3 Periplasmic Space and Rigid Layer

3.1 The Periplasmic Space

The region between cytoplasmic and outer membrane of the Gram-negative bacteria is called the periplasmic space. It contains a concentrated gel-like matrix, the periplasm. Embedded in it is a rigid layer (peptidoglycan). Its width has been electron microscopically determined as 13-25 nm, a variation range that may be explained by differences in cultivation or preparation conditions. The total volume of the periplasmic space has been determined as 20-40% of the whole cell; this value, however, is not identical with that calculated from the width, which would allow a volume of only 8-16%. Because of its great importance for the vital processes of the bacteria, the existence of a space at least similar to the periplasmic is also thought to be present in Gram-positive bacteria (Dijkstra and Keck 1996).

The composition of the periplasm differs distinctly from that of the surrounding medium. It contains an aqueous solution of mono- and oligosaccharides, amino acids, peptides, soluble biosynthetic precursors of the peptidoglycan and other small molecules, but also degrading and detoxifying enzymes. Thus, at the membrane limiting the space to the outside, a Donnan potential of about 30 mV is created, the physiological importance of which is still unknown. Shielding of the cytoplasmic membrane, formation of a protonmotive force, regulation of the extent of opening the membrane pores and the influencing of surface organelles, such as, for instance, the flagella, are under discussion.

Besides the dissolved ones, there are also substances in the periplasm which are bound to one of the membranes or to the peptidoglycan.

It is difficult to determine the composition of the periplasm. A selective lysis, using, e.g. osmotic shock or treatment with chloroform, comprises only the suspended periplasmic components and even these not always completely and/or exclusively. The use of spheroplasts which are more easy to destroy may have variations in composition as a consequence. Some components can be specifically detected in situ, e.g. enzymes, by using diffusible substrates or proteins by labelling with diffusible cross-linking reagents. Histochemical and immunologic methods have also been described. It is recommended to always apply more than one method in parallel and to combine the results.

From the volume of the periplasm and the quantity and nature of the materials dissolved in it, it follows that the solution must be highly viscous and it occurs most likely in a gel-like state. This state as well as the sieving function of the peptidoglycan embedded in the periplasm drastically reduce the motility of the

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dissolved substances (to about 0.1% compared to an aqueous solution) and thus may support a formation of specific microenvironments with particular physiological assignments.

Since the cytoplasmic membrane is only marginally osmostable, cytoplasm and periplasm have to be nearly iso-osmotic. Therefore the bacteria possess fast-reacting regulatory mechanisms which keep the periplasmic osmotic pressure constant. Currently, the nature of the osmosensor is unknown. The osmotic stabilisation occurs in particular via the content of membrane-derived oligosaccharides (MDO), a mixture of oligosaccharides consisting of 6-12 glucose units in \(\beta-(1\rightarrow2)\)- and \(\beta-(1\rightarrow6)\)-linkage which are statistically substituted with sn-1-phosphoglycerol, 2-phosphoethanolamine and O-succinyl ester residues. It was found that osmotic differences between cytoplasm and periplasm can trigger the synthesis of MDO. The overall negative charge of the MDO represents one factor in the formation of the Donnan potential.

The proteins in the periplasm are basically assigned to three functional classes: enzymes (catabolic and detoxifying enzymes for protection against penetrated harmful substances as well as enzymes necessary for the biosynthesis of cell wall components and higher-molecular secretion products), chaperones and high-affinity binding proteins for vitally important substrates (amino acids, peptides, sugars, vitamins, coenzymes, nucleotides, inorganic ions and many others) which are important for the following transport across the cytoplasmic membrane. An important periplasmic protein, TonB, has already been described (see Sect. 2.3.2.3.3). All these proteins contribute to the function of the periplasm, i.e. represent an essential coordinating point for transports from the outside to the inside and vice versa. Some of these proteins are also present in Gram-positive bacteria in which they are anchored in the outer surface of the cytoplasmic membrane.

Outer and cytoplasmic membrane are not separated from each other at all sites of the cell wall. In electron micrographs, adhesion zones between both membranes (so-called Bayer’s patches, 100-200 per cell, zone width 20-100 nm) can be detected which are mainly found in exponentially growing cultures. Therefore it is supposed that these sites play a role in the biosynthesis of the cell wall or serve as perisepal anuli for the subcompartimentalisation of the periplasmic space as well as marking sites for a future cell division. However, there are opinions that the Bayer’s patches represent artefacts created during fixation of the preparations.

Bibliography