Biodiversity of psychrotrophic microbes and their biotechnological applications

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ABSTRACT

The extreme cold environments harbor novel psychrotrophic microbes. The psychrotrophic microbes have been reported as plant growth promoters and biocontrol agents for sustainable agriculture, in industry such as cold-adapted hydrolytic enzymes and in medicine as secondary metabolites and pharmaceutical important bioactive compounds. Inoculation with psychrotrophic/psychrotolerant strains significantly enhanced root/shoot biomass and nutrients uptake as compared to non-bacterized control. The psychrotrophic microbes play important role in alleviation of cold stress in plant growing at high hill and low temperature and conditions. The psychrotrophic microbes have been reported from worldwide from cold habitats and belong to all three domain archaea, bacteria, and eukarya including different phylum such as Actinobacteria, Armatimonadetes, Basidiomycota, Chloroflexi, Chlamydiae, Planctomycetes, Cyanobacteria, Euryarchaeota, Firmicutes, Gemmatimonadetes, Verrucomicrobia, Mucoromycota, Proteobacteria, Spirochaetes, Thaumarchaeota and Nitrospirae. The most dominant genera belong to Arthrobacter, Bacillus, Exiguobacterium, Paenibacillus, Providencia, Pseudomonas, and Serratia have been reported from the cold habitats. The Psychrotrophic microbes have biotechnological applications in agriculture, industry, medicine. The cold-adapted microbes attracted the attention of the scientific community due to their aptitude in plant growth promotion, adaptation of plants at low-temperature conditions.

The novel microbes have been isolated using the culture-dependent techniques from cold environments worldwide including Actinomadetenchis spitensis, RMV-378, Agrocococcus lahaulensis, K22-21, Arthrobacter psychrotrophinophilus, GP3, Azospirillum himalayense, ptr-3, Bacillus lehensis, MLB2, Desulforhopalus vacuolatus, Itk10, Dioszea arctica, ANT-03-116, Eixguobacterium hingiirinensis, K22-26, Eixguobacterium soli, DVS 3Y, Flavobacterium frigidarium, A2, Flavobacterium omnivorum, ZF-8, Flavobacterium phocarcin, SE14, Flavobacterium urumqienese, Sr25, Gelidibacter algens, ACAM 536, Geysypchothacter electrodephilus, Al, Glaciecola pallidula, ACAM 615, Glaciomonas frigoris, N1-38, Halobacterium lacusprofundi, ACAM 32, Hymenobacter rubripertinctus, NY03-3-30, Massilia eurypychrophila, B528-3, Nocardipsisantarctica, ACAM 32, Paenibacillus glacialis, KFC91, Pedobacter arcticus, A12, Pseudomonas deceptionensis, M1, Psychrobacter pocilopora, S6-60, Spiribacterium antarctica, 4BY, and Sulfitobacter brevis, EL-162 (Table 1).

The cold habitats such as cold deserts, glaciers, and subglacial lakes are hot spots of a great microbial diversity of psychrophile, psychrotolerant, biotechnological agricultural and industrial applications of beneficial and efficient microbes for diverse sectors including agriculture, industry, and medicine.
and psychrotrophic microorganisms. The cold-adapted microbes possess diverse genes responsible for cold adaptation and genes for diverse molecules and alleles with potential applications in diverse fields. There are several reports on whole genome sequences of novel and potential psychrotrophic microbes such as *Arthrobacter agilis* [37], *Cenarchaeum symbiosum* [38], *Clavibacter* sp. [39], *Colwellia chukchansi* [40], *Colwellia psychrerythraea* [41], *Exiguobacterium antarcticum* [42], *Exiguobacterium oxidotolerans* [43], *Exiguobacterium sibiricum* [44], *Methanococcoides burtonii* [45], *Octadecabacter antarcticus* [46], *Paenibacillus* sp. [47], *Planomicrobium glaciei* [48], and *Rheinheimera* sp. [Table 2] [49]. The whole genome sequences of cold-adapted microbes help to understand the adaptation on microbes under the extreme cold habitats and also potential genes for functional attributes, for example, *A. agilis* L77, are an important psychrophilic

Table 1: Novel psychrotrophic microbes from diverse cold habitats

| Novel microbes                        | Habitats         | References |
|--------------------------------------|------------------|------------|
| *Actinalloteichus spitensis*, RMV-378°| Spiti Valley     | [11]       |
| *Arthrobacter flavus*, CMS 19Y°      | Antarctica       | [90]       |
| *Azospirillum himalayense*, pII-3°   | Chamba Valley    | [14]       |
| *Bacillus cecembensis*, PNS5°        | Pindari Glacier  | [91]       |
| *Bacillus lehensis*, MLB2°           | Leh, JK         | [15]       |
| *Cenarchaeum symbiosum*, Fosmid 4B7  | Sponge Symbiotic| [92]       |
| *Chryseobacterium imtechense*, MW 10°| Bay of Bengal    | [93]       |
| *Cryobacterium psychrotolerans*, 05497° | China No. 1 glacier | [94] |
| *Cryobacterium roopkundense*, RuGl7° | Roopkund Lake   | [95]       |
| *Desulfurhopalus vacuolatus*, ltk10  | Kysing Fjord    | [16]       |
| *Dyadobacter hamtensis*, HHS 11°    | Hamta glacier    | [96]       |
| *Exiguobacterium himigrensis*, K22–26° | Spiti Valley | [18]       |
| *Exiguobacterium soli*, DVS 3Y°     | Antarctica       | [19]       |
| *Flavobacterium frigidarium*, A21°  | Antarctica       | [20]       |
| *Flavobacterium omnivorum*, ZF-8°   | China No. 1 glacier | [21] |
| *Flavobacterium xinjiangense*, ZF-6°| China No. 1 Glacier | [21] |
| *Gelidibacter algens*, ACAM 536     | Burton Lake      | [24]       |
| *Geopsychrobacter electrodiphilus*, A1° | Marine Sediment   | [25]       |
| *Glacimonas frigoris*, N1-38°       | Siberian Permafrost | [27] |
| *Halobacterium lacusprofundi*, ACAM 32° | Antarctic Lake    | [28]       |
| *Halobasta litchfieldiae*, tADL1   | Antarctic Lake   | [97]       |
| *Hymenobacter rubripertinctus*, NY03-3-30° | Antarctica       | [29]       |
| *Kocuria himachalensis*, K07-05°    | Spiti Valley     | [98]       |
| *Massilia eurypsychrophila*, B528-3°| Muztagh Glacier  | [30]       |
| *Nocardiopsis antarcticus*,         | Antarctica       | [31]       |
| *Octadecabacter arcticus*, 307°    | Antarctica       | [99]       |
| *Octadecabacter arcticus*, 238°    | Antarctica       | [99]       |
| *Oleispira antarctica*, RB-8°      | Antarctic        | [100]      |
| *Orrthinimicrobium kibberense*, K22-20° | Spiti Valley | [101]     |
| *Paenibacillus gelidus*, KFC91°     | Kafni Glacier    | [32]       |
| *Polaromonas vacuolata*, 34-P°      | Antarctic        | [102]      |
| *Pseudomonas extremeaustralis*, 14-3° | Antarctic      | [103]      |
| *Psychrobacter pociloporum*, S6-60° | Andaman Sea     | [35]       |
| *Psychroflexus torquis*, ACAM 623°  | Sea Ice Antarctica | [104] |
| *Psychromonas aquimarina*, JAMM 0404° | Kagoshima, Japan | [105] |
| *Rhodobacter changlensis*, JA139°  | Changla Pass, HP | [106]      |
| *Rhodotorula himalayensis*, 3A°    | Roopkund Lake   | [107]      |
| *Sheanwella frigidimarina*, ACAM 591| Antarctic Sea Ice | [108] |
| *Sheanwella gelidimarina*, ACAM 456| Antarctic Sea Ice | [108] |
| *Sphingobacterium antarcticus*, 4BY| Antarctica       | [35]       |
| *Sphingobacterium psychroaqualicum*, L-1° | Michigan Lake | [109] |
bacteria isolated from Pangong lake, Northwest (NW) Himalayas, India. The strain L77 has abilities to produced cold-adapted hydrolytic enzymes and shows that the plant growth-promoting (PGP) attributes are different low-temperature conditions. The whole genome sequences of psychrophilic bacteria revealed different genes for adaptation and metabolic activities [37]. The novel psychrophilic/psychrotolerant microbes and their products will be applicable in broad range of agricultural, industrial, and medical processes. The cold-tolerant psychrotrophic microbes can be valuable in agriculture as inoculants biofertilizers and biocontrol agents. The present review describes the microbial diversity analysis from cold habitats and its potential applications in agriculture, industry, medicine, and allied sectors.

2. BIODIVERSITY PSYCHROTROPHIC MICROBES

The extreme of cold represents hot spots of microbial biodiversity for psychrotrophic, psychrophilic, and psychrotolerant microbiomes [9,50,51]. The biodiversity of psychrotrophic microbes inhabiting cold habitats has been extensively investigated worldwide and has been reported from phylum, namely Actinobacteria, Gemmatimonadetes, Ascomycota, Acidobacteria, Bacteroidetes, Basidimycota, Chlamydiae, Chloroflexi, Proteobacteria, Cyanobacteria, Firmicutes, Mucoromycota, Verrucomicrobia, Nitrospirae, Planctomycetes, Spirochaetes, Thaumarcheota, and Euryarchaeota [Figure 1]. The microorganisms of cold habitats including the subglacial lakes, Antarctic, Arctic glacier, permanently ice-covered sea, permafrost, and Himalayan and Mountain lakes have been investigated for the diversity of psychrotrophic, psychophilic, and psychrotolerant microbes [52-56,19,57-62].

The biodiversity of cold-adapted bacteria was deciphered from northern hills zone of India. A total of 247 culturable bacteria have been isolated using serial dilution and spread plate methods from different sites in Indian Himalayan regions. The bacteria have been identified using 16S rRNA gene sequencing and BLAST analysis. All sequences have been analyzed for phylogenetic profiling and revealed that the sequences are affiliated to four phyla, namely Firmicutes, Proteobacteria, Bacteroidetes, and Actinobacteria. The selected strains have been found to be PGP attributes, which included phosphorus, K, and Zn solubilization; NH₄, HCN, indole-3-acetic acid (C₆H₃NO₂), and Fe-chelating compounds production; and the activity of 1-aminocyclopropane-1-carboxylate (ACC) deaminase and biological nitrogen fixation. The psychrotrophic bacteria also possess biological control against the different pathogens such as Macrophomina phaseolina, Rhizoctonia solani, and Fusarium graminearum. These PGP psychrotrophic and psychrotolerant bacteria could be applicable as biofertilizers and biocontrol agents for crops cultivated under the low-temperature conditions and hilly regions [2].

The Indian cold deserts are suitable for the selection of psychrotrophic and psychrotolerant bacteria, archaea, and fungi with potential biotechnological application in diverse sectors, microbes. Yadav et al. [63] investigated microbiome of the cold deserts of Northwestern Himalayas, India, using culture-dependent and culture-independent
method and reported different genera, belonging to different phyla, namely Bacteroidetes, Firmicutes, Actinobacteria, and Proteobacteria. The selected microbe showed PGP attributes of the production of \( \text{NH}_3 \), HCN, gibberellic acid, Fe-chelating compounds (catecholates...
Table 3: Psychrotrophic microbes with multifunctional plant growth promoting attributes

| Psychrotrophic microbes                    | P     | Sid | ACC | References |
|-------------------------------------------|-------|-----|-----|------------|
| Aeromonas hydrophila                      | 31.5±1.8 | +   | -   | [63]       |
| Arthrobacter methlyolophous               | 55.9±1.4 | +   | +   | [2]        |
| Arthrobacter sulfonivorans                | 25.6±1.2 | +   | -   | [64]       |
| Bacillus amyloliquefaciens                | 54.2±1.5 | +   | +   | [123]      |
| Bacillus firmus                           | 35.2±3.3 | +   | +   | [64]       |
| Bacillus licheniformis                    | 19.2±1.0 | +   | -   | [66]       |
| Bacillus pumilus                          | 36.1±0.8 | +   | -   | [64]       |
| Bacillus subtilis                         | 19.8±0.5 | +   | +   | [64]       |
| Cellulosimicrobium cellulans             | 15.5±1.1 | -   | +   | [64]       |
| Desemzia incerta                          | 47.5±1.2 | +   | -   | [64]       |
| Paenibacillus tylopili                    | 48.4±2.4 | +   | -   | [66]       |
| Pantoea dispersa                          | 44.5±0.2 | +   | -   | [124]      |
| Pseudomonas fluorescens                   | 768.3±0.2 | -   | +   | [125]      |
| Pseudomonas fluorescens                   | 90.2±1.7 | -   | +   | [126]      |
| Pseudomonas fragi CS11RH1                 | 514.9±0.2 | -   | +   | [127]      |
| Pseudomonas vancovenensis                 | 66.3±0.2 | +   | +   | [128]      |
| Rahelina sp.                              | 805.0±0.1 | +   | +   | [129]      |
| Sanguibacter antarcticus                  | 20.1±0.1 | +   | +   | [64]       |
| Sanguibacter suarezii                     | 18.1±0.5 | +   | +   | [63]       |
| Stenotrophomonas maltophilia              | 55.7±0.5 | +   | +   | [2]        |

P: Phosphorus, Sid: Siderophores, ACC: 1-aminocyclopropane-1-carboxylate

Cold-adapted microbial communities can be studied using culture-dependent and culture-independent techniques. The microbiomes reported using both techniques culture dependent and culture independent revealed the occurrence of different and diverse major groups viz., Actinobacteria, Ascomycota, Bacteroidetes, Verrucomicrobia, Thaumarchaeota, Spirochaetes, Proteobacteria, Planctomycetes, Nitrospirae, Mucoromycota, Gemmatimonadetes, Firmicutes, Euryarchaeota, Cyanobacteria, Chloroflexi, Chlamydiae, and Basidiomycota. On review of isolated cold-adapted microbes, it was found that proteobacteria were most dominant phyllum followed by Firmicutes and Actinobacteria [10].

3. BIOTECHNOLOGICAL APPLICATIONS

The psychrotrophic microbes exhibited multifarious PGP attributes such as ACC deaminase activity, potassium zinc and phosphorus solubilization, biological N₂ fixation, and production of different bioactive compounds such as gibberellic acids, ammonia, cytokinins, Fe-chelating compounds, hydrogen cyanide, and indole-3-acetic acid. The use of PGP microbes improves plant growth by supplying plant nutrients, which can help sustain environmental health and soil productivity [10]. Psychrotrophic PGP microbes were found in several genera, including Arthrobacter, Bacillus, Burkholderia, Pseudomonas, Exiguobacterium, Janthinobacterium, Lysinibacillus, Methylobacterium, Microbacterium, Paenibacillus, Providencia, and Serratia [67-70]. The microbes having ACC deaminase activity help plant to alleviate cold stress [Table 3] [2,66,71,72].

Sustainable agriculture requires the use of strategies to increase or maintain the current rate of crops and food production using eco-friendly manners. PGP microbe can affect plant growth directly under the low-temperature condition through nitrogen-fixing bacteria.

The PGP psychrotrophic bacilli were investigated from different sites in NW Himalayas India [66] and bacteria have been reported from different genera, namely Desemzia, Exiguobacterium, Lysinibacillus, Sporosarcina, Jeotgalicoccus, Planococcus, Sinobaca, Pontibacillus, Staphylococcus, and Sporosarcina. The identified genera affiliated to different families Bacillales incertae sedis, Camobacteriaceae, Bacillaceae, Planococcaceae, Paenibacillaceae, Staphylococcaceae, and Sporolactobacillaceae. The selected isolates found to exhibit cold-active enzymes such as amylase, chitinase, pectinase, β-glucosidase, protease, cellulase, xylanase, β-galactosidase, laccase, and lipase by different genera, namely P. terrae, Bacillus amyloliquefaciens, Exiguobacterium indicum, Bacillus marisflavi, Pontibacillus sp., Sporosarcina globispora, and Sporosarcina psychrophila.

The subglacial lakes are also hot spots of microbial diversity of psychrotrophic and psychrotolerant bacteria with functional attributes of cold-adapted and cold stable active extracellular hydrolytic enzymes productions [65]. On the basis of DNA isolation, polymerase chain reaction amplification of 16S rRNA gene and their sequencing using universal primers revealed that isolated bacilli belong to different genera, namely Exiguobacterium, Virigibacillus, Staphylococcus, Lysinibacillus, Jeotgalicoccus, Desemzia, Bacillus, Paenibacillus, Planococcus, Pontibacillus, Sinobaca, and Sporosarcina. The identified genera affiliated to different families Bacillales incertae sedis, Camobacteriaceae, Bacillaceae, Planococcaceae, Paenibacillaceae, Staphylococcaceae, and Sporolactobacillaceae. The selected isolates found to exhibit cold-active enzymes such as amylase, chitinase, pectinase, β-glucosidase, protease, cellulase, xylanase, β-galactosidase, laccase, and lipase by different genera, namely P. terrae, Bacillus amyloliquefaciens, Exiguobacterium indicum, Bacillus marisflavi, Pontibacillus sp., Sporosarcina globispora, and Sporosarcina psychrophila.

Cold-adapted microbes are ubiquitous in nature and can be isolated from permanently ice-covered lakes, cloud glaciers, and hilly regions [8]. Bacteria recovered using isolation techniques using different growth media as selective and complex and using 16S rRNA gene sequencing the bacteria were affiliated to genera Stenotrophomonas, Virigibacillus, Citricoccus, Enterobacter, Brevundimonas, Providencia, Pseudomonas, Flavobacterium, Pantoea, Planococcus, Paenibacillus, Pontibacillus, Methylobacterium, Psychrobacter, Cellulosimicrobium, Exiguobacterium, Janthinobacterium, Lysinibacillus, Rhodococcus, Sanguibacter, Arthrobacter, Sphingobacterium, Bacillus, Staphylococcus, and Sporosarcina. The identified bacteria affiliated to different phyllum on the phylogenetic profiling using Actinobacteria, Proteobacteria, Basidiomyota, Chlamydiae, Chloroflexi, Bacteroidetes, Cyanobacteria, and Firmicutes using Mega 4 analysis.
such as *Arthrobacter*, *Azorarcus*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Enterobacter*, *Glucanacetobacter*, *Herbaspirillum*, *Klebsiella*, *Pseudomonas*, and *Serratia* [1,2,69,73,74]; ACC deaminase activity by *Acinetobacter*, *Achromobacter*, *Agrobacterium*, *Alcaligenes*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Pseudomonas*, *Ralstonia*, *Serratia*, and *Rhizobium* [75-78] and through indirect mechanism by releasing siderophores, β-1, 3-glucanase, chitinases, antibiotics, and fluorescent pigment or by cyanide production by *Alcaligenes* sp., *Bacillus pumilus*, *B. subtilis*, *B. megaterium*, *Clavibacter michiganensis*, *Curtobacterium* sp., *Flavobacterium* sp., *Kluvera* sp., *Microbacterium* sp., *Pseudomonas alcaligenes*, *P. putida*, and *P. fluorescens* [79-85].

The psychrophilic, psychrotolerant, and psychrotrophic microbes are important for many reasons, particularly because they exhibited antifreezing compounds, antibiotics, and bioactive compounds production [1] and production of extracellular hydrolytic enzymes with potential biotechnological applications in different processes. These enzymes included β-glucosidase, β-galactosidase, xylanase, protease, pectinase, laccase, lipase, chitinase, cellulase, and amylase [37,65,86]. Cold-active enzymes are produced by psychophilic microbes, namely *Acinetobacter*, *Aquaspirillum*, *Arthrobacter*, *Moraxella*, *Bacillus*, *Moritella*, *Carnobacterium*, *Planococcus*, *Clostridium*, *Cytophaga*, *Shewanella*, *Vibrio*, *Flavobacterium*, *Marinomonas*, *Paeinbacillus*, *Pseuodaltermonas*, *Pseudomonas*, *Psychrobacter*, and *Xanthomonas* [9,37,65,87-89]. Enzymes from psychophilic and psychrotrophic microbes have become interesting for different processes in industry, pharmaceuticals, medicine, and food and feed industry. Antifreezing compounds from psychrophilic microbes are useful in cryosurgery and also in the cryopreservation of whole organisms, isolated organs, cell lines, and tissues [1,9,37].

4. CONCLUSION AND FUTURE VISION

The psychophilic, psychrotolerant and psychrotrophic microbiomes have been isolated from different cold habitats worldwide. The microbial diversity of cold environments has attracted the consideration of the scientific community due to production of cold active enzymes production, anti-freezing compounds, secondary metabolites and bioactive compounds by psychrotrophic microbes. The psychrotolerant/psychrotrophic microbes have potential biotechnological applications in industry, pharmaceuticals, medicine, food and feed for human. The psychrotrophic microbes with multifarious

PGP attributes could be used as biofertilizers and biocontrol agents for crops growing in hilly and low temperature condition for enhance crops production and soil health for sustainable agriculture. The psychrotrophic microbes having biodegradation ability could be used for bioremediation, and waste water treatments for sustainable environments. These cold-adapted microbes may be used for biofuels and biodiesel production for future energy systems. The psychrotrophic microbiomes are widely distributed and have been reported to promote plant growth and alleviation of cold stress in plants. Although the most research work conducted so far has largely focused on psychrophilic and psychrotolerant microbes, it is a welcome sign that many agriculturally important resourceful microbes are being described from various parts of the earth.

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