12.1 Introduction

Permafrost, which is defined as a subsurface frozen layer that remains frozen for more than 2 years, makes up more than 20% of the land surface of the earth, including 82% of Alaska, 50% of Russia and Canada, 20% of China, and most of the surface of Antarctica (Harris 1986; Williams and Smith 1989; Storad 1990). Permafrost poses unique challenges to its resident biota because of the permanently cold temperature of the soils, averaging −10 to −12°C, and the length of time over which the soils were frozen, which may be from a few thousand to even 2–3 million years.

To survive at subfreezing temperatures in permafrost, microbes have apparently developed various adaptive mechanisms. Electron microscopic examination of bacterial cells in a chip of permafrost core revealed that bacterial cells may survive due to reduction of cell size and formation of “dwarf” curved forms similar to nanoforms. The in situ permafrost bacteria, further characterized by thickened cell walls, altered structure of cytoplasm, compact nucleoid, showed similarities to cyst-like resting forms of non-spore-forming bacteria (Soïna et al. 2004). The survival mechanisms may include reduction of the polar polysaccharide capsular layer, decrease of the fractional volume of cellular water, increase of the fraction of ordered cellular water, or extraction of energy by catalyzing redox reactions of ions in thin aqueous films in permafrost (McGrath and Gilichinsky 1994; Ostroumov and Siegert 1996; Mindock et al. 2001; Gilichinsky 2002). Among such adaptive processes, not only the bacteria themselves might be affected by environmental low temperature and induced cold-adapted features, but also the production of cold-induced organic molecules within them, such as polysaccharides, proteins and enzymes that sustain their metabolism at low temperatures.

Progress on low-temperature adaptation research has been achieved mainly through genomic or physiological studies. Proteomic analysis provides the dynamic information of cells which reflects the actual live status of cells. Protein patterns demonstrated that growth temperature substantially reprogrammed the proteome.
Identification of all the proteins, including those differentially expressed under different conditions, will facilitate the understanding of the adaptation process. Comparative proteomic studies of various microorganisms during growth at different temperatures could be found (Sinchaikul et al. 2002; Goodchild et al. 2005; Kawamoto et al. 2007). Some of these differentially produced proteins displayed temperature trends: some proteins accumulated to high levels at low temperatures, while other protein expressions are elevated at high temperatures. Here we review the proteomic studies of cryoadaptation of permafrost bacteria.

### 12.2 Proteomic Studies of Low-Temperature Adaptations in Permafrost Bacteria

In the discussion of bacterial low-temperature adaptation, specific sets of cold-induced proteins (CIPs) have been considered to facilitate and allow cell growth at low temperature. CIPs are defined as proteins that are preferentially or uniquely present at low temperatures, and are thought to contribute specially to the ability of organisms to function at low temperatures (Fukunaga et al. 1999). CIPs could be further classified into cold-shock proteins (CSPs) and cold-acclimation proteins (CAPs). The term “CSPs” is used here for proteins that are transiently over-expressed after an abrupt shift to a low temperature, and the term “CAPs” is used for the proteins synthesized at a greater level during continuous growth at low temperatures as compared with high temperatures. CSPs and CAPs have been considered to facilitate and allow cell growth at low temperatures, and both sets of proteins may share functionality at both the molecular and cellular level (Whyte and Inniss 1992; Bayles et al. 1996; Berger et al. 1996; Panoff et al. 1997). Similarities between the CSPs and CAPs may suggest that these proteins are of significance to both shock recovery as well as constant growth in a new environment. The synthesis of CIPs in response to continuous growth at low temperatures in comparison to optimal growth temperature has been studied in two strains of the genus *Exiguobacterium* and two strains of the genus *Psychrobacter* isolated from Siberian permafrost and water brine samples (Table 12.1).

#### 12.2.1 Cold-Inducible Proteins (CIPS)

The detection and identification of CIPs present during growth at 16°C, 4°C, and −4°C (salinity remained constant at 5%) by two-dimensional electrophoresis has been reported in *Psychrobacter cryohalolentis* K5 (Bakermans et al. 2007). Changes in the growth temperature regime differentially induce the synthesis of a large set of specialized proteins needed to maintain growth and reproduction at different temperatures. Twenty-eight of the CIPs were identified in *P. cryohalolentis* K5.