Adaptive mechanisms for stress tolerance in Antarctic plants

S. M. Singh, N. Pereira and R. Ravindra*

During the 23rd Indian Antarctic Expedition (IAE) in the summer 2003 at Schirmacher Oasis, Antarctica, it was observed that some plants changed their colour as an adaptation strategy to prevent bleaching of the chlorophyll molecule due to high intensity of UV light. The molecular basis of cold adaptation and the transduction of thermal-quanta signals in Antarctic plants is still a matter of debate. Life forms of Antarctica have a unique survival and functioning mechanism in the extremes of environment. This fragile continent has been burdened with increasing human pressure in the form of scientific expeditions and tourism activities adversely impacting the biodiversity of Antarctica. This article explores the life strategies displayed in algae, mosses and lichens as a result of adaptation to harsh climatic conditions with a focus on ozone depletion and its effects on these plants.

Keywords: Antarctica, adaptation strategies, extreme climate, ozone, plant life, UV-radiation.

ANTARCTICA is an icy continent having harsh climatic conditions hindering growth and survival of organisms. In addition to the extreme climatic conditions, the organisms also experience the ill effects of depletion of stratospheric ozone and a consequent increase of UV-B, a harmful component of sunlight. Antarctic life is mainly confined to ice-free areas of coastal outcrops, offshore islands, inland nunataks, mountain ranges and oases. Cyanobacteria and algae are known to exist in glacial ice, streams, lakes, sea coast, permafrost, temporary snowfields and soil environment[1]. These plants contribute to the Antarctic biomass production by the process of oxygenic photosynthesis and are well adapted to the environment, marked by an absence of both competition and grazing pressures[2]. Phytoplankton is the basic primary producer in the Antarctic Ocean that supports other components of the ecosystem such as zooplankton, krill, fish, etc. Hence, a change in their community structure or productivity due to ozone depletion can have lasting effects on the ecology of the Southern Ocean. Pigment concentrations of phytoplankton such as chlorophyll and carotene are used as markers to gauge the damage done by the UV exposure.

On a visit to the Schirmacher Oasis of Antarctica (Figure 1), it was seen that *Buellia*, *Lecanora*, *Caloplaca* and *Umbilicaria* (Figure 2 *a*) were the most dominant genera of lichens. Among the mosses were *Bryum* (Figure 2 *b*), *Ceratodon*, *Orthogrimmia* and *Syntrichia* genera. *Oscillatoria*, *Phormidium*, *Nostoc* (Figure 2 *c*) and *Stigonema* (Figure 2 *d*) were the dominant representatives of cyanobacteria. It was seen that some samples of lichens, mosses and cyanobacterial mats (Figure 2 *e*) had changed from a lighter shade during early summer to a darker one in late summer. The exact reason for this phenomenon remains unknown though it could be hypothesized that the change of colour in Antarctic plants is an adaptation strategy to prevent the bleaching of chlorophyll molecule in the high intensity of UV light. In order to understand the adaptive responses of the inhabitants of the icy continent, it becomes crucial to consider the rapid climatic fluctuations comprising changes in water state (liquid to ice) and temperature followed by enormous changes in irradiation, salinity, pH and other ecological factors. A range of physical and ecological life strategies have evolved in the polar terrestrial algal communities to circumvent the extreme changes in environment.

Prokaryotic cyanobacteria, eukaryotic algae along with bacteria, lichens and certain mosses with a tolerance for dessication in varying degrees are grouped under poikilohydric organisms. The cold resistance observed in these organims is mainly due to the absence of vacuoles. In these organisms, the outside environment controls the metabolic activity by regulating the presence or absence of water in either liquid or vapour forms. Poikilohydricity coupled with shelter strategies, cellular and physiological adaptations guard the oxyphototrophic microorganisms against stress generated by vigorous temperature and water gradients[2]. The presence of secreting structures and compounds such as mucilage, sheaths and multilayered

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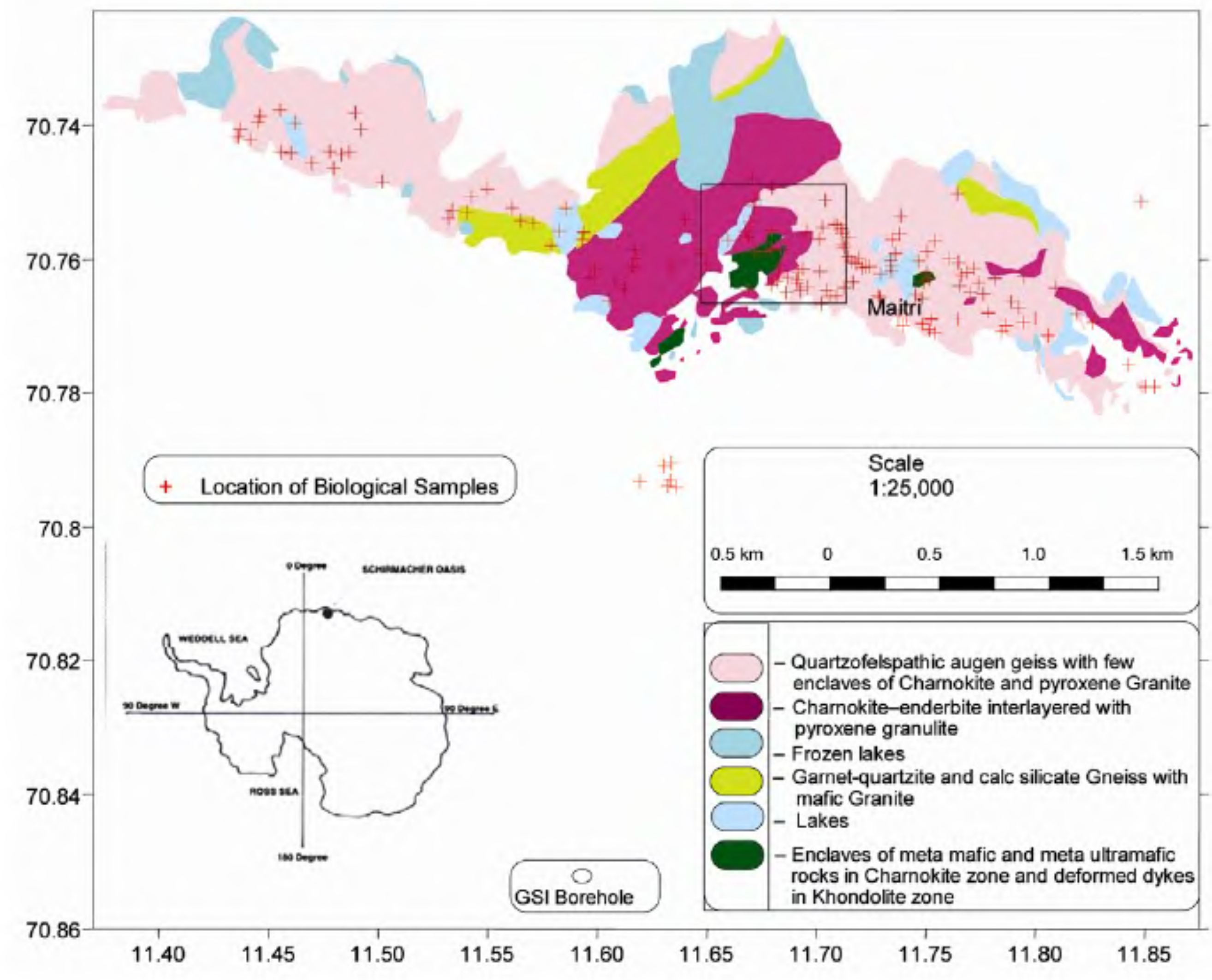

Figure 1. Diversity rich area in Schirmacher Oasis, East Antarctica.

cell walls in polar algae and cyanobacteria has been widely studied[3]. The multilayered cell walls contain sporopollenin, a resistant biopolymer that strengthens the cell walls of algae. Studies on a cyanobacterium *Chroococcidiopsis* have shown that organisms have the ability to alter their cell wall composition by changing the proportion of polysaccharides, lipids and proteins[2]. Understanding the life strategies developed by the polar organisms to cope with low temperature and associated stresses offer rousing prospects in the field of cryobiology (study of life in frozen state). These organisms are termed as extremeophiles and have become cryobiological research tools due to their specialized adaptive responses. The application of soluble protective agents such as sugars, polyols and glycerol as cryoprotectants in germplasm cryoconservation suggests the cryoprotective responses of polar organisms. An extensive deployment of natural cryoprotectants in applied cryobiology is demonstrated by the use of trehalose and sucrose. Trehalose has been used in cryopreservation of plant suspension cultures as well as in cryoprotection of thermophillic bacteria like *Lactobacillus bulgaricus*[4]. The use of molecular tools has enabled the ecologists to identify the genetic basis of the adaptive mechanisms. Whereas there is intensification of research, there are also concerns about possible environmental degradation rising from anthropogenic pressure. An increasing human presence and pollution on the icy continent in the form of tourism and scientific establishments have raised issues about possible alteration to the Antarctic environment.

Geographical features of Antarctica

The continent lies within the Antarctic circle (lies around 60°S area of earth); along with its islands and ice shelves it covers about 13.66×10^6 km^2, containing about 80% of the world's freshwater and represents 10% of the world's

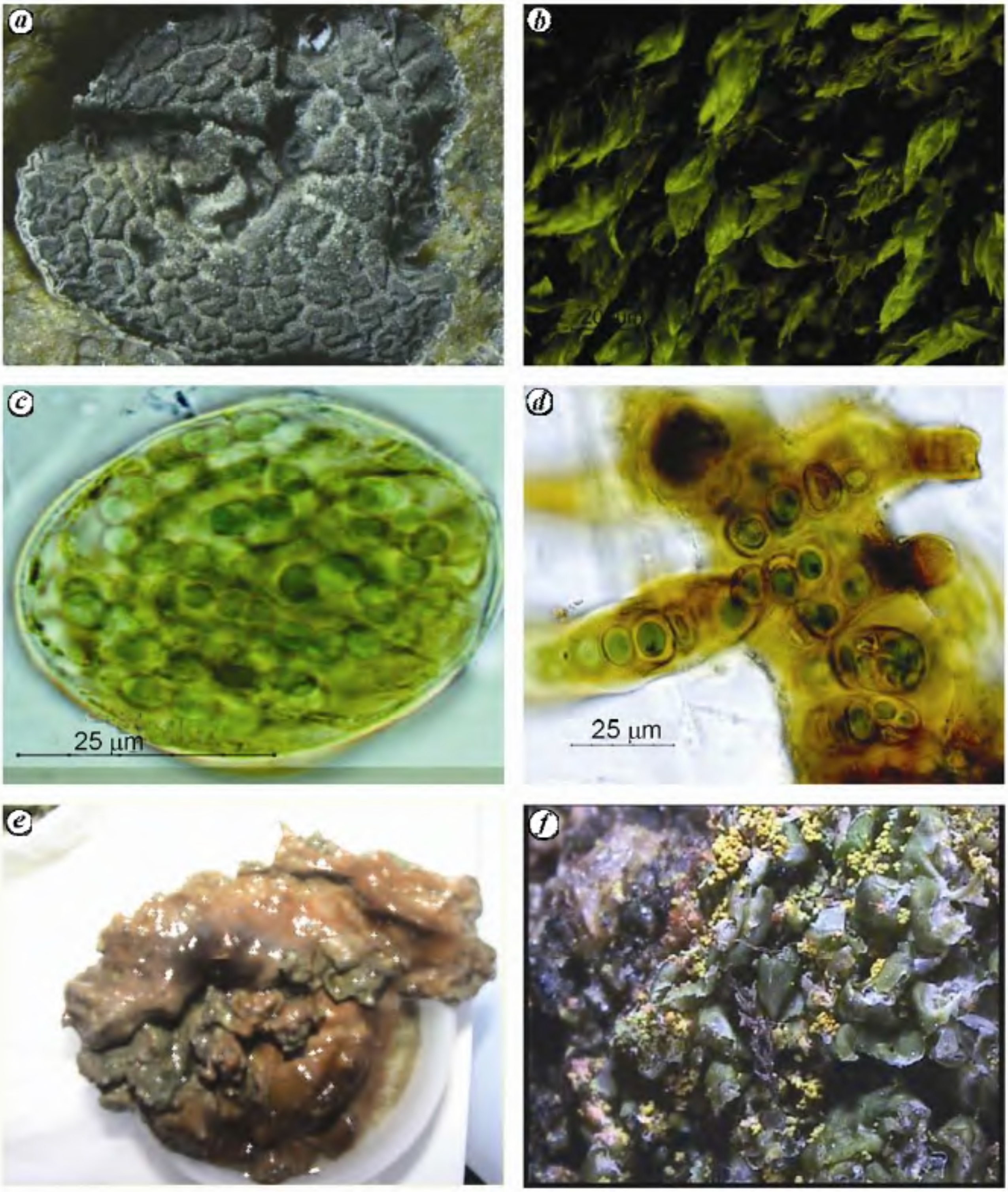

Figure 2. ***a***, *Umbilicaria decussata* (lichen); ***b***, *Bryum* (moss); ***c***, *Nostoc commune* (cyanobacteria); ***d***, *Stigonema minutum*; ***e***, Change of colour in cyanobacterial mat; ***f***, *Prasiola crispa* (green alga).

land surface[5]. Formation of Antarctica dates back to 180–200 million years ago when the southern portion of Pangea, known as Gondwana, drifted south to form the southern continents including Antarctica. The commencement of circumpolar current that led to the expansion of ice caps around 25 million years ago had an intense impact on the climate of Antarctica. Recent research findings show that Antarctica is getting warmer since the last

50 years. The summer temperature ranges from –30°C on the plateau to –4°C at coastal locations whereas minimum temperature is observed in July or August with –70°C on the plateau and –25°C at the coast. Only 0.3% of the area is ice-free during the summer period[6]. The lowest temperature measured on Antarctica was –89.5°C at the Russian Vostok station.

Current status of the Antarctic biodiversity

Due to extreme climatic conditions, Antarctica harbours the narrowest biodiversity amongst continents. The biodiversity has significant gradients and it can be defined on the basis of latitude, altitude and depth. The distribution patterns and biodiversity in the terrestrial and marine ecosystems of Antarctica are governed by temperature, water, ice cover, oxygen and light respectively.

The plant life constituted by algae, mosses and lichens occurs in low temperature terrestrial environments. The vegetation of Antarctica comprises two flowering plants, 27 liverworts[7], 111 species of mosses[8], 380 species of lichens[9], and about 300 species of algae and cyanobacteria[10]. Lichens thus dominate the Antarctic flora both in terms of species diversity and in terms of total biomass. The vegetation of Indian base area in Schirmacher Oasis includes eight species of mosses[11], 57 species of lichens[12], 7 genera of fungi[13] and 109 species of cyanobacteria[14]. The biodiversity of cyanobacteria and algae in fresh water and terrestrial ecosystems of the Schirmacher Oasis in the Antarctica revealed that ecosystems differ significantly from each other. The species composition of N_2-fixing species, both heterocystous and unicellular diazotrophs, was greatest in the middle region of the oasis. *Cosmarium*, an algal species was predominant in association with cyanobacteria. Among the cyanobacteria, *Oscillatoria*, *Phormidium* and *Nostoc* were dominant in both aquatic and moist habitats. How the life invaded, colonized and inhabited the Antarctic region is a matter of considerable debate. Studies on Antarctic organisms have suggested that physiological plasticity may be the limiting factor for colonization in Antarctica.

Effects of UV-B radiation on plants of Antarctica

Emissions of chlorofluorocarbons in the atmosphere have led to a depletion of the stratospheric ozone layer since the 1980s (ref. 15). The springtime stratospheric ozone depletion in Antarctica occurs in October and November and enhances the UV-B radiation (280–320 nm). Ozone depletion is known to affect both the structure and functioning of plants in Antarctica by creating an imbalance in spectral processes such as photosynthesis, photoinhibition and photoprotection consequently reducing primary productivity in the Marginal Ice Edge Zone of Antarctica[16,17]. Terrestrial plants such as algae, lichens and bryophytes possess UV absorbing compounds and exhibit differential responses to UV exposure. Experimental studies on the Antarctic moss *Sanionia uncinata* revealed that though an enhanced UV-B radiation did not have a significant impact on photosynthesis, it increased the level of DNA damage. However, the DNA damage induced during the day was repaired overnight. This phenomenon probably suggests that the presence of UV-A radiation in nature might be responsible for mitigating the negative impacts of enhanced UV-B radiation[18]. UV-A is known to be instrumental in photorepair process. The presence of high Photosynthetic Active Radiation (PAR) in Antarctic could lead to photoinhibition in photoautotrophic organisms though poikilohydric organisms like lichens may withstand this unfavourable condition in a desiccated dormant state. Studies conducted on various Antarctic lichens exhibit varying responses to UV-B depending on the protection strategy induced by its algal and fungal component. Phytoplankton are found to be most vulnerable to the damaging effects of UV-B in an area with dissipated ice cover, stratified water column and high primary productivity, as observed in the Marginal Ice Edge Zone[19]. The snow-free fast ice is said to transmit almost 10% of UV-B in October when ozone levels are least and declines to 0.25% in late November with the snow cover leading to reduced transmittance.

Studies conducted on diatom records from anoxic basins of Antarctica fjords over two decades reveal that UV-B has slight impact on composition of phytoplanktonic diatom, though a drop in the sedimentation rate in species like *Nitzschia stellata* and *Berkeleya rutilans* is seen. This was supported by *in vitro* studies conducted on sea-ice algal culture wherein an increased irradiance led to a 5% drop in primary productivity[19]. An increased UV radiation reportedly led to a drop in photosynthesis coupled with destruction of chlorophyll *a*, chlorophyll *c* and alteration of other accessory pigments such as fucoxanthin, 19′ hexanoyloxyfucoxanthin, diadinoxanthin, diatoxanthin and β carotene[20].

Antarctic green alga *Prasiola crispa* (Figure 2*f*) contains low concentration of compounds with absorbance level as those found in mosses. UV-B was shown to have negative effects on the PS-II reaction centres of the alga, which consequently decelerated photosynthesis. It has been studied that the production of UV absorbing compounds was dependent on the intensity of UV irradiance[21]. The algae produce these compounds as a survival strategy against high levels of UV. A study of airborne alkaline pollution on lichens and mosses at Casey station[22] showed that mosses such as *Ceratodon* were apparently unaffected whereas lichens *Usnea* and *Umbillicaria* were found to be discoloured. Due to their inability to excrete toxic compounds, lichens were susceptible to alkaline cement dust contamination as witnessed by the loss of black pigment and chlorophyll. Mosses *Grimmia antarctici* and *Bryum pseudotriquetrum* contain UV filtering compounds with absorption capacity of 323 nm that reaches its highest capacity in early summer. It was inferred that damage to the characteristic black pigment of lichens and prolonged daylight could be responsible for bleaching and shrivelling of the lichen thallus.

Signalling of low temperature and cold adaptation in cyanobacteria

Cyanobacteria are photosynthetic organisms surviving since the Precambrian time of the geological past[23,24]. Cyanobacteria are unicellular, filamentous and colonial microorganisms capable of producing microbial mats near moist and watery habitats as an adaptation to hostile environment. It has a lipid composition that is similar to those of chloroplast membranes of higher plants, thus making it a model organism for studies of molecular mechanisms of stress responses and acclimation[25].

Presence of mucilage and multilayered walls protects the cyanobacteria against freezing and dessication damage during prolonged cold and icy winter period as observed in species of *Nostoc* and *Phormidium*. During low temperature, a high internal sugar-phosphate concentration helps *Nostoc* whereas *Anabaena variabilis*, *Synechocystis* and thermophilic species *Synechococcus vulcanus*[26,27] are found to benefit from the increased level of unsaturated fatty acids.

The fluidity of membrane lipids depends upon the extent of desaturation of membrane lipids[28]. The analysis of gene transcript during the downward shift in temperature revealed that the increase in desaturation occurs due to stimulation of the expression of the genes for the appropriate desaturases[29,30]. Impact of cold temperature induces the expression of several genes for ribosomal proteins[31,32], indicating the presence of a temperature sensor in the cytoplasmic membrane of cyanobacteria that perceives a change in the physical motion of membrane lipids and transmits the signal to a mediator that activates the expression of genes for desaturases[25]. Cold temperature regulation in cyanobacteria is performed by a cold-sensing histidine kinase system, which regulates the gene expression responses to low temperature shock. Recent studies on the mutant form of *Hik33* revealed that not all cold-inducible genes are controlled by histidine kinase[32] and speculates the existence of other cold sensors that probably control gene expression by some unknown mechanism[32,33].

Freezing adaptation in Antarctic lichens

The life form associations observed in the polar terrestrial environment include physiological and metabolic benefits. The most common association observed in this location is that of algae/cyanobacteria with fungi in lichens. Lichens are known to be sensitive to stresses such as air pollution and enhanced UV-B. This is known to affect photosystem II and can be measured by means of chlorophyll *a* fluorescence. Antarctic lichens are capable of passively absorbing water from the gaseous phase[33–36] and taking up water directly from snow[37]. In the poikilohydrous lichens, drought stress occurs due to continuous drying and wetting cycles consequent to changes in ambient moisture levels. Laboratory studies on the crustose lichen *Placopsis contortuplicata* show difference in physiological performance between the green algal and cyanobacterial photobionts despite being in the same thallus. This finding supports the crustose lichen's preference for wet sites in maritime Antarctica due to the requirement of liquid water by the cyanobacterial photobiont[38]. Cold adaptation in the lichen thallus could be attributed to a mechanism that protects the thallus from the ice crystal growth during freezing. The production of a cryoprotective sugar trehalose found in lichens, was seen to correspond with partial dehydration during low temperature acclimatization[39]. Until now, the mystery of freezing protection mechanism is not clear but a cryoprotective role of sugars and polyols has been suggested by Hamada[40].

Human invasion: a threat to Antarctic biodiversity

Though considered to be an unpolluted region in the world, tourism and research activities have led to anthropogenic pressure and pollution in the area. The sinking of *Bahia Paraiso* in 1989 resulted in a diesel fuel spill of 600,000 litres and affected nearly 20 islands and has been a case study for international cooperation in environmental monitoring of Antarctica[41]. The amount of solid waste discharged by expedition ships in the ocean may be seriously adding alien species in regions of Southern Ocean and Antarctica. Waste such as plastic acts like a substratum and transports the organisms to areas they would never be able to reach on their own. The alien invaders among animals comprise bryozoans, barnacles, polychaete worms, hydroids, crabs and mollusks, whereas grasses such as *Avena*, *Plantago* and *Poa* have been reported as alien plants from Marion Island[42]. An estimated 18 vascular plants have taken root in Antarctica as a result of human activities. Since the Antarctic Treaty Consultative meeting in 1964, there have been concerns over introduction of alien species. While some have disappeared, others are spreading rapidly. Gremmen[42] suggests a regular botanical survey to detect new introductions of alien species as well as a strict adherence to quarantine measures to avoid further introductions. The implementation of the Protocol for the Protection of the Antarctic Environment has made environmental impact assessments mandatory to safeguard the biodiversity of the frail ecosystem.

The environmental impact assessment studies on Antarctic flora have shown a negative impact on the routes of vehicle movement and near the workshop. Lichens and mosses are good bioindicators for airborne pollution caused by heavy metals and radioactive debris as they have a unique ability to accumulate pollutants (inorganic ions) from the atmosphere. Hence, they are used as tools for environmental monitoring in Antarctica[43–45]. The lichen species collected from the surroundings of Indian base Maitri station and Vettiyya Nunatak area were analysed for heavy metals. The samples reported an absence of heavy metal content, suggesting that the area in and around Maitri station is relatively free from pollution[46].

Conclusion

Floristic mapping, comparison of biodiversity in the recent past with the present by modern molecular tools may shed light on the percentage of erosion, invasion and evolution of new species in the area. There is need for an internationally coordinated programme to study the impact of UV on Antarctica to confirm the UV-B induced changes on biological systems, in order to predict the consequences arising out of global changes such as increasing atmospheric carbon dioxide and warming[47]. Cryobiologists have begun to simulate nature's survival responses to cryopreserve both native biodiversity and genetic resources of agricultural and forestry species. It is also useful for development of new medicines to treat human ailments. Many of the unique chemicals produced by living organisms as a part of the survival strategy also have valuable pharmaceutical properties. Antarctic biodiversity benefits humankind, because it allows us to understand the world we live in better and to make informed decisions about the future. The Antarctic treaty system has been responsible for conservation of this region in the past and is expected to be effective in the future too. With the provision of legal measures and cooperation of various governments, Antarctic is expected to remain a source of new discoveries for mankind[48].

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