Psychrotrophs of the genus *Janthinobacterium* with potential to weather potassium aluminosilicate mineral

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Abstract

In the present investigation, five strains of *Janthinobacterium* obtained from Rohtang Pass, Himachal Pradesh, India along with one strain of *Bacillus decolorationis* (IARI-SL-13) were screened qualitatively and quantitatively for their ability to solubilize K at different temperatures ranging from 5 to 30 °C. All the selected strains do not produce violet colonies, instead produced pink or red coloured colonies. In a plate assay, among all the strains tested, *Janthinobacterium* sp. IARI-R-81 was most efficient in solubilization of K at lower temperatures of 5 and 10 °C and was closely followed by *Janthinobacterium lividum* (IARI-R-71). *Janthinobacterium* sp. IARI-R-70 did not produce any detectable halo zones at all temperatures except 10 and 25 °C. Quantitative analysis revealed that all the selected pigment-producing strains could solubilize potassium-bearing mineral at low temperature (5 °C). *J. lividum* IARI-R-50 strain was most efficient in solubilizing K ($29.87 \pm 1.22 \mu\text{g K/mL}$) from its mineral at 5 °C. This strain was typical as it solubilized almost the same amount of K both at 5 and 30 °C indicating its capability to adapt to different temperatures. All other strains showed a significantly higher concentration of solubilized K at 30 °C as compared to other temperatures tested. The non-pigmented *B. decolorationis* showed solubilization only at 25 and 30 °C and the concentration of K solubilized at 30 °C was significantly higher than at 25 °C. There was no correlation between pigment production and solubilization of potassium. This is the first report depicting solubilization trait of members of genus *Janthinobacterium* and confirms its evolutionary relatedness to Collimonads.

Keywords Mineral weathering potential · Genus *Janthinobacterium* · Pigment analysis · 16S rRNA gene sequencing

Introduction

Microorganisms isolated from extreme environments have increased curiosity among the researchers because of their adaptation for surviving in such extreme conditions (Bottos et al. 2008; Liu et al. 2009; Niederberger et al. 2008). Such adaptations showed some specific physiological and biochemical characteristics like pigmentation, cold-shock proteins production, and synthesis of polyunsaturated branched-chain fatty acids in the cytoplasmic membrane (Russell and

Nichols 1999). Several psychrophilic bacteria have been reported from cold environments such as sub-glacial Himalayan lakes, Antarctica, and deep-sea sediments (Feller et al. 1996). Among bacteria, members of the genus *Janthinobacterium* have been reported from many cold environments (Gillis and De Ley 2006; Lincoln et al. 1999; Schloss et al. 2010; Shoemaker et al. 2015). The members of this genus are psychrophilic and produce a violet colour pigment (Gillis and De Ley 2006; Lincoln et al. 1999; Schloss et al. 2010). However, there are reports of strains that have lost the ability to produce violacein and instead of producing violet colonies they produce red or pink colonies (O'Brien et al. 2018).

Members of the genus *Janthinobacterium* have never been reported to solubilize minerals, in particular, K, P, and Zn. In a comparative study between Collimonads and closely related genera like *Herbaspirillum* and *Janthinobacterium*, it was reported that Collimonads could solubilize minerals while *Herbaspirillum* and *Janthinobacterium* lack this ability. Based on the ability to solubilize minerals, it was concluded that the Collimonads and the closely related genera

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Janthinobacterium and *Herbaspirillum* might have evolved separately (Uroz et al. 2009). However, the presence of the members of the genus *Janthinobacterium* in large numbers in the cold deserts where the nutrients are always limiting suggests that they might be involved in the solubilization of minerals. Moreover, it is worthwhile to study the importance of pigment production by these isolates and its correlation with the dissolution process. Bacteria recovered from different cold habitats have been reported to often show pigmentation, which is a natural protection mechanism against free radicals and UV radiations (Russell 2009). However, no correlation between the degree of exposure to UV and the pigment production has been reported (Russell 2009). *Microrococcus roseus* and *Sphingobacterium antarcticus* strains isolated from Antarctica showed the production of several polar and non-polar carotenoids. In both strains, increased production of polar carotenoids as well as decreased production of non-polar carotenoids was observed when grown at a low temperature in comparison to grown at room temperature (Chattopadhyay and Jagannadham 2001).

Potassium is a major macronutrient for growth and development of plants. The role of potassium in growth, yield, and disease resistance has been demonstrated in a wide variety of plant species (Huang and Han 2014). The concentration of available potassium in soil varies from 0.04 to 3% and is often limiting (Sparks and Huang 1985). The major percentage of potassium (90–98%) in soil is in the form of soil minerals which are not available to the plants for uptake (Goldstein 1994). Many reports are now available in the literature wherein microbes, particularly bacteria have been implicated in solubilization of K from minerals and making it available to the plants (Bagyalakshmi et al. 2017; Bakhshandeh et al. 2017; Zhang and Kong 2014). Solubilization of minerals to release K or P has been reported through secretion of organic acids by different microorganisms (Bennett et al. 1998; Rajawat et al. 2016; Toba et al. 1991; Welch and Vandevivere 1994). Secretion of carboxylic acids such as citric acid, tartaric acid, and oxalic acids, and capsular polysaccharide are involved in the solubilization of feldspar by *Bacillus mucilaginosus* and *Bacillus edaphicus* (Lin et al. 2002; Richards and Bates 1988). *Janthinobacterium* has been reported to lack the ability to produce gluconic acid and hence fails to dissolve K from minerals (Uroz et al. 2009). Hence, the present study was aimed to screen pigment-producing psychrotolerant isolates of *Janthinobacterium* obtained from cold deserts of Rohtang Pass to solubilize potassium from potassium-bearing silicate minerals and to provide evidence to their evolutionary relatedness with Collimonads based on this attribute.

Materials and methods

Bacterial cultures

Five pigment-producing cultures belonging to the genus *Janthinobacterium* isolated from soil sediments and water samples collected from Rohtang Pass, Himachal Pradesh, India (32°22'17"N, 77°14'47"E) were obtained from a laboratory culture collection, Division of Microbiology, Indian Agricultural Research Institute, New Delhi. The cultures were revived, purified, and stored at 4 °C for further work. A strain of *Bacillus decolorationis* (IARI-SL-13) isolated from Sambhar salt lake, India and efficient for K solubilization was used for comparative study.

Screening of K-solubilization efficiency of pigment-producing psychrotolerant isolates on agar plates

Purified psychrotolerant isolates were grown in nutrient broth for inoculum preparation and screened on Aleksandrov agar medium (Aleksandrov et al. 1967) containing potassium aluminosilicates as an insoluble source of potassium (Hu et al. 2006). The cultures were screened for their efficiency to solubilize potassium in triplicates by spotting on Aleksandrov agar medium plates and incubated at 25 °C for 5 days. Halo zone formed by bacteria on plates was measured by subtracting colony size from total size.

Evaluation of K-solubilization efficiency of pigment-producing psychrotolerant isolates at different temperature conditions

Qualitative evaluation of K-solubilization efficiency

Five pigment-producing *Janthinobacterium* isolates along with *B. decolorationis* (IARI-SL-13) were qualitatively examined for their efficiency to solubilize potassium from insoluble potassium minerals at different temperatures ranging from 5 to 30 °C (5 °C, 10 °C, 20 °C, 25 °C, and 30 °C) by spot-inoculation on Aleksandrov medium. After incubation for 5 days, the plates were observed for the formation of the halo zone around the colonies. Halo zone size formed at different temperatures was measured by subtracting colony size from total size.

Quantitative evaluation of K-solubilization efficiency

Potassium solubilization at different temperatures mentioned earlier was carried out in Aleksandrov broth containing potassium aluminosilicates as insoluble potassium mineral.

All experiments were carried out in triplicates in 150 mL conical flasks containing 40 mL Aleksandrov broth. Conical flasks were inoculated with each isolate separately and incubated at different temperatures for 5 days at 150 rpm. Autoclaved uninoculated medium served as control. After incubation, the pH of the broth cultures was measured. The broth cultures were centrifuged at 10,000 rpm for 15 min, the supernatant was collected and analyzed for solubilized potassium by a flame photometer (Jackson 1973).

Pigment extraction and UV–visible absorption analysis

Bacterial cultures showing the pigment production were streaked on Aleksandrov agar plates and incubated at 25 °C for 10 days. After incubation, bacterial cells were scrapped and suspended in methanol for pigment extraction. Pigments from bacterial cells were extracted by sonication. Sonication of bacterial cells was carried out at 30 amplitude and 15 cycles of 30 s on/off pulse. After sonication, the pigment was separated by centrifugation at 10,000 rpm for 10 min. The supernatant was collected and analyzed for spectrum analysis of pigment at different wavelengths. Wavelength scan was performed in the visible region ranging from 400 to 600 nm.

Molecular characterization of isolates

The partial sequences of 16S rRNA gene for all the cultures used in the present study with NCBI GenBank Accession numbers (JX429043, JX429048–51, JX645207) were used to construct the phylogenetic tree using the neighbour-joining (NJ) method (Saitou and Nei 1987) and MEGA 7.0 program (Kumar et al. 2016). Bootstrap analysis (Felsenstein 1985) was performed on 1000 random samples taken from the multiple alignments.

Statistical analysis

Obtained data were analyzed statistically by using SPSS 16.0 statistical software. The critical difference between the bacterial cultures and solubilization at different temperatures was determined. The mean values and the critical difference between treatments were calculated at 5% level of significance and denoted as critical difference (CD) in the tables.

Results

Screening of pigment-producing psychrotolerant bacteria

All the five strains of *Janthinobacterium* producing pink–red pigment and a non-pigment-producing *B. decolorationis* (IARI-SL-13) showed the formation of halo zone around the colonies at 25 °C when spot-inoculated on Aleksandrov medium supplemented with potassium aluminosilicate indicating the solubilization of K from the mineral. Among them, IARI-R-81 recorded the maximum halo zone of 8.5 mm followed by IARI-R-71 (Table 1).

Evaluation of K-solubilizing efficiency at different temperatures

The selected strains exhibited variations in qualitative and quantitative assays. In plate assays, no halo zone was observed around the colony for strains IARI-SL-13 and IARI-SL-70 at low temperatures (Table 1). However, in a quantitative assay, these strains could solubilize K that could be detected by flame photometer (Table 2). In general, the selected strains of genus *Janthinobacterium* and *B. decolorationis* IARI-SL-13 exhibited potential to solubilize potassium aluminosilicate mineral in both plate assay and liquid medium at low temperatures.

Qualitative evaluation of K-solubilization efficiency

Incubation temperature had an influence on the K-solubilizing efficiency of the pigment-producing bacteria. Among all the strains tested, *Janthinobacterium* sp. IARI-R-81 was most efficient in solubilization of K at lower temperatures of 5 and 10 °C and was closely followed by *Janthinobacterium lividum* (IARI-R-71). *Janthinobacterium* sp. IARI-R-70 did not produce any detectable halo zones at all temperatures except 10 and 25 °C. Size of halo zone of solubilization of silicate minerals on agar plates (Fig. 1) formed by the isolates at different temperatures ranged from 0 to 9.33 mm (at 30 °C), 0.50–8.50 mm (at 25 °C), 0–6.0 mm (at 20 °C), 1.50–9.17 mm (at 10 °C) and 0–9.33 mm (at 5 °C) (Table 1).

Quantitative evaluation of K-solubilization

Quantitative analysis showed that selected pigment-producing strains have the efficiency to solubilize potassium-bearing mineral at low temperature (5 °C). All the isolates exhibited a unique trend in their efficiency to solubilize K at different temperatures. At 10 °C there was a dip in the values of K solubilized for all the isolates and there was a gradual

Fig. 1 Formation of halo zone on Aleksandrov agar plate amended with potassium aluminosilicate mineral at 5 °C, 10 °C, 20 °C, 25 °C, and 30 °C, respectively (from left to right)

Table 1 Identity of strains used and its ability to solubilize potassium in Aleksandrov agar plates at different temperatures

Isolates	Identity of isolates	Pigment colour	NCBI GenBank accession number	Halo zone size (in mm) on Aleksandrov agar plates at different incubation temperatures (°C)						
				5 °C	10 °C	20 °C	25 °C	30 °C	SEM	CD (5%)
IARI-R-50	<i>Janthinobacterium lividum</i>	Pink	JX429043	5.50	2.00	3.50	3.00	4.00	0.679	1.52
IARI-R-70	<i>Janthinobacterium sp.</i>	Carrot	JX429048	0.05 ^a	1.50	0.05 ^a	0.50	0.05 ^a	0.153	0.34
IARI-R-71	<i>Janthinobacterium lividum</i>	Light pink	JX429049	6.83	9.17	6.00	3.50	5.83	0.811	1.81
IARI-R-72	<i>Janthinobacterium sp.</i>	Dark pink	JX429050	1.83	2.00	3.83	2.50	3.67	0.364	0.81
IARI-R-81	<i>Janthinobacterium sp.</i>	Dark pink	JX429051	9.33	8.67	5.83	8.50	9.33	0.734	1.64
IARI-SL-13	<i>Bacillus decolorationis</i>	Creamish	JX645207	ND	ND	ND	0.75	1.50		
			SEM	0.509	0.345	0.565	0.658	0.274		
			CD (5%)	1.14	0.77	1.26	1.47	0.61		

^aNo halo zone formation on Aleksandrov agar plates and mean value of data shown in table

Table 2 Quantitative estimation of available K by flame photometer in liquid Aleksandrov medium by selected strains at different temperatures

Isolates	Available K (µg/mL) in liquid medium at different incubation temperatures (°C)						
	5 °C	10 °C	20 °C	25 °C	30 °C	SEM	CD (5%)
Control	4.80 ± 0.53	5.13 ± 0.12	5.27 ± 0.70	6.13 ± 1.89	5.73 ± 0.90	0.591	1.32
IARI-R-50	29.87 ± 1.22	9.73 ± 0.42	14.60 ± 0.69	19.07 ± 1.40	26.80 ± 0.72	0.463	1.04
IARI-R-70	14.90 ± 2.65	8.20 ± 0.40	13.93 ± 0.70	19.33 ± 1.03	26.20 ± 0.92	1.035	2.31
IARI-R-71	19.27 ± 4.99	9.73 ± 0.42	16.47 ± 0.61	21.40 ± 1.25	29.40 ± 1.11	1.725	3.86
IARI-R-72	18.63 ± 2.02	8.60 ± 0.40	14.47 ± 0.90	21.07 ± 0.83	27.13 ± 1.01	0.812	1.82
IARI-R-81	15.07 ± 2.04	7.73 ± 0.61	13.87 ± 0.64	19.73 ± 1.10	26.33 ± 1.01	0.714	1.60
IARI-SL-13	5.1 ± 1.15	6.73 ± 1.33	11.43 ± 1.42	19.90 ± 1.40	30.93 ± 2.03	1.835	4.11
SEM	1.545	0.351	0.423	0.799	0.648		
CD (5%)	3.46	0.78	0.95	1.79	1.45		

increase in solubilized K from 15 to 30 °C (Table 2). The amount of K solubilized at 5 °C and 30 °C was statistically at par for strain IARI-R-50 indicating its adaptability to different temperatures. All other strains showed a significantly higher concentration of solubilized K at 30 °C as compared to other temperatures tested. The non-pigmented *B. decolorationis* showed solubilization only at 25 and 30 °C and the concentration of K solubilized at 30 °C was significantly higher than at 25 °C (Table 2).

Pigment analysis

Pigments extracted from isolates were examined for absorption maxima at different wavelengths by UV–visible spectrophotometer. Wave length-scanning spectra showed that the isolates IARI-R-50, IARI-R-72, and IARI-R-81 have three absorption maxima at 470 nm, 495 nm, and 535 nm whereas isolates IARI-R-70 and IARI-R-71 showed two absorption maxima at 495 nm and 535 nm (Fig. 2). The

Fig. 2 Absorption spectra of extracted pigment from *Janthinobacterium* strains

peaks are typical for the group carotenoids, where the peaks at 470 nm and 535 nm represent prodigiosin pigment while the peak at 495 nm is indicative of keto carotenoids.

Phylogenetic analysis of 16S rDNA gene sequences of pigment-producing psychrotolerant bacteria

Selected isolates were sequenced and the sequence data were analyzed by NCBI BLASTn followed by the nearest match from NCBI GenBank database was recorded. DNA sequencing and phylogenetic analysis revealed that selected isolates showing the K-solubilization efficiency have 98–100% similarity with the sequences within the NCBI GenBank. Phylogenetic tree constitutes mainly two clusters. Among them,

Fig. 3 Phylogenetic tree of selected isolates based on 16S rRNA gene sequences by neighbor-joining method

Janthinobacterium strains showed > 95% similarity among them. Each strain of *Janthinobacterium* genus represents an individual clad during the taxonomical study (Fig. 3). *B. decolorationis* IARI-SL-13 represents a separate cluster. For the taxonomical study, *Halolamina* sp. IARI-CDK2 was used as an outgroup for tree construction.

Discussion

The genus *Janthinobacterium* includes non-fermentative and psychrophilic bacteria producing violet colonies due to the presence of violet pigment violacein (Gillis and De Ley 1993; Kanelli et al. 2018). In the present investigation, five strains identified as species of *Janthinobacterium* were screened for K solubilization. However, none of the strains exhibited the typical violet coloured colonies on Aleksandrov medium. They all produced pink or red coloured colonies. There are reports of partly pigmented and non-pigmented variants of *J. lividum* naturally isolated from Sikkim Himalayas that also produce light pink colour colonies (Kumar et al. 2018; Suman et al. 2015). Variations have also been reported with regards to its ability to grow at different temperatures. Both psychrophilic and psychrotrophic isolates have been described within the genus *Janthinobacterium* (Kumar et al. 2018; Shivaji et al. 1991). Shivaji et al. (1991) described eight bacteria, members of genus *Janthinobacterium*, isolated from soil samples collected in the islands of Scotia Ridge and the Antarctic Peninsulas as psychrotrophs that could grow in the temperature range of 4–28 °C but not at 30 °C or above (Shivaji et al. 1991; Kumar et al. 2018; Baricz et al. 2018). They all exhibited optimum growth at 15 °C. The five strains used in the present study are also

psychrotrophs that could grow in the temperature range of 4–30 °C. Lipson et al. (2009) in their study on high elevation coniferous forest reported fast growing, cold-adapted *Janthinobacterium* to be the dominant species during winters (Lipson et al. 2009). Pyrosequencing revealed that *Janthinobacterium* sp. dominate both the source meltwater and microcosm communities in Arctic glacier surface (Rassner et al. 2016). The predominance of members of *Janthinobacterium* in different cold environments indicates that this group might have some role in nutrient cycling besides the production of antibiotics as reported in many studies (Suman et al. 2015). However, no reports are available on solubilization or mineralization of any nutrient element by *Janthinobacterium*. A single report available also indicates that *Janthinobacterium* lacks the ability to solubilize minerals except for biotite by one isolate (Uroz et al. 2009).

The five strains of *Janthinobacterium* obtained from Rohtang Pass, Himachal Pradesh, India were found to be positive for their ability to solubilize K from Potassium aluminosilicates both in qualitative and quantitative assays at different temperatures. This is the first report that describes mineral weathering potential of strains ascribed to genus *Janthinobacterium*. The concentration of K solubilized from aluminosilicates at 30 °C is at par to that solubilized by non-pigmented *B. decolorationis* IARI-SL-13 used for comparison in this study. The red or pink coloured colonies of *Janthinobacterium* could be due to the presence of carotenoid as reported earlier (Kumar et al. 2018). The peak at 495 nm represents keto carotenoids (Llansola-Portoles et al. 2017) whereas the peak at 470 nm and 535 nm represent prodigiosin pigment (Darshan and Manonmani 2017; Andreyeva and Ogorodnikova 2015). A psychrotrophic strain of *J. lividum* from a cold Alaskan soil have been reported to produce prodigiosin (Schloss et al. 2010).

However, the presence or absence of pigment has no bearing on the amount of K solubilized from insoluble sources. The ecological niche from where the isolation has been made also has the bearing on the potential of the microorganism to solubilize nutrients. It has been reported that Collimonads isolated from nutrient-poor environments had high mineral weathering efficacy as compared to those isolated from agricultural fields (Uroz et al. 2009). The biotite weathering isolate of *Janthinobacterium agaricidamnosum* DSM9268, the only one reported for solubilization and mobilization, was recovered from the mushroom and is a soft rot pathogen (Lincoln et al. 1999; Uroz et al. 2009). The cultures used in the present study are from the cold deserts of Rohtang Pass typically characterized by low nutrient availability. Hence all the five isolates exhibited the trait of K solubilization to a different extent. The results of the present study are in contrast to an earlier report that delineated *Janthinobacterium* from Collimonads based on their inability to weather minerals (Uroz et al. 2009). The additional advantage with

these strains was their ability to solubilize K even at low temperatures. This makes them as a suitable candidate for selection as a bioinoculant, particularly for hill agriculture.

Conclusion

Strains belonging to genus *Janthinobacterium* possess the ability to release K from insoluble K-minerals at low temperature. The mineral-solubilizing ability further provides evidence for its evolutionary relatedness to Collimonads. The ability to solubilize K at low temperatures make them a suitable candidate to develop microbial formulations for augmenting K in crops grown in hills.

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Author contributions MR and AS designed the experiment. RS, MR and AS participated in coordination and interpretation of results. MR and AS wrote the manuscript with contributions of RS and DS. All authors reviewed the manuscript.

Compliance with ethical standards

Conflict of interest Authors declare that they have no conflict of interest.

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