4 Adaptation in Algae to Environmental Stress and Ecological Conditions

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Abstract

Algae (including *Cyanobacteria*) are aquatic organism and ubiquitous in distribution. They are found not only in fresh and marine waterbodies but also on terrestrial habitats such as soil, tree trunk and man-made substrates. As they heavily depend on water, it becomes a limiting factor for their survival. However, algae are found growing abundantly in extreme habitats indicating their adaptation to the harsh environment which we try to explore in this chapter. The response of algae to desiccation stress is widely studied. They produce specialized spores that would remain dormant during harsh period and revive once the favourable conditions return. Their thick cell walls would have further protective layers of chemical substances and also mucilage sheath which helps in the delay of desiccation. Algae produce and accumulate varieties of organic osmolytes that protect them from desiccation, high irradiation and UV light. Algae also have *de novo* biosynthesis mechanism to manage the damage occurred due to desiccation. Algae occurring in colder habitats have substances in their cells that would withstand sub-zero temperatures. Algae growing in saline habitats accumulate salt and maintain ionic balance with the cellular concentration. Although algae are also found in hot springs, not many studies are available to explain their adaptive strategies.

Keywords

Desiccation · Hot spring · Resting spores · Extreme environments · Evolution · Astaxanthin

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4.1 Introduction

Algae are aquatic, oxygen-evolving, photosynthetic autotrophs that are unicellular, are colonial or are constructed of filaments or composed of simple tissues (Guiry 2012). As algae contain photosynthetic pigments, they are considered as plants, but unlike vascular plants, they lack true stems, roots, leaves, vascular tissue and flowers. Algae include organisms that are not closely related to each other and are mostly classified based on their pigments, reserve food material and mode of reproduction. While some of the authors consider only eukaryotes as algae (Allaby 1992; Nabors 2004), some also include prokaryotes *Cyanobacteria* (blue-green algae) (Fritsch 1935, 1945).

Algae are important component of biodiversity and an integral part of the ecosystem. Their contribution to the existence of life on earth is immense. Algae are the primary producers in the aquatic environment, and the oxygen that all organisms depend on was generated by numerous cyanobacteria during the Achaean and Proterozoic Eras. It is estimated that marine algae contribute to about 70–80% of the oxygen in the atmosphere. The chloroplast with which plants photosynthesize is actually a cyanobacterium living within the plant's cells. More than 100 species of algae serve as food to human beings. Use of seaweeds as food in China or Japan and high-protein-yielding *Chlorella* and *Spirulina* products available in the market are few examples. Some algae yield antibiotics, for example, chlorellin is obtained from green alga *Chlorella*, that inhibits the growth of certain bacteria. Because of high iodine contents, brown algae are used in the manufacture of various goitre medicines (McCledon 1993). Due to their ability to fix atmospheric nitrogen algae, especially *Cyanobacteria* are important source of biofertilizers. Many algae yield certain chemical products that have huge industrial applications such as agar-agar, alginates and carrageenin (Borowitzka and Hallegraeff 2007). Sometimes algae can also be harmful; algal bloom that increases the biological oxygen demand of water and obstructs light penetration results in death of aquatic animals. In the sea, red tides are best examples for mass destruction of fishes and contaminating seafood with toxins (Hallegraeff 1993).

4.2 Habitat Range for Algal Colonization

Algae are ubiquitous in distribution and represent a huge diversity in the world with an estimate of 72,500 species (Guiry 2012). They are free-living, prominent in waterbodies and also common in terrestrial environments such as soil, tree bark and rock. Sometimes algae are extremophiles, found growing in extreme environments such as hot springs, deserts, cold waterbodies, polar regions, permafrost, high or low pH and high levels of CO_2 (Seckbach 2007). Algae are also symbiotic, living in association with other organisms. For example, alga and fungus associate to form lichens wherein both the partners lose their original identity to behave as single entity (Nash 1996). Dinoflagellates are often endosymbionts in the cells of the corals, where they accelerate host-cell metabolism by generating sugar and oxygen through photosynthesis using incident light and the carbon dioxide produced by the host (Lesser et al. 2016). Some algae are parasites of plants such as *Cephaleuros* that causes red rust on tea and coffee leaves (Joubert and Rijkenberg 1971).

4.3 Adaptation to Desiccation Stress

Algae are poikilohydric organisms and don't have control over their water balance. They equilibrate with surrounding moisture, and when fully hydrated, intact cells will be able to function physiologically (Karsten and Holzinger 2012). Therefore, availability of water or moisture is the most important limiting factor for their survival. Water availability includes precipitation, condensation and water vapour. Algae growing in terrestrial habitats such as soil, rock, ephemeral ponds, ditches, seasonal streams, bark and man-made substrates experience severe desiccation, especially during summer. However, in places like alpine regions, water availability fluctuates from fluid droplets after rain or snow to extended periods of dryness or freezing (Holzinger and Karsten 2013). These algae adapt several survival strategies to exist in such stressed environment and are referred as desiccation-tolerant organism. The desiccation tolerance can be defined as the ability to survive drying to about 10% remaining water content (equivalent to 50% of relative humidity) at 20 °C (Oliver et al. 2010).

4.3.1 Stress Avoiders

Avoiding desiccation would be one of the strategies of the unicellular or filamentous algae. They aggregate into colonies and form multilayered mats and biofilms. While the outer layer is exposed and susceptible to damage, the cells underneath are protected, which can be referred as self-shading. The outer layer may be bleached or change its colour and acts as light screen in case of low-light-requiring communities. This strategy is more useful when more than one community is involved in grouping as in case of biological soil crusts. The whole community is protected by the contribution of each individual (Holzinger and Pichrtova 2016). Lüttge and Büdel (2010) observed that green algal biofilms on tree bark showed a pronounced desiccation tolerance up to 80 days and the recovery of photosynthetic activity was faster after shorter periods of dehydration. Similarly, green algae from biological soil crusts in the desert can survive at least 4 weeks (Gray et al. 2007). Desert algae survived desiccation for at least 4 weeks and recovered to high levels of photosynthetic quantum yield within 1 h of rehydration when experimented in laboratory condition (Gray et al. 2007).

The primary effect of dehydration in algae may be shrinkage process which may reduce the cells to less 60% of their original value (Karsten and Holzinger 2012). In case of *Klebsormidium* cells subjected to desiccation experiment, overall the cytoplasm appeared extremely dense and cell organelles including the nucleus and chloroplast were visible. The number of plastoglobules in chloroplasts was increased indicating capability of cell organelles to reorganize during desiccation (Karsten and Holzinger 2012). The plastoglobules are lipoprotein subcompartments of the chloroplast which contain biosynthetic metabolic enzymes that are responsible for desiccation tolerance (Fenández-Marín et al. 2013).

4.3.2 Resting Spores

Algae form specialized cells as strategy to survive adverse conditions. These stress-tolerant cells may be dormant zygotes, oospores and zygospores resultant of sexual reproduction and capable of continuing life cycle of the alga (Fig. 4.1a–c). The zygotes have thicker cell wall and inner wall of cortical cells, sometimes encrusted with lime and referred as gyrogonites (Leliaert et al. 2012). In *Coleochaete*, the inner zygote cell wall layers contain material similar to sporopollenin, which provides protection from both desiccation and UV radiation (Delwiche et al. 1989; Kroken et al. 1996). The dormant zygote is revived by the change in environmental conditions such as moisture, temperature and light. The oospores are overwintering cells that can survive anoxic condition on lake bottom in case of *Charophyceae* (Holzinger and Pichrtova 2016). The zygospores reported in *Coleochaetophyceae* (Delwiche et al. 1989) and *Zygnematophyceae* (Stancheva et al. 2012) are triple layered and contain crucial stress tolerance enzymes and acetolysis-resistant materials. Other specialized spores may be parthenospores, akinetes, hormogonia and aplanospores. The parthenospores are resultant of incomplete conjugation, and they are the gametes that did not find compatible sexual partner. The akinetes are developed directly from vegetative cells and have thick cell wall due to deposition of wall material (Fig. 4.1d, e). Hormogonia are motile filaments of cells produced by *Cyanobacteria* when exposed to environmental stress. Hormogonia are common in *Nostocales* and *Stigonematales* formed during asexual reproduction (Fig. 4.1f, g). They are capable of establishing symbiotic association with plant for nitrogen fixation. Aplanospores are formed within the vegetative cells while protoplast is shirking (Kadlubowaska 1984). *Haematococcus*, a green alga, is known to produce aplanospores (also called as haematocysts, hypnoblasts) during stress conditions. Suseela and Toppo (2006) observed that during summer, several seasonal ponds and lakes in Palampur, India, turned red due to the presence of *H. pluvialis* (Fig. 4.1h). As the water starts to dry, green algae lose their flagella and become spherical, and their cell wall becomes thick and turns red producing aplanospores rich in astaxanthin. The astaxanthin is a pink (or red)-coloured ketocarotenoid, which protects the alga from adverse environmental changes such as photo-oxidation and cell membranes and other sensitive structures against free radical attack (Suseela and Toppo 2006).

4.3.3 Dormant Vegetative Cells

In several cases, algae do not produce specialized cells to survive stress. They remain dormant in vegetative state with reduced physiological activity. They can be considered as true desiccation-tolerant species. The stress-tolerant vegetative cells

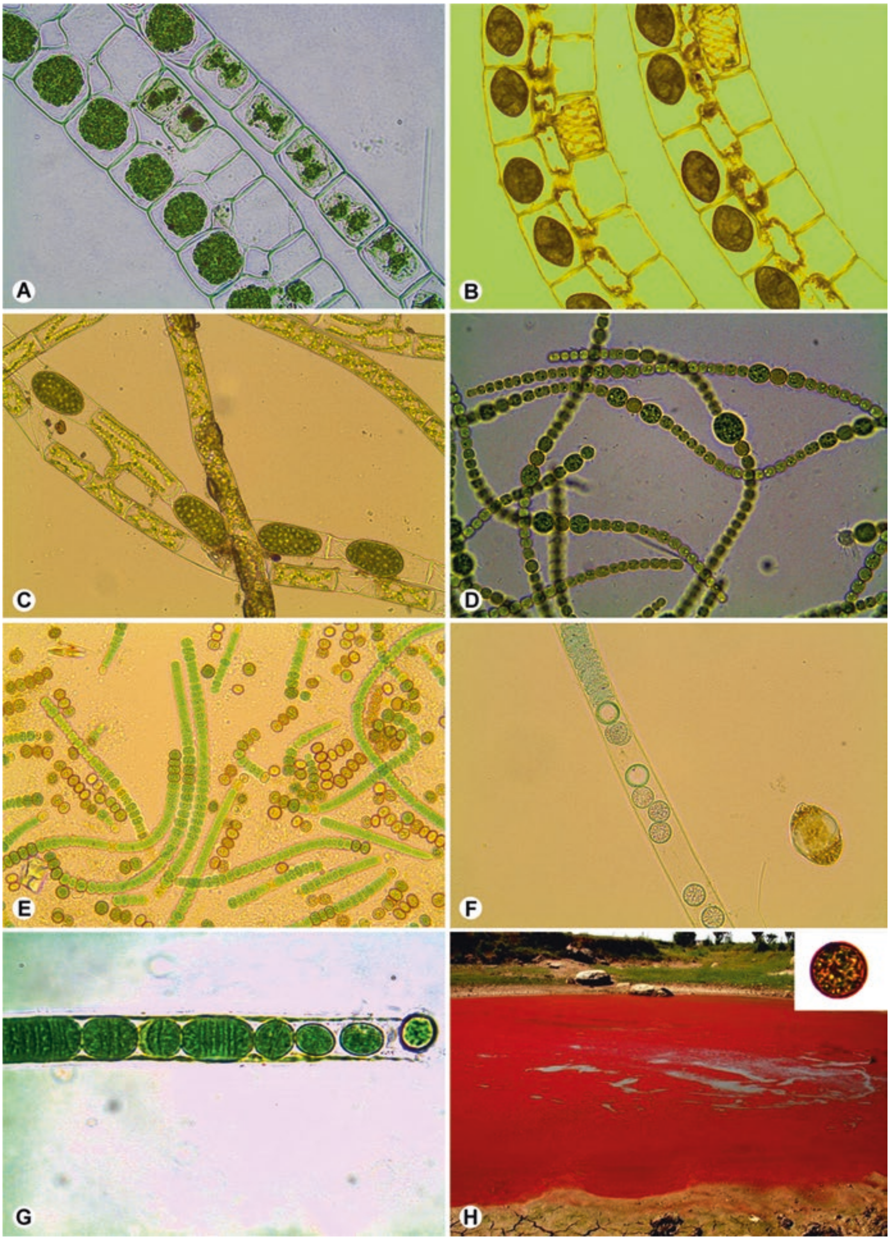

Fig. 4.1 Resting spores seen in algae. (**a**) Zygospore formation in *Zygnema* sp. (**b** and **c**) Different species of *Spirogyra*. (**d** and **e**) Akinetes in *Anabaena* spp. (**f** and **g**) Hormogonia (**f**) *Lyngbya* sp. (**g**) *Oscillatoria* sp. (**h**) Lake turned red in Palampur, Himachal Pradesh, due to the presence of *Haematococcus pluvialis*; inset aplanospore

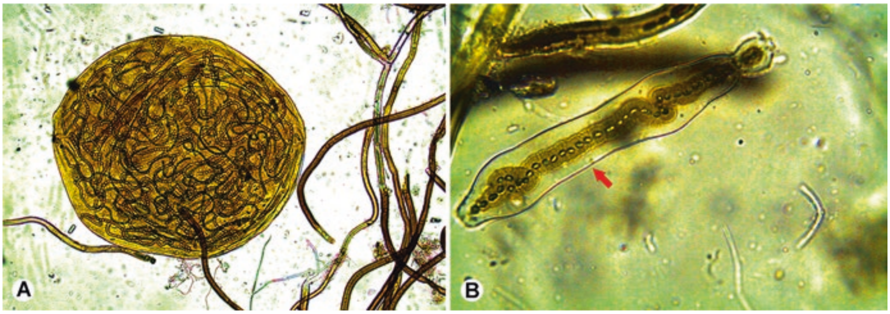

Fig. 4.2 Thick mucilage sheath protecting *Cyanobacteria*. (**a**) *Nostoc* colony enveloped by mucilage. (**b**) Single filament of *Nostoc* sp. with thick mucilage sheath

resume their physiological activity when favourable condition returns. Such hardened stress-tolerant vegetative cells are called as 'pre-akinete' or 'mature cell' and are proven strong for desiccation as well as freezing (Herburger et al. 2015). Upon desiccation, carbohydrate and lipid contents increased, and protein content decreased (Morison and Sheath 1985). However, recent proteomic analyses of the lichen green alga showed that dehydration caused an increase in the relative abundance of few proteins, while the proteins associated with Calvin cycle were decreased (Gasulla et al. 2013).

The presence of external mucilage cover on the algal cells not only delays desiccation process but also helps in quickly absorbing moisture (Fig. 4.2a, b). The mucilage layer has also been suggested to play a significant role in UV protection (Lütz et al. 1997). These cells may also have thick cell wall which further facilitates the stress tolerance. The cell wall of the algae is made of complex substances that may be similar to land plants. For example, charophyte cell wall contains polymers that are similar to cellulose, pectins, hemicellulose, arabinogalactan proteins, extensin and lignin (Sørensen et al. 2011; Domozych et al. 2012). Some of these cell wall components might facilitate prolonged water-holding capacities and tolerate desiccation stress. Callose found in cell wall is a flexibilizing compound that can protect algae from desiccation-induced damage when they follow the shrinkage of the protoplast. In some algae such as *Klebsormidium* in desiccated samples, undulating cross-walls were observed. This indicates the high degree of mechanical flexibility and structural integrity in the dried state that allows cell to maintain turgor pressure for prolonged period during dehydration process (Holzinger and Pichrtova 2016).

4.3.4 Physiological Changes

Physiologically, desiccation results in reduction of the cellular water potential and increases cellular ionic concentration (Holzinger and Karsten 2013). Desiccation also directly affects photosynthesis, the electron transport system in thylakoid membranes in algae, and hence may result in photoinhibition or even photodamage

(Wieners et al. 2012). There will be rapid reduction of photosynthesis during desiccation and quick recovery after rewetting. The loss of water in the presence of light increases the stress leading to generation of reactive oxygen species (ROS) (Fernandez-Marin et al. 2016). ROS are the most possible source of damage to nucleic acids, proteins and lipids. Particularly, the hydroxyl radical is extremely reactive and easily hydroxylates purine and pyrimidine bases of DNA, thus enhancing mutation rates (Halliwelli 1987). To fight the oxidative stress tolerant species upregulate photoprotection mechanism through photoinhibition (Roach and Krieger-Liszkay 2014). Some high-light-tolerating algae also contain increased concentration of zeaxanthin in PSII antenna (Stamenkovic et al. 2014) and phenolic compounds (Pichrtova et al. 2013). The CO_2 exchange is another important physiological parameter that is affected during desiccation. In case of alga *Apatococcus lobatus*, most favourable carbon assimilation was measured at 97–98% relative humidity (RH); however, lower limit of carbon assimilation was observed at 68% RH (Bertsch 1966).

4.3.5 Stress-Tolerant Substances

Algae produce and accumulate a variety of metabolites such as organic osmolytes that protect them from stress conditions and act as antioxidants, cryoprotectants and heat protectants. These organic osmolytes are chemically diverse, comprising sugars (sucrose, glucose, raffinose, xylose, galactose, mannose, inositol, fructose, glycerol, mannitol, sorbitol), amino acids and their derivatives (Welsh 2002; Yancey 2005; Kaplan et al. 2012). Among them, sucrose seems to be the major organic osmolyte found in several stress-tolerant algae. For example, the extraction of soluble sugars from Antarctic *Zygnema* yielded 95% of the sucrose (Hawes 1990). Concentration of composition of amino acid has been observed during desiccation.

In the algae growing in high UV radiation (cold desert, alpine areas), mycosporine-like amino acids are produced as UV screening compounds. Mycosporines are colourless, water-soluble substances with peak absorbance between 310 and 360 nm (Shick and Dunlap 2002). They can function also as antioxidants and are involved in osmotic regulation (Oren 2007). The phenolics are the other group of substances that are useful in screening UV. Some phenolic substances cause strong pigmentation of the vacuoles, and so they protect photosynthetic apparatus from excessive PAR irradiation (Holzinger and Pichrtova 2016). Purple pigmentation (purpurogallin derivatives) can be seen in some algae such as *Mesotaenium berggrenii* growing in alpine and Arctic glacier (Remias et al. 2012). Production of red astaxanthin by *H. pluvialis* is already discussed earlier, and recently, Shah et al. (2016) discussed in detail the biochemistry, pathway, function and use of this substance. During low nitrogen concentration and high solar irradiation, algae such as *Dunaliella* may produce more than 12% of its dry weight as β-carotene. β-Carotene is a provitamin A carotenoid and a natural antioxidant, which has been used as food and animal feed additive and cosmetic ingredient (Seckbach 2007).

4.3.6 *De novo* Mechanism

Algae have inbuilt repair and *de novo* biosynthesis mechanism to manage the damage occurred due to desiccation. DNA is found to be the only biomolecule that is steadily maintained and repaired, while other molecules such as proteins are degraded and *de novo* synthesized (Holzinger and Krasten 2013).

4.4 Adaptation for Cold

Winter season, temperate and alpine region of the terrestrial habitat impose cold stress to the algae. The cold deserts such as Leh, Ladakh, Antarctica and Arctic are other colder areas where algae are found growing. Algae are also seen in snow, ice, glaciers and permafrost. The occurrence of algae in these habitats indicates that they are psychrotrophs, well adapted to cold. Algae growing in cold desert suffer not only desiccation but also light stress with bright and high UV radiation. In *Zygnema* strains studied from Arctic and Antarctic habitats, a high amount of antheraxanthin and zeaxanthin was observed as light-tolerating mechanism (Pichrtova et al. 2013). Further, the highest de-epoxidation state was found in an Arctic strain, which went along with the highest concentration of phenolic compounds (Pichrtova et al. 2013). Glacier is one of the most extreme habitats on earth, and very few algae reported from here belong to the class *Zygnematophyceae* (Holzinger and Pichrtova 2016). These algae are found mostly in vegetative state, and spores or cysts are not produced even during overwintering. Alpine strains of *Klebsormidium* are markedly resistant to osmotic stress (Kaplan et al. 2012) and can survive freezing at −40 °C (Elster et al. 2008). We have observed that some of the algae, especially cyanobacteria (*Anabaena sp.*), growing in alpine areas are much darker in colour than in lower altitudes (Fig. 4.3a). The optimum temperature for growth of snow algae is generally below 10 °C. During summer months, the snow algae result into blooms giving red, orange, green or grey coloration to the snow depending upon the species. The colouration is due to the transformation of green vegetative cells to colourful resting spore stages. The pigments protect the algal cells from high light and UV radiation damage during the summer months. The spores also have thick walls and large amounts of reserve food in the form of lipid, polyols and sugars. Such spores are able to withstand sub-zero temperatures in winter and desiccation in summer. The cells of some species also secrete large amounts of mucilage which enable them to adhere to one another and to snow crystals and prevent them from being washed away by meltwater. As discussed earlier, the mucilage also forms a protective coat and delays desiccation. It may have an additional function as an UV shield. We have observed in the algal taxa, especially desmids collected from colder area had thick sheath of mucilage giving a feather-like appearance (Fig. 4.3b, c). The other strategies include algae incorporate polyunsaturated fatty acids with decreased chain-lengths into the membrane to maintain membrane fluidity at low temperatures. They also produce compatible solutes (e.g. trehalose) that help to reduce the freezing point of the intracellular fluid. This strategy also reduces cell desiccation as less water is needed to retain

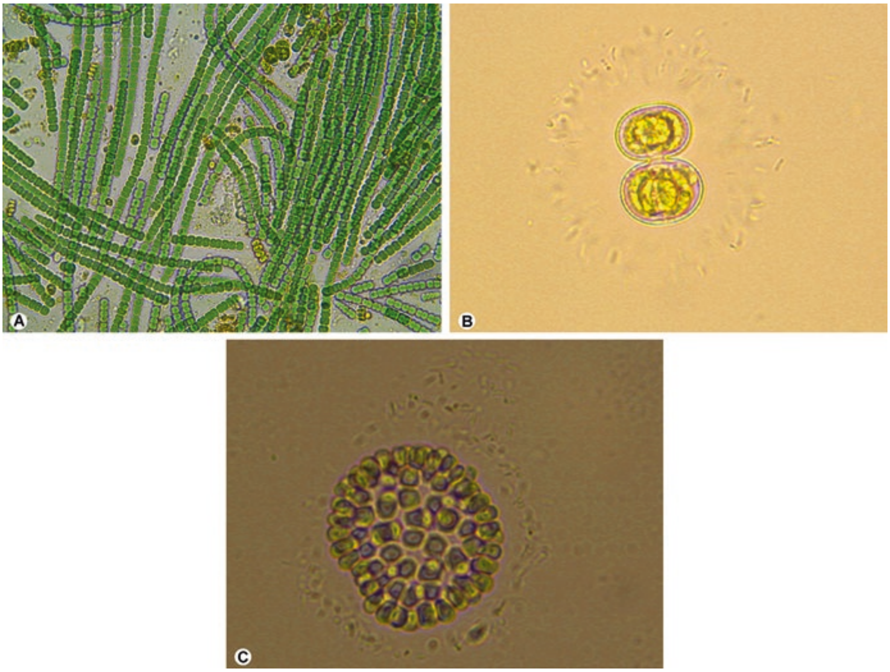

Fig. 4.3 Algae in alpine areas. (**a**) *Dark green* colouration of *Anabaena* sp. in higher-altitude areas, (**b**) feather-like mucilaginous structure around *Cosmarium* cells, and (**c**) *Sphaerocystis* sp.

the osmotic equilibrium (Welsh 2002). Further, extracellular compounds such as polymeric substances help to reduce ice nucleation around the cells (Vincent 2007).

4.5 Algae in Saline Habitats

According to evolutionary theories, algae originated from sea which has high-saline environment. However, during evolution, algae lost their degree of salt resistance (Fodorpataki and Bartha 2004). Apart from sea and ocean, algae also occur in saline water such as saline pond, lakes and brine channels in the sea. In these algae, the increase in the salt concentration in the environment is countered by accumulation of salt by algae to maintain osmotic balance. They uptake inorganic ions to balance the extracellular ion concentration and produce organic osmolytes as long-term survival strategies (Oren 2000). *Dunaliella salina*, an alga which grows in saline environment, is used as convenient model organism to study general mechanisms of salt adaptation in algae and plants. Katz et al. (2007) identified 55 novel membrane-associated proteins in *D. salina* and showed how changes in the structure and composition of the membrane may help this organism to adapt to high salt content. Algae such as *Scenedesmus opoliensis* excrete high amount of mucilage in which the individuals form extended aggregates (Fodorpataki and Bartha 2004).

4.6 Algae in Hot Springs

Algae are also known to occur in hot springs, and such thermophiles are considered as closest living relatives of microorganism present on early earth (Stetter 2006). They are most abundant at temperatures of 55 °C (131 °F) or below. Several studies dealing with the diversity of algae in hot springs are available; however, the information about their adaption is scarce. Prasad and Srivastava (1965) collected 24 taxa of *Cyanobacteria* from four (Tapovan, Badrinath, Manikaran, Bashisht) hot springs of Himalayas wherein temperature ranged from 45 to 97 °C. Recently, Bhakta et al. (2016) enumerated 50 species of algae (*Cyanobacteria*, Chlorophyceae, Bacillariophyceae) from hot springs in Odisha state where water temperature ranged from 35 to 60 °C. We have ourselves collected a total of seven genera of algae from Bashisht hot spring, Himachal Pradesh, and their further identification is in progress. The microbial diversity is lower in hot springs, but they exhibit remarkable genomic and metabolic flexibility. The diversity of microbes significantly depends on physicochemical parameters of water as well as geographical location. Badhai et al. (2015) observed that environmental physicochemical parameters of the hot spring not only control microbial composition and diversity but also play an important role in the dispersal of biological functions and adaptive responses of the communities.

4.7 Conclusion

Adaption is a dynamic evolutionary process wherein phenotypic or adaptive trait with functional role is passed on to the successive generation through natural selection. The evolution of land plants from aquatic algae was through gradual colonization of algae to moist habitats in proximity of water and from there to dry land. Later, the loss of vegetative desiccation tolerance led to the development of water-regulating structures such as xylem elements to transport water or stomata to regulate transpiration (Holzinger and Karsten 2013). Therefore, it can be concluded that terrestrial algae which have well adapted to harsh environmental conditions are in evolutionary process of achieving next cellular organization like plants. While algae produce several biological substances for their own protection, they also serve as important biomolecules for human welfare. Astaxanthin is one such highly beneficial substance having multiple usage such as antioxidant, treatment of Alzheimer's and Parkinson's disorders, etc. (Suseela and Toppo 2006).

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