. © 2008 Elsevier GmbH. All rights reserved.

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Introduction

The term compatible solute reflects the ability of small molecular weight organic compounds to accumulate in cells in response to external increases in osmotic pressure without compromising cell physiology [5]. Dissolved salts commonly determine the amount of water available to cells and NaCl, in particular, is a major cause of water stress in aquatic environments. The vast majority of microorganisms are capable of

responding, within intrinsic limits, to changes in the salt concentrations of the environment and many resort to the accumulation of compatible solutes to counterbalance the external decrease in water availability and consequent decrease in internal turgor pressure. Neutral zwitterionic compatible solutes such as trehalose, glycine betaine, ectoine and proline are frequent osmolytes in many mesophilic bacteria [11]. On the other hand, negatively charged organic solutes like di-*myo*-inositol-phosphate and mannosylglycerate (MG) have been often identified in hyper/thermophilic bacteria and archaea [45]. However, some compatible solutes have crossed the boundaries of a role in osmoadaptation and play a broader range of biological functions [11,12]. It is

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currently believed that nature's economy has provided alternative functional and structural missions for compatible solutes. Trehalose, for example, is involved in the protection of cells against a plethora of different types of stress such as freezing and heat tolerance, in addition to the classical role in osmoadaptation [12]. Furthermore, trehalose is also a structural component of the cell walls of several bacteria [38].

In this review we will address some of the factors known to elicit the accumulation of MG and glucosylglycerate (GG) in members of the three domains of life as well as their presence in larger macromolecules with apparently unrelated functions. We will also illustrate the diversity of pathways governing MG and GG biosynthesis as well as the genes and enzymes involved, and their distribution.

Mannosylglycerate distribution and physiological roles

Mannosylglycerate in red algae

The first report of the occurrence of a low molecular weight organic solute composed of mannose and glycerate, named digeneaside, which we designate as MG, was published by Colin and Augier in the red seaweed *Polysiphonia fastigiata* (*Rhodophyceae*) in 1939 [7]. Only later, was its structure established by Bouveng et al. [4]. Although MG has initially been found in members of the order *Ceramiales*, and considered a taxonomic marker for this order, it has recently been detected in other red algae of the orders *Gelidiales* and *Gigartinales* and its taxonomic significance has been refuted [30]. However, the concentration of MG does not always respond to increases in the salinity nor does it accumulate at levels suitable to contribute to the internal osmotic pressure of most species under salt stress, a role attributed to polyols, namely mannitol [29].

Mannosylglycerate in thermophilic bacteria and archaea

Mannosylglycerate was later identified in the thermophilic bacteria *Thermus thermophilus* and *Rhodothermus marinus* [37]. MG accumulates in the majority of strains of *T. thermophilus*, under salt stress but, in many cases, trehalose is the major compatible solute [1]. Trehalose has also been detected in many of the organisms that accumulate MG and a synergistic role for the two solutes was proposed by Santos and da Costa [45]. The construction of MG- and trehalose-negative *T. thermophilus* mutants and the concomitant response to osmotic stress led to the confirmation that MG is essential for low-level osmotic adjustment, while trehalose accumula-

tion is required for growth at higher salt concentrations [2,48]. Mannosylglycerate also behaves as a compatible solute in *R. marinus*, where its concentration increases with the salinity of the medium, along with very low levels of glutamate and trehalose. Oddly, a neutral form of MG designated mannosylglyceramide (MGA) replaced MG at higher salinities [47]. Furthermore, MG was also implicated in the response of *R. marinus* to thermal stress [3]. Mannosylglycerate also accumulates in members of the genus *Rubrobacter*, which represent a deep-branching lineage of the phylum *Actinobacteria* [17]. These organisms are extremely γ -radiation resistant and the species *R. xylanophilus* (optimal growth temperature 60 °C) is the most thermophilic member of this genus that includes two additional species, *R. radiotolerans* and *R. taiwanensis* which also accumulate MG [6]. However, *R. xylanophilus* shows constitutive accumulation of MG and neither salt or thermal stress, nor the medium composition had significant effects on MG levels [17].

Mannosylglycerate has been identified in the hyperthermophilic archaea of the genera *Pyrococcus*, *Thermococcus*, *Palaeococcus*, *Aeropyrum*, *Stetteria* and in some strains of *Archaeoglobus*, where it accumulates concomitantly with the increasing levels of NaCl in the growth medium [46]. The apparent restrictedness of MG to thermophilic bacteria and hyperthermophilic archaea (Fig. 1) contributed to the hypothesis that MG is important in thermal resistance. However, several studies with hyperthermophilic archaea have shown that upon thermal stress, di-*myo*-inositol-phosphate (DIP) is the dominant intracellular organic solute [46]. Curiously, the hyperthermophilic archaeon *Palaeococcus ferrophilus*, which does not accumulate DIP, was found to accumulate high levels of MG both under salt or thermal stresses strengthening the hypothesis of a role for MG in thermal adaptation [36].

Glucosylglycerate occurrence and biological functions

Glucosylglycerate as a compatible solute of bacteria and archaea

The organic solute GG is a structural analogue of MG that was originally identified in the marine cyanobacterium *Agmenellum quadruplicatum* grown under nitrogen-limiting conditions [31]. GG was also recently shown to behave as a compatible solute in the γ -proteobacterium *Erwinia chrysanthemi* under combined salt stress and nitrogen-limiting conditions, replacing glutamate and glutamine, the major compatible solutes when abundant sources of nitrogen are present in the medium [22]. Therefore, it is possible that

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