Vertika Shukla · Sanjeev Kumar
Narendra Kumar   *Editors*

Plant Adaptation Strategies in Changing Environment

Springer

Plant Adaptation Strategies in Changing Environment

Vertika Shukla • Sanjeev Kumar
Narendra Kumar

Editors

Plant Adaptation Strategies in Changing Environment

Springer

Editors
Vertika Shukla
School of Environmental Sciences
Babasaheb Bhimrao Ambedkar University
Lucknow, UP, India

Sanjeev Kumar
School of Environmental Sciences
Babasaheb Bhimrao Ambedkar University
Lucknow, UP, India

Narendra Kumar
Department of Environmental Science,
School of Environmental Sciences
Babasaheb Bhimrao Ambedkar University
Lucknow, UP, India

Preface

Plants are sessile organisms, and to cope up with disturbed/altered ambient conditions, they have evolved diverse adaptation strategies to support their growth and development. The ability of various plant groups to tolerate the extremes posed by natural (arid/cold) conditions and/or chemically rich environments involves both morphological and physiological adaptation as well as changes in ecological behaviour to sustain in relatively protected niches within an extreme environment. These adaptations are manifested as changes in enzyme activity, cellular organization, metabolomics and ultimately genetic alterations expressed as mutations.

The present compilation addresses various stress conditions to which plants are exposed to and how they resist or avoid the particular stress condition/s. Plants endure temperature fluctuations and varying solar irradiance and also tolerate anthropogenic emissions. Lichens, pioneers of plant succession, are among the most ubiquitous organisms which are widely distributed in polar regions and cold deserts. They are highly mechanized to freezing and desiccation. Resurrection strategy in plants presents an interesting aspect for research, which requires thorough investigation at the cellular and genetic levels.

Similar to lichens, algae are also present globally, occurring in a range of habitats. Algae are found growing abundantly in extreme habitats indicating their adaptation to harsh environments. Lower plant groups not only adapt to natural alterations but also have been potential sequesters of anthropogenic emissions especially. Pteridophytes are widely utilized as hyperaccumulators of metals. Fly ash-induced metabolic adaptation in different fern species provides an insight into the metabolic adaptations adopted by ferns to tolerate higher levels of metals. Further utility of these species in phytoremediation of toxic metals from fly ash as well as ecorestoration of fly ash landfills is an added advantage.

In view of the increasing urbanization and industrialization, metallic emissions are posing a risk at spatio-temporal scale, but crops have adapted to the high levels by various detoxification processes.

A number of physiological and biochemical changes occur under heavy metal (HM) toxicity including alteration in water uptake and transport, root and shoot growth and generation and scavenging of reactive oxygen species (ROS) and

changes in HM-complexing ligands for sequestration of these HMs into vacuoles to reduce the HM concentration in the cytoplasm. Physiological and biochemical responses of plants to HM toxicity have been discussed in detail along with shedding light on uptake and transport mechanisms of HMs in brief.

Agriculture productivity is greatly affected by the salinity of the soil. Crop growth and yield are severely decreased by salt stress. Proteomic-based techniques have emerged as a powerful tool to reveal the molecular mechanisms of salt stress responses. Several salt-responsive proteins have been identified for crops by using these techniques. It will be possible to change salt-sensitive crops to salt-tolerant crops in the near future by using these proteins and their corresponding genes. In the past few years, great progress has been made towards understanding plant salt stress responses and tolerance mechanisms, but still many challenges lie ahead. Both molecular breeding and advanced biotechnology methods should help scientists to develop crops with enhanced salt tolerance. Apart from the proteomics approach, usage of plant-based biochar increases plant growth and biomass under salt stress. Biochar-treated soil increases the photosynthesis, nutrient uptake and modified gas exchange characteristics in plants; the details about omics approaches and biochar have also been well discussed in the chapters.

Plants which are adapted to toxic chemicals (hyperaccumulating plants) show an important part in the terrestrial food web and are significant in both agricultural and natural ecosystems. These plants are frequently utilized for phytoremediation of contaminated sites. The chapters provide an understanding about the applicability and mechanism of the phytoremediation process.

Plants biosynthesize and store a variety of metabolites especially carbon-based secondary compounds that protect plants from stress conditions by acting as antioxidants, cryoprotectants and heat protectants. These organic compounds are chemically diverse, comprising sugars (sucrose, glucose, xylose, galactose, mannose, inositol, fructose, glycerol, mannitol, sorbitol), fatty acids and amino acids and their derivatives. Use of hyphenated instrumentation techniques like LC-MS/MS, GC-MS, etc. provides the high-throughput estimation of metabolic profile changes in valuable plant resources. Variation in sugar, amino acid and fatty acids in plant species exposed to different environmental conditions has been discussed in detail.

Lichens are known to synthesize more than 1000 metabolites. The range of chemicals synthesized underlines their ecological importance. Lichens are potential natural resources of a wide range of chemicals having a potential biological role in sustainability in a diverse range of habitats and extreme conditions. The chapter reviews the progress made in the past 30 years in the field of lichenology to isolate and characterize bioactive constituents.

The overview on plant adaptation to outer space environment and survival capability of some plants underlines the importance of lithopanspermia process, i.e. the transport of living organisms by meteorites in the Solar System between the planets of the Earth type is an interesting aspect for studies on existence of extraterrestrial life in the universe and origin of life on Earth.

Overall the book provides comprehensive information on the strategies adopted by various plant groups to sustain changing environmental condition whether natural or man-made. Ultimately it is the strategy based on 'survival of the fittest' which has resulted in the evolution of various plant groups. This book aims to serve as a valuable knowledge resource especially for beginners, students and researchers from different academic backgrounds of basic research and applied sciences.

Lucknow, UP, India   Vertika Shukla
                                                                                                 Sanjeev Kumar
                                                                                                 Narendra Kumar

Contents

Editors and Contributors

About the Editors

Vertika Shukla received her M.Sc. in organic chemistry and Ph.D. (2003) on *Chemical Study of Macrolichens of Garhwal Himalayas* from H.N.B. Garhwal University, Srinagar (Garhwal). She currently teaches chemistry to undergraduate applied geology students at Babasaheb Bhimrao Ambedkar (Central) University, Lucknow. Dr. Shukla has completed three postdoc fellowships awarded by the Department of Science and Technology (DST, New Delhi) at CSIR National Botanical Research Institute and Babasaheb Bhimrao Ambedkar (Central) University. She has published 64 scientific articles, mostly in respected international SCI journals. She has also coauthored and coedited three books published by Springer. Currently, she is the chief editor of the journal *Cryptogam Biodiversity and Assessment*, the official journal of Indian Lichenological Society.

Dr. Shukla has more than 10 years of research and teaching experience. She has carried out extensive research on air pollution and climate change in Garhwal Himalayas. She has contributed much on secondary metabolite chemistry, accumulation and spatio-temporal behaviour of persistent organic pollutants (POPs) and metals in high-altitude ecosystems.

Sanjeev Kumar is an assistant professor at the School for Environmental Science, Babasaheb Bhimrao Ambedkar University, Lucknow. He received his Ph.D. degree in environmental sciences from Babasaheb Bhimrao Ambedkar University, Lucknow, in 2015. He has published several research articles in national and international journals and has several book chapters in national and international books to his credit. He has been awarded a "Fellow of Society of Plant Research" and has also received the "Significant Contribution in Academic Activities" award from Babasaheb Bhimrao Ambedkar University, Lucknow. He is joint secretary of the Prof. H.S. Srivastava Foundation for Science and Society and the Society for Science of Climate Change and Sustainable Environment and is coeditor of the multilingual magazine *KAHAAR*. Dr. Sanjeev Kumar has also worked as assistant

editor for international journals such as *Functional Plant Biology*, *Physiology and Molecular Biology of Plants* and the *Journal of Climate Change and Environmental Sustainability*.

Narendra Kumar obtained his M.Sc. and Ph.D. degrees in environmental science from the Babasaheb Bhimrao Ambedkar University, Lucknow. Dr. Kumar is an active researcher and academician with almost 15 years of postgraduate teaching and research experience. Dr. Kumar started his academic career as a project fellow at National Botanical Research Institute (NBRI-CSIR), Lucknow, U.P., India. He is currently working as an assistant professor at the Department of Environmental Science, Babasaheb Bhimrao Ambedkar University (a Central University), Lucknow. Dr. Kumar has successfully guided more than 50 M.Sc. environmental science students for their dissertation work and produced one Ph.D.

Dr. Kumar has published more than 20 international and national research papers as well as many articles in the leading newspapers. He has published five book chapters with reputed national and international publishers.

Contributors

Shamshad Ahmad Department of Environmental Sciences, Babasaheb Bhimrao Ambedkar University, Lucknow, UP, India

Richard A. Armstrong Department of Vision Sciences, Aston University, Birmingham, UK

Ankita Asati Analytical Chemistry Division, CSIR-Indian Institute of Toxicology Research, Lucknow, India

Surabhi Awasthi CSIR-National Botanical Research Institute, Lucknow, India

Institute of Environment & Sustainable Development, Banaras Hindu University, Varanasi, India

A. Casanova-Katny Veterinary school, Faculty of Natural Resources, Catholic University of Temuco, Temuco, Chile

Paromita Chakraborty Department of Civil Engineering, SRM Research Institute, SRM University, Kattankulathur, Tamil Nadu, India

Water Science Laboratory, University of Nebraska-Lincoln, Lincoln, NE, USA

Reshu Chauhan CSIR-National Botanical Research Institute, Lucknow, India

Department of Biotechnology, Kumaun University, Bhimtal, Bhimtal, Nainital, Uttarakhand, India

Farah Deeba Biotechnology Department, CSIR-Central Institute of Medicinal & Aromatic Plants, Lucknow, India

Valery M. Dembitsky National Scientific Center of Marine Biology, Vladivostok, Russia

H. Harańczyk Institute of Physics, Jagiellonian University, Cracow, Poland

Puja Khare Agronomy and Soil Science Division, CSIR-CIMAP, Lucknow, India

Hina Khatoon Department of Environmental Science, G.B. Pant University of Agriculture and Technology, Pantnagar, Uttarakhand, India

Richa Kothari Department of Environmental Sciences, Babasaheb Bhimrao Ambedkar University, Lucknow, UP, India

Amit Kumar Cytogenetic and Plant Breeding Lab, Department of Botany, University of Lucknow, Lucknow, India

Dhananjay Kumar Department of Environmental Science, Babasaheb Bhimrao Ambedkar (Central) University, Lucknow, UP, India

Mahesh Kumar Department of Environmental Science, Babasaheb Bhimrao Ambedkar University, Lucknow, UP, India

Shailender Kumar Department of Environmental Studies, University of Delhi, New Delhi, Delhi, India

Alka Kumari Department of Botany, University of Lucknow, Lucknow, UP, India

Arun Kumar Maurya Department of Botany, Multanimal Modi PG College, Modinagar Ghaziabad, UP, India

Sanjeeva Nayaka Algology Section, CSIR-National Botanical Research Institute, Lucknow, India

M. Olech Institute of Botany, Jagiellonian University, Cracow, Poland

Institute of Biochemistry and Biophysics, Polish Academy of Sciences, Warsaw, Poland

Veena Pande Department of Biotechnology, Kumaun University, Bhimtal, Nainital, Uttarakhand, India

Vivek Pandey Plant Ecology & Environmental Sciences Division, CSIR-National Botanical Research Institute, Lucknow, India

Apourv Pant Department of Environmental Science, G.B. Pant University of Agriculture and Technology, Pantnagar, Uttarakhand, India

Anju Patel School of Earth Sciences, Banasthali Vidyapeeth, Banasthali, Rajasthan, India

Devendra K. Patel Analytical Chemistry Division, CSIR-Indian Institute of Toxicology Research, Lucknow, India

D.D. Patra Bidhan Chandra Krishi Viswa Vidyalaya, Nadia, West Bengal, India

Poonam Department of Environmental Sciences, Babasaheb Bhimrao Ambedkar University, Lucknow, UP, India

Ravindra Prasad Department of Environmental Studies, University of Delhi, New Delhi, Delhi, India

J.P.N. Rai Department of Environmental Science, G.B. Pant University of Agriculture and Technology, Pantnagar, Uttarakhand, India

Anita Rani Department of Botany, Dyal Singh College, Delhi University, Delhi, India

Manoj Semwal ICT Department, CSIR-Central Institute of Medicinal & Aromatic Plants, Lucknow, India

Amit Pal Singh CSIR-National Botanical Research Institute, Lucknow, India

Ritu Singh Department of Environmental Science, School of Earth Sciences, Central University of Rajasthan, Ajmer, Rajasthan, India

Neerja Srivastava Department of Biochemistry, IBSBT, CSJMU, Kanpur, UP, India

Sudhakar Srivastava Institute of Environment & Sustainable Development, Banaras Hindu University, Varanasi, India

K. Strzałka Malopolska Centre of Biotechnology, Jagiellonian University, Cracow, Poland

Faculty of Biochemistry, Biophysics and Biotechnology, Jagiellonian University, Cracow, Poland

Kiran Toppo Algology Section, CSIR-National Botanical Research Institute, Lucknow, India

Rudra Deo Tripathi CSIR-National Botanical Research Institute, Lucknow, India

Dalip K. Upreti Lichenology Laboratory, CSIR-National Botanical Research Institute, Lucknow, India

Sushma Verma Algology Section, CSIR-National Botanical Research Institute, Lucknow, India

Anuj Kumar Yadav Department of Zoology & Environmental Sciences, Gurukula Kangri Vishwavidyalaya, Haridwar, Uttarakhand, India

Adaptation of Lichens to Extreme Conditions

Richard A. Armstrong

Abstract

Lichens exhibit the classic features of stress-tolerant organisms, viz. slow growth rates, considerable longevity, low demand for nutrients, and the presence of specific adaptations to survive in the most inhospitable environments on Earth. The ability of lichens to tolerate the extremes posed by deserts, polar regions, and chemically rich environments involves both morphological and physiological adaptation and changes in ecological behaviour so that species adapt to relatively protected niches within an extreme environment. This chapter discusses those aspects of the lichen symbiosis relevant to survival in extreme conditions and then describes the adaptation of lichens to (1) wet forests, (2) deserts, (3) the Arctic, (4) alpine regions, (5) Antarctica, (6) chemically rich environments, and (7) extraterrestrial environments such as outer space and Mars. It is evident that the lichen symbiosis is more tolerant to hostile conditions than its symbionts, morphological and physiological adaptations are intimately associated, and convergent evolution has resulted in similar changes in different environments.

R.A. Armstrong (✉)
Department of Vision Sciences, Aston University, Birmingham, UK
e-mail: R.A.Armstrong@aston.ac.uk

Abbreviations

ABC transporter	ATP-binding casette transporter
EBF	European BIOPAN Facility
GSH	Glutathione
GST	Glutathione S-transferase
ISS	International Space Station
nPS	Net photosynthesis
ROS	Reactive oxygen species
S/V	Surface/volume ratio
SOD	Superoxide dismutase
THEMIS	Thermal Emission Imaging System
UV	Ultraviolet

1.1   Introduction

Lichens occur in every major ecosystem on Earth from the poles to the tropics. Although many species are found in the tropics, they only become a significant component of the vegetation in more extreme environments such as the hot arid and semiarid deserts and the cold polar regions (Mattick 1954). Lichens are influenced by many environmental factors including the long-term effects of climate, local changes in microclimate, and a variety of factors associated with the substratum such as type of rock, bark, or soil, substrate chemistry, and the degree of nutrient enrichment by birds, salinity, or pollution (Armstrong 1974, 2015; James et al. 1977). Plants in general have been divided into three groups according to whether a ruderal, competitive, or stress-tolerant life-cycle strategy predominates (Grime 1979). In this scheme, lichens are considered to be stress-tolerant organisms and therefore to occur in communities in which competition is unlikely to play a significant role. Such organisms would be characterized by slow growth rates, considerable longevity, low demands for nutrients, and the presence of specific adaptations to survive in stressful conditions (Grime 1979). The ability of lichens to tolerate extreme conditions involves both morphological and physiological adaptation as well as changes in ecological behaviour so that they adapt to relatively protected niches within an extreme environment. This chapter discusses those aspects of the lichen symbiosis relevant to survival in extreme conditions and then describes the adaptation of lichens to (1) wet forest, (2) desert, (3) the Arctic, (4) alpine regions, (5) Antarctica, (6) chemically rich environments, and (7) extraterrestrial environments such as outer space and Mars.

1.2   The Lichen Symbiosis

1.2.1   Morphology

A lichen is composite, symbiotic organism comprising two or more constituents, the most frequent being an alga and a fungus. In cross section (Fig. 1.1), a typical lichen is composed mainly of fungal tissue, but embedded in the upper cortical layers are eukaryotic algal cells. Some lichens are also associated with cyanobacteria (blue-green algae) found in special structures called cephalodia, and lichens may also associate with other microorganisms. Hence, a lichen can be considered as an 'ecosystem' in which several constituent organisms collaborate (Farrar 1976). The algal partner carries out photosynthesis and supplies the fungus with carbohydrate, but there is little experimental evidence that the fungus supplies nutrients directly to the alga (Smith and Douglas 1987). Nevertheless, a thick upper cortical layer and associated hyphae may protect the algal cells from rapid water loss and intense radiation but at the expense of slower uptake of materials (Rundel 1988). There are three major types of lichen growth form (Fig. 1.2), viz. the crustose type composed of a thin crust that is tightly attached to the substratum, the foliose type that comprises a series of radially arranged leaflike lobes, and the fruticose type in which the lichen thallus is attached to the substratum at a single point and forms a complex branched structure. Most habitats in which lichens are frequent have a mixture of all three growth forms. These growth forms have very different surface to volume (S/V) ratios, which is maximal in fruticose lichens and an important factor
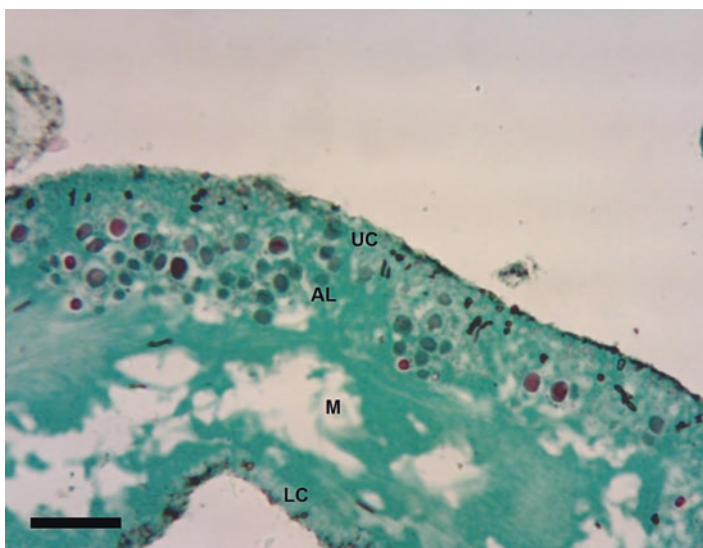
Fig. 1.1 Vertical section through a thallus of the foliose lichen *Xanthoria parietina* (L.) Th. Fr. showing the various layers: *UC* Upper cortex, *A* algal layer, *M* medulla, *LC* lower cortex. Some desert lichens subvert this structure and have a ventral rather than a dorsal algal layer
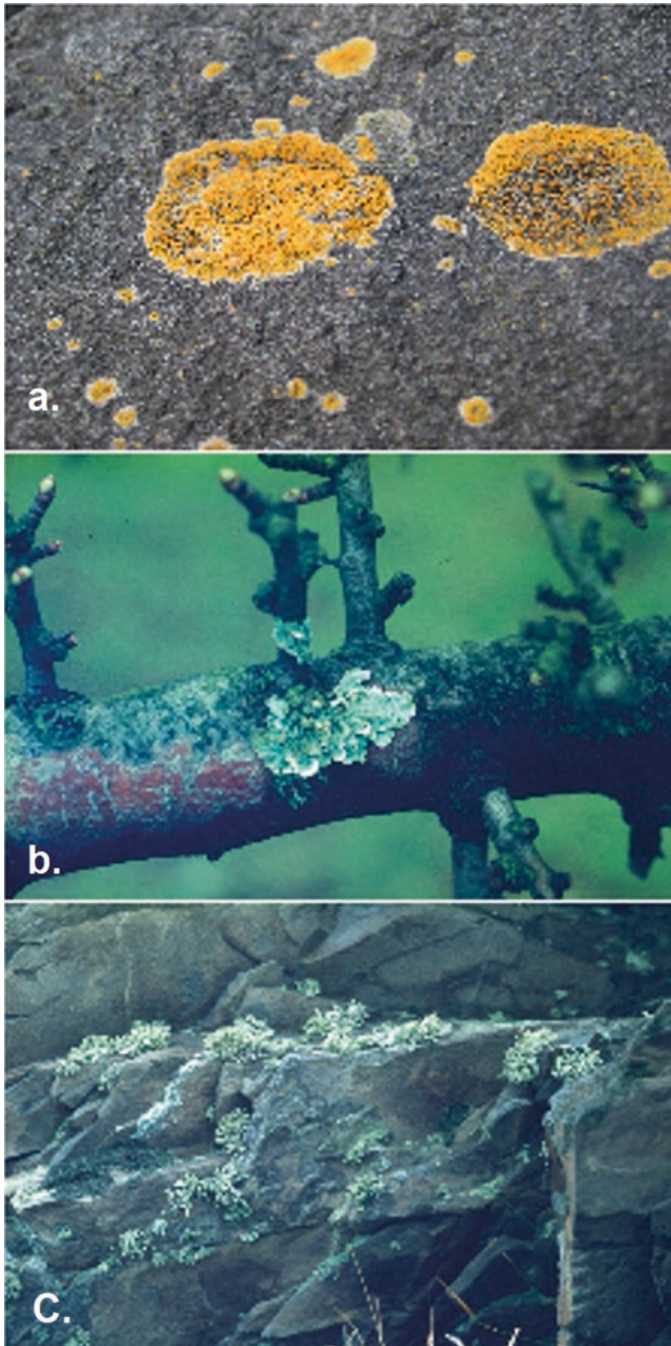
Fig. 1.2 The three main growth forms of lichens: (**a**) the crustose lichen *Caloplaca marina* (Wedd.) Zahlbr. Ex Du Riez, (**b**) the foliose lichen *Parmelia sulcata* T. Tayl., and (**c**) the fruticose lichen *Ramalina subfarinacea* (Nyl. ex Cromb.) Nyl. The proportions of these three growth forms often vary with type of extreme environment

determining water uptake and evaporative loss. Various morphological adaptations in lichens result in an increase in this ratio by changing growth form, branching pattern, or thallus thickness (Larson 1984). Hence, the development of a prothallus by many crustose species, often observable as a ring of fungal tissue at the thallus margin, may be particularly important in the uptake and accumulation of water. Additional growth forms include the 'placodioid' type in which a largely crustose thallus has distinct marginal lobes as in some species of *Buellia* and *Caloplaca*, a 'powdery' type ('leprose'), as in *Lepraria*, and a 'gelatinous' type in which algal cells are generally distributed throughout the thallus, as in *Collema* and *Leptogium.* Many lichens exclusively produce fungal spores, and reproduction involves 'lichenization' which results when a germinating spore contacts a suitable alga. However, many species have also evolved vegetative 'diaspores' which disperse the fungal and algal symbionts together (Bailey 1976). The most common methods of vegetative reproduction include isidia (Armstrong 1981), soredia (Armstrong 1991), and thallus fragments (Armstrong 1990a).

1.2.2 Growth and Physiology

The foliose and crustose types of lichen grow radially over the substratum rather like a fungus on an agar plate, but growth rates can be very slow. Foliose species have rates of radial extension between 2 and 5 mm per year (Armstrong and Bradwell 2011), but many crustose lichens grow much more slowly with rates of less than 0.5 mm year (Armstrong 2005, Armstrong and Bradwell 2010). Some species grow so slowly that larger thalli growing in the Arctic may live to be over 5000 years old and thus may be some of the oldest living organisms on Earth (Beschel 1961). The slow growth of lichens is not attributable to slower than normal physiological processes but to the fact that they may spend a considerable portion of their time in a dehydrated state and metabolically inactive. Moreover, when the lichen is wetted, there is a loss of carbon due to respiration (Smith and Molesworth 1973). After wetting, photosynthesis begins to replace the carbon lost, but the lichen has to remain wet for a sufficient period in the light to make good the carbon losses and then to make new carbon for growth (Armstrong 1976). Hence, frequent rain showers combined with rapid rates of drying in the sun may continually deplete carbon sources with little available for growth. As a result of slow growth, however, a lichen may make relatively little demand on the environment for nutrients, thus enabling the organism to grow in potentially nutrient-poor habitats.

A large group of lichens contain the green alga *Trebouxia* as the algal partner in which carbohydrate is released from the alga as the polyol ribitol and then converted into arabitol and mannitol by the fungus (Richardson et al. 1968). In some foliose and fruticose lichens, transfer of carbohydrate occurs within an extracellular envelope of hydrophobic proteinaceous material creating an 'apoplastic continuum', but this system is unlikely to be present in crustose lichens where the mechanism of transfer is less clear (Honegger 1978). Hence, algal cells in *Rhizocarpon lecanorinum* Anders are not penetrated by haustoria, a mechanism which can extract

Table 1.1 Mean concentrations (µg mg^{-1} extracted tissue) of the poyols ribitol, arabitol, and mannitol in the foliose lichen *Xanthoparmelia conspersa* (Ehrh ex Ach) Hale and crustose lichen *Rhizocarpon geographicum* (L.) DC

Species	Region	Ribitol	Arabitol	Mannitol
X. conspersa	Marginal lobes	7.26	19.78	19.66
R. geographicum	Prothallus	1.16	6.58	4.25
	Areolae	8.73	22/73	11.20

Data from Armstrong and Smith (2009)

nutrients in lichens with a lesser degree of thallus organization (Clayden 1998). In *Trebouxia*-containing lichens, arabitol and mannitol are used as carbohydrate reserves, arabitol as a respiratory reserve, while mannitol having a more protective function (Farrar 1973). In Table 1.1, for example, the concentrations of arabitol and mannitol are similar in the foliose lichen *Xanthoparmelia conspersa* (Ehrh ex Duby) Hale, but the level of arabitol is greater than mannitol in *Rhizocarpon geographicum* (L.) DC., especially in the prothallus. In addition, the arabitol to ribitol ratio is similar in the areolae of *R. geographicum* and in *X. conspersa*, but in the more vulnerable marginal prothallus of the former, the arabitol and mannitol to ribitol ratio is greater suggesting a greater proportion of the photosynthate is stored as arabitol and mannitol (Armstrong and Smith 1987). Hence, lichens may maintain pools of polyols as a stress-tolerant mechanism, and the relative level of these polyols in different parts of the thallus is a useful indicator of the stress response in lichens (Farrar 1973, 1976).

A number of other stress-tolerant mechanisms are likely to be present in lichens including an antioxidant system (Li and Wei 2016). Hence, Kranner et al. (2005) investigated the effect of desiccation and irradiation on the level of reactive oxygen species (ROS) in *Cladonia vulcani* Savicz. Antioxidant and photoprotective mechanisms were more effective by an order of magnitude compared with the isolated symbionts. In addition, it was concluded that the alga and fungus could induce increased regulation of the protective systems in the other evidence that the lichen symbiosis is more stress resistant than either of its partners (Table 1.2).

1.3   Adaptations of Lichens to Extreme Conditions

1.3.1   Wet Forest

There are two types of wet forest environment on Earth. First, the temperate wet forest, also known as temperate rainforest, which occupies regions along the west coast of North America from California to Alaska. This region is characterized by higher temperatures than normal for boreal forest environments, relatively limited seasonal variation, and high levels of humidity (Odum 1971). Rainfall is high, usually between 30 and 150 in a year, with periods of fog compensating for lower rainfall in the more southern regions of the forest. Humidity is usually very high throughout the forests with a precipitation/evaporation ratio which is very favourable for plant growth. In southern regions, fog may account for two to three times

Table 1.2 Summary of morphological and physiological adaptations of lichens to extreme environments

Environment	Type	Adaptations
Wet forest	Morphological	Often shade adapted: thinner thalli, less fertile, and less pigmented. Tomentum may be present. Upper or lower surface impermeable to water
	Physiological	Can tolerate high temperatures when wet. Some species show little depression of nPS at thallus saturation. May use lichen substances as defensive allelochemicals
Desert	Morphological	Thin crustose growth form. Light-coloured thalli in some areas, darkly pigmented when very arid
		Increasing cortical thickness in some species. Inversion of structure with ventral algal layer. May contain photoprotective pigments (yellow/orange species). Increase of surface area in foggy regions with fruticose, pendulous, or tufted growth form
	Physiological	nPS may be optimal at high temperatures and recorded at very low thallus water potentials
The Arctic	Morphological	Crustose or fruticose. Dark pigmentation with light-coloured forms in more protected niches. Fruticose species in dense columnar mats
	Physiological	Takes advantage of short favourable periods
		Tolerant of freezing: strong recovery of nPS and respiration after storage at low temperature
		Increasing levels of soluble carbohydrates especially trehalose
Alpine regions	Morphological	Greater area of black prothallus in some species at higher altitudes
	Physiological	Accumulate UV-absorbing phenolic usnic acid. Storage of pools of polyols. Takes advantage of short favourable periods. Changes in protein and fatty acid composition with altitude
Antarctic	Morphological	Crustose species dominant and fruticose species also present. Develop stipitate and pulvinate growth. Increase in cortical thickness. Dark pigmentation with yellow-green forms in cracks and fissures. Endolithic growth form in dry valleys
	Physiological	Similar to Arctic. Photoprotective pigment melanin present in some species
Chemically rich	Morphological	Increased surface hydrophobicity with pores to provide 'breathable' surface
		Increased surface 'roughness'
	Physiological	Tolerance of high pH. Physiological control of intracellular ions. Use of stress ethylene and lichen substances. Differential expression of heat shock proteins, glutathione S-transferase, and ABC transporter. Antioxidant resistance mechanisms

more of the available water than annual rainfall and on some trees, and 50 in of rain has been recorded dripping down the trunk in a year (Oberlander 1956). By contrast, tropical rainforest occurs in low-altitude regions near the equator and comprises the Amazon and Orinoco basin in South America; the Central American isthmus; the Congo, Niger, and Zambezi basin of Central/West Africa and Madagascar; and the Indo-Malay-Borneo-New Guinea region (Odum 1971). These regions are characterized by greater than 80–90 in of rain a year, which is well distributed across seasons, with usually one or more shorter dry seasons. Temperature variation is small across the seasons as a whole and often less than the diurnal variation.

Wet forest is a surprising environment to be considered as extreme for lichens. Nevertheless, a combination of high thallus water contents over long periods, which can depress net photosynthesis (nPS), and intense competition from rapidly growing bryophytes and other plants can be challenging (Fig. 1.3). As a consequence, despite the large number of individual species present, 50% of all known lichen species being recorded from tropical areas (Mattick 1954), individual lichen species are rarely dominant in these forests. The lichens of wet forests exhibit a range of morphological and physiological adaptations (Kappen 1988), light being a strong limiting factor (Awasthi and Agrawal 1970). Hence, lichen morphology often varies with light regime, thalli in shade being less pigmented, having a thinner cortex, fewer apothecia, and more abundant soredia (Riehmer 1932). Such species also appear to be able to tolerate higher temperatures while wet (Kappen 1988). Some species possess a 'tomentum' on the surface (Kappen 1988), which may be waterholding adaptation, reducing the chance that the thallus will become saturated for long periods. In some species, e.g. *Peltigera praetextata* (Flörke ex Summerf.)

Fig. 1.3 The wet forest of the Olympic Peninsula, Washington State, USA. Lichens in these environments are subjected to extremely wet conditions and intense competition from bryophytes and higher plants

Zopf, the upper thallus surface is impermeable to CO_2 and covered by a thick water film after rain (Matthes 1980), whereas in species of *Sticta* and *Pseudocyphellaria*, only the upper surface allows exposure to rain or runoff, the lower surface being sealed at high water contents to enable CO_2 to diffuse through pores (Green et al. 1981). The extent of the depression of nPS at high thallus water contents varies among species in the wet forest, a 15% reduction being observed in species of *Sticta* while 45% is more typical of *Pseudocyphellaria*. In addition, lichens were soaked, sprayed, and shaken and then allowed to dry slowly so that their response could be compared with samples of thalli continuously exposed to a wet environment (Lange et al. 1993). Several types of photosynthetic response were observed at high water contents including species exhibiting no depression, little depression, or large degrees of depression suggesting considerable variations in the ability of different species to adapt to very wet conditions.

A major problem faced by lichens in the wet forest is competition from bryophytes and higher plants (Fig. 1.3), and as stress-tolerant organisms, they are unlikely to be successful in communities in which competition is intense (Armstrong and Welch 2007). Nevertheless, a large number of lichen species have been recorded especially in tropical forests (Mattick 1954). One possibility is that lichens use chemical substances as a defensive strategy. Over 500 secondary metabolites have been reported in lichens of which 350 are unique to the symbiosis (Lawrey 1995). Most of these metabolites are weak phenolic compounds produced by the fungal partner and which accumulate in the outer walls of the hyphae. For many years, there have been claims that such compounds, when leached from the thallus, may suppress adjacent lichens and mosses (allelopathy) (Lawrey 1995). A prediction of Grime's hypothesis (Grime 1979) is that the production of secondary compounds in stress-tolerant organisms is essentially defensive. In addition, Rogers (1990) concluded that competitors produce offensive allelochemicals while stress-tolerant organisms produce defensive (antimicrobial) allelochemicals. Hence, Hilmo (1994) and Glenn et al. (1995) reported that the presence of usnic acid and other secondary compounds may reduce grazing by microarthropods and generalist herbivores, while John (1989) suggested that crustose lichens use allelochemicals as a contact avoidance strategy. Hence, defensive allelochemicals could be part of an adaptive strategy to survive the intense competition of wet forests.

1.3.2 Desert

Either desert regions are characterized as having less than 10 in of rainfall a year, or if more than 10 in is present, there is a greater uneven distribution across the seasons (Odum 1971). The scarcity of rainfall can be attributable to three main causes: (1) high subtropical pressure, e.g. in the Saharan and Australian deserts; (2) location in rain shadows, e.g. in western North American deserts; or (3) high altitude, e.g. the Tibetan, Bolivian, and Gobi deserts. Most deserts receive some rain and therefore have a sparse cover of vegetation with the possible exceptions of the extremely arid regions of central Sahara and north Chile (Odum 1971).

Availability of water is clearly the main problem facing desert lichens, and although the dry conditions may favour some species, lichens may be absent in some sandy deserts (Kappen 1973, 1988). There is a balance in lichen thalli between exposing the maximum water absorbing surface and being able to restrict water loss (Rundel 1988), and there are a number of adaptations reflecting this dilemma. First, there is an increase in the frequency of thin, crustose species as conditions become increasingly dry, which exposes the maximum degree of horizontal surface accompanied by internal anatomical adaptations to increase the density and thickness of hyphal walls (Rundel 1988). Second, there are changes in pigmentation, many species being either light coloured (Galun 1963) or possessing light-coloured powdery 'pruina' on a darker thallus (Weber 1962). In extremely dry conditions, dark-coloured lichens containing blue-green algae as the algal partner ('cyanolichens') have been reported (Marton and Galun 1981), while on the gravel plains of Namaqualand, orange/yellow lichens are frequent, a pigmentation which is protective against light (Kappen 1983). Third, dry thalli regardless of pigmentation can resist high temperatures of up to 70 °C without heat damage (Lange 1953). Fourth, increasing cortical thickness relative to the other layers has been reported in some desert lichens reaching a maximum where thalli are frequently exposed to sand blast (Kappen 1988). Fifth, some taxa, e.g. species of *Buellia*, may exhibit an 'inversion' of thallus structure in which the sensitive algal layer is located towards the base of the lichen rather than near its surface, an adaptive response to high light intensity (Broady 1986).

A number of physiological adaptations have been observed in desert lichens. Hence, in *Chondropsis semiviridis* (F. Muell. Ex. Nyl.) Nyl., growing in South Australia, the optimum temperature for nPS is approximately 30 °C, one of the highest recorded in lichens, indicating a specific adaptation of the algal partner (Rogers 1971). In the Sonoran Desert in North America, temperature optima for nPS are significantly lower, and there are adaptations to the cooler dimmer conditions characteristic of winter rain periods in this region (Nash et al. 1982a, b). Cyanolichens in the Judean Desert and Arava valley occur exclusively in rain tracks as they cannot utilize water vapour for photosynthesis (Llimona 1982). By contrast, *Ramalina maciformis* (Delise) Bory can use water vapour in the Negev desert very efficiently, nPS being recorded at very low water potentials (Lang and Bertsch 1965). Many lichens can use atmospheric water vapour (Lange and Kilian 1985), and hence, some desert lichens take advantage of occasional periods of fog (Kappen 1988). Such lichens often have a large surface area to trap moisture and hence have a fruticose, pendulous, or tufted growth form. Such adaptation is also seen in some essentially crustose species, e.g. *Caloplaca coralloides* (Tuck.) Hulting, which adapt a pulvinate, branched, or coralloid form.

Some desert lichens exhibit changes in ecological behaviour in response to the extreme conditions. Hence, in the Negev desert, thalli frequently occur on northerly exposed rocks or at more shaded sites, while in the Namib, south-westerly exposed sites are favoured or sites located under translucent rocks (Vogel 1955). In addition, in the Negev, a differential distribution with reference to small pebbles has been observed with different taxa present either at the top or sides of the stones (Kidron 2002). The top of the pebbles receive twice the average daily dew compared with

their margins, but there is greater moisture at the margin after rain as a result of capillary action in soil adjacent to the pebble. In the driest parts of the Atacama Desert in Chile, weakly welded rhyolitic ignimbrite is frequently colonized by lichens that grow within the rock ('endolithic lichens'), the porous interior of the rock which, as well as encouraging hydration, also protects the thalli from damaging UV radiation and excessive levels of visible light (Wierzchos et al. 2013). In addition, the endolithic species *Verrucaria rubrocincta* Breuss inhabits the 'caliche plates', resulting from subsurface precipitates dominated by calcite, exposed on the surface of the Sonoran Desert where temperatures may exceed 60 °C in summer and fall to 0 °C in winter (Garvie et al. 2008). An upper micrite layer within the rock is highly reflective, thereby reducing light intensity levels experienced by the alga.

1.3.3   The Arctic

The Arctic is characterized by low average heat input, a long severe winter with temperatures usually less than −40 °C, and a short growing season of less than 60 days (Odum 1971). The soil remains frozen except for the upper few inches in summer months, the predominantly frozen deeper layers known as 'permafrost'. Over most of the region, the vegetation is essentially a wet grassland composed of lichens, grasses, sedges, and dwarf shrubs. In addition, there is a gradient from tundra through Arctic 'desert' to regions with permanent ice. The vegetation is often divided into two zones: (1) low Arctic composed of a thick spongy mat of living, non-decomposed vegetation often saturated with water and associated with scattered often frozen ponds and (2) high Arctic which may be completely bare apart from rare patches of lichens and grasses (Odum 1971). A relatively new stress factor for Arctic lichens is climate change which can cause acute but short-lasting winter warming periods (Bjerke et al. 2011).

Arctic lichens face many stress factors and morphological adaptation may be in response to high radiation, low temperature, short periods when metabolic activity is possible, drought or wetness, long-lasting snow cover, and the erosive action of wind (Kappen 1988). Most species are crustose or fruticose, and there is considerable morphological variation. Hence, in *Cladonia uncialis* (L.) Web., variations in morphology occur along a gradient from Southern Finland into the Arctic with the ratio of length to thickness of internodes and area of algal cell layer being at their lowest but relative percentage of pycnidia and perforate axils highest in the Arctic (Kärenlampi and Pelkonen 1971). Microtopography can also have a significant effect with degree of slope as an important factor (Link and Nash 1984), and many species are finding shelter against the cooling of the wind in small depressions. Some of these species are darkly pigmented, an adaptation to absorb heat and therefore to increase availability of water by melting snow more rapidly (Nordhagen 1928). By contrast, lichens in deeper depressions are light coloured often 'greenish', which may be an adaptation to lower light conditions under snow. The Arctic can be strongly heated in summer but subject to slower rates of evaporation. Hence, widely distributed taxa such as *R. geographicum* (Armstrong 2013) may change

their ecological behaviour, being characteristic of well-lit southern-facing surfaces in temperate regions (Armstrong 2002) but north-facing rocks in the Arctic (Pitman 1973). In addition, fruticose lichens often occur in dense light-coloured mats which dissipate solar radiation and cause cooler soil surface temperatures, thus conserving moisture (Kershaw 1978).

Arctic lichens exhibit a variety of physiological adaptations to take advantage of short, favourable environmental events after being dormant for long periods (Kappen 1988). Hence, the growth of the fruticose species *Cetrariella delisei* (Bory ex Schaer.) Kärnefelt and A. Thell. was measured in the high Arctic (Uchida et al. 2006). Positive nPS was recorded when thallus water contents were high, photosynthetic rates being lower on clearer days due to lower thallus water content. Most Arctic species are tolerant of freezing with many taxa exhibiting CO_2 uptake (Kallio and Heinonen 1971) and recovery of photosynthesis and respiration after storage at low temperatures (Lange 1966). Soluble carbohydrates in cryptograms are often highest in spring and summer especially trehalose, a non-reducing disaccharide which accumulates as a result of heat, cold, or osmotic stress (Avonce et al. 2006) and which may be involved in acclimation to low temperature and partial dehydration (Monteil 2000; Armstrong and Smith 2009). Hence, trehalose is present at higher concentration in the more vulnerable marginal prothallus of *R. geographicum* compared with the central areolae (Armstrong and Smith 2009).

Arctic species subjected to higher light conditions often exhibit the same strategies as more temperate species, i.e. they show high efficiency of nPS in winter. Nevertheless, availability of nitrogen may be an important limiting factor for Arctic lichens and in other cold temperature regions (Bliss 1962; Russel 1940; Haag 1974). Lichens capable of fixing nitrogen are particularly common in the polar regions either being cyanophilous or possessing cephalodia as in species of *Peltigera*, *Nephroma*, *Solorina*, and *Stereocaulon*.

1.3.4   Alpine Regions

The challenges posed by an alpine environment are generally similar to those of the Arctic (Billings and Mooney 1968; Billings 1973; Bliss 1962). However, the growing season is longer, i.e. up to 7 months below 3000 m at favourable sites and up to 2 months at higher latitudes. On clear days, alpine environments are characterized by alternating high temperatures and frost (Kershaw 1983). In addition, there is a significant difference in day length with greater angles of the sun and of both long-wave and global radiation (Thomson 1982). Diurnal temperature changes are generally more extreme in alpine environments, and differences with the Arctic increase significantly with decreasing latitude (Bliss 1956; Vareschi 1956).

An advantage of mountainous environments is the ability to investigate the influence of environmental gradients with increasing altitude. Nevertheless, here have been relatively few such studies involving lichens. The lichen flora of Nepal between altitudes of 200 and 7400 m was studied by Baniya et al. (2010) who found the highest richness of species at 3100–3400 and 4000–4100 m. Crustose lichens reached a

peak of species richness at higher altitudes, viz. 4100–4200. By contrast, Pinokiyo et al. (2008) found that in Northeast India, medium altitudes had the greatest diversity of taxa. More specifically, Fahselt (1998) found that *Rhizocarpon superficiale* (Schaerer) Vainio and *Lecidea tessellata* Flörke occurred at different elevations in Canada, with apothecia production being significantly lower at higher altitudes where growth conditions were more limiting. Altitude could limit the variety of algal partners available to the fungal partner and therefore could influence a wide variety of different lichens (Piercey-Normore and Dediche 2011).

Lichens may exhibit several adaptations to the increasingly severe conditions experienced at high altitude. Hence, *Cetraria nivalis* (L.) Ach. accumulates the UV-absorbing phenolic usnic acid in the upper cortex at higher altitudes (Bjerke et al. 2002). In addition, lichens at high altitudes experience alternating periods of desiccation and hydration, and pools of polyols are likely to contribute to the protection of cellular constituents and the preservation of intracellular structures during desiccation (Aubert et al. 2007). Hence, high rates of nPS when wet at low temperatures help alpine lichens to take advantage of brief periods of hydration such as melting ice. In addition, in Chile, high altitude may change the haplotype of the algal partner compared with lower altitudes where there is higher water availability in the form of fog, condensation, and precipitation. In *Pseudevernia furfuracea* (L.) Zopf., changes in protein composition occur with altitude, with certain sizes of proteins increasing and others decreasing (Strobl et al. 1994). In addition, changes in fatty acid composition have been reported with decreasing levels of unsaturation with altitude possibly reflecting changes in cellular membrane composition (Piervittori et al. 1994).

A number of morphological changes in the crustose lichen *Rhizocarpon geographicum* (L.) DC. have been observed at sites on Mount Pilchuck, Washington State, USA (Fig. 1.4). At the highest sites, including the summit, there were fewer marginal areolae, a wider peripheral prothallus, smaller central areolae, less spacing between areolae, and more apothecia per central areole (RA Armstrong, unpublished data). Marginal areolae were either randomly distributed or clustered on the
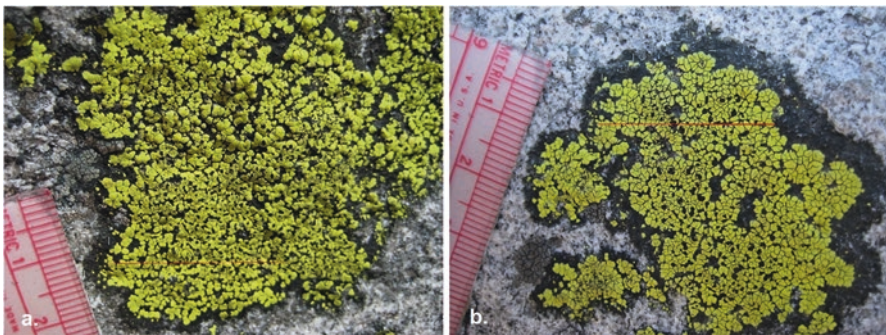
Fig. 1.4 Morphological changes in thalli of the crustose lichen *Rhizocarpon geographicum* (L.) DC. in response to altitude on Mount Pilchuck, Washington State: (**a**) lower altitude, (**b**) higher altitude

Fig. 1.5 The SO$_2$ pollution-tolerant lichen *Lecanora conizaeoides* Nyl. Ex Cromb., growing in Central Birmingham in 1976. In the 1960s and 1970s, this species was often the only lichen to be recorded consistently on trees in the centre of large cities in the UK. The surface of the thalli is 'super hydrophobic' but with breathable pores

marginal prothallus but with no clear relationship with altitude. Similarly, there was a more marked decline in the frequency of marginal areolae with size at the highest altitudes but with no simple relationship between the shape of the size distribution and altitude being log-normal at all sites. Hence, the exposure of a greater area of dark prothallus at the highest altitudes may be an adaptation to absorb heat and melt snow similar to that seen in some darkly pigmented Arctic species (Nordhagen 1928). The SO$_2$ pollution-tolerant lichen *Lecanora conizaeoides* Nyl. Ex Cromb. grows in Central Birmingham in 1976. In the 1960s and 1970s, this species was often the only lichen to be recorded consistently on trees in the centre of large cities in the UK. The surface of the thalli is 'super hydrophobic' but with breathable pores (Fig. 1.5).

1.3.5　Antarctica

Lichens are the dominant feature of the Antarctic continent and its adjacent islands (Llano 1965; Ahmadjian 1970; Longton 1979; Lindsay 1978; Smith 1984, 1995). Annual rainfall is not a limiting factor in the maritime Antarctic, but there is a marked moisture gradient from the coast to inland regions with degree of salinity, nutrient availability, oxygenation, and ice cover as additional variables (Convey et al. 2014). Drifting snow can also be important in part of the region, but snowfall is rare in the south of the Antarctic circle resulting in a 'polar desert' (Smiley and Zumberge 1971). Consequently, there is a decline in species diversity, coverage, and

growth rates from the maritime Antarctic to the continental dry valleys (Raggio et al. 2016) with water availability and length of the growing period as the most likely determining factors.

Adaptations of Antarctic lichens are often similar to those seen in arctic and alpine species (Ahmadjian 1970). Hence, Schroeter and Scheidegger (1995) examined the effects of extreme cooling in water-saturated thalli of *Umbilicaria aprina* Nyl. from the continental Antarctic. When thalli were slowly cooled to subzero temperatures, ice nucleation occurred at −5.4 °C followed by extracellular freezing leading to cytorrhysis in algal cells and vacuolation in fungi hyphae, changes which were reversible on warming. Reproduction in Antarctic lichens is often via vegetative diaspores such as soredia rather than lichenization, and early development is very slow (Ott 2004). Cortical thickening occurs commonly with the addition of 'dead' layers of hyphae and structures to ensure strong fixation to the ground to withstand wind (Dodge 1973). There is a dominance of crustose species but fruticose lichens also occur, being stunted in form compared with their temperate relatives (Dodge 1973). Some crustose species also develop a 'stipitate' or 'pulvinate' type of growth, which may be an adaptation to the higher humidity as a result of fog in maritime regions (Kappen 1988). In addition, Antarctic species of *Usnea* usually grow vertically on rocks, but there are also relatively unattached prostrate forms which may result from competition with rapidly growing bryophytes (Kappen 1985). As in the Arctic, many of the continental species are darkly pigmented, while yellow to green thalli often predominate in cracks and fissures (Hertel 1984).

The endolithic growth form found in deserts also occurs in Antarctica, with *Lecidea phillipsiana* Filson being a common species in the east of the region (Friedmann 1977). Three types of endolithic organisms have been described from Antarctica: (1) 'chasmoendoliths' which occupy fissures and cracks in rocks but the organism may be partially exposed on the surface, (2) 'cryptoendoliths' which occupy pores and pre-existing structural cavities, and (3) 'euendoliths' that bore into relatively soluble rock substrates such as those rich in carbonate (Lawrey 1984). The dominant flora of the dry valleys is often chasmoendolithic and cryptoendolithic lichens which occupy a narrow zone of the subsurface of the rock 10 mm thick and form colonies from a few cm to a metre in diameter (Friedmann 1982). The lichens exhibit a similar structure to those that live on the surface, but a true fungal zone is absent, with instead the fungal hyphae filling the available pore space. In cross section of a typical rock, there is a black zone just below the surface containing the alga *Trebouxia* and below that a white zone of fungal tissue, a green layer of non-lichenised green algae, and finally, in some species, a layer of cyanobacteria. The subsurface layers are often solubilized by fungal hyphae resulting in the upper surface peeling away to expose the lichen tissue. Further penetration of the rock results in more rock layers being lost, and the consequence of this 'biogenic weathering' is a characteristic pockmarked surface.

The physiological adaptations of Antarctic lichens are variable depending on location (Kappen 1988). Contrary to the maritime Antarctic, snow-covered regions often retain the severe cold of winter for long periods preventing any early warming (Pannewitz et al. 2003). Hence, the lichens are at subzero temperatures for a

prolonged period, and major activity occurs only when snow finally disappears. However, CO_2 gas exchange experiments suggest that nPS and dark respiration can occur at subzero temperatures in continental Antarctica (Schroeter and Scheidegger 1995). Nevertheless, there is a substantial decline in growth rates from the warmer, wetter peninsula to the colder dry valleys (Sancho et al. 2007) with higher photosynthetic rates and a wider temperature range of response than their counterparts on the continent. An extremely low nPS rate is particularly characteristic of endolithic species in the dry valleys. In studies of species of *Umbilicaria* and *Caloplaca*, there is a considerable difference in duration of activity in relation to microclimate, as measured by chlorophyll 'a' fluorescence, between the maritime regions and dry valleys, with *Caloplaca* species in particular exhibiting strategies to improve thallus hydration (Raggio et al. 2016). Successful adaptation of lichens to continental Antarctic conditions also involves the algal partner as a result of the strong adverse effects of radiation on nPS (Cao et al. 2015). Hence, no photoinhibition was observed in entire thalli of *Umbilicaria decussata* (Vill.) Zahlbr., when the photoprotective pigment melanin was present (Sadowsky and Ott 2016). In addition, the effect of high light exposure was studied on *Umbilicaria antarctica* E. Frey and M. Lamb, causing increased levels of oxidized glutathione and the conversion of violaxanthin to zeaxanthin, both of which are involved in antioxidant resistance (Bartak et al. 2004).

1.3.6 Chemically Rich Environments

Lichens are characteristic of several chemically rich environments including highly eutrophicated sites and those influenced by salinity, pollution, and heavy metals. As many species are unable to grow successfully in these conditions, they can also be regarded as extreme environments for lichens.

Several studies suggest that the degree of nutrient enrichment of a substratum, especially by birds, has a significant influence on lichens (Hale 1967). Bird droppings can influence lichens by smothering the thalli, altering the pH, or adding inhibitory and stimulatory compounds (Armstrong 1984). Hence, experiments in which droppings from a variety of birds were applied as a thick paste or as a suspension in deionized water had differential effects on species of foliose lichens (Armstrong 1984), e.g. increasing the radial growth of *X. conspersa*, a species common on well-lit nutrient-enriched rocks, but inhibiting the growth of *Parmelia saxatilis* (L.) Ach., a species relatively rare on bird perching stones. Uric acid, the most abundant nitrogenous component of bird droppings, did not influence growth when applied as a suspension to either species (Armstrong 1984). Hence, tolerance of a lichen to these conditions may depend on the ability to adapt to either the increased pH or excess inorganic chemical ions in the bird droppings.

Chemical factors may also be important in influencing lichens on maritime rocks where a distinct zonation is often present (Fletcher 1976). Ramkaer (1978) found that the response of four different lichen fungi to salinity correlated well with their zonation on maritime rocks. In addition, some coastal lichens can use hygroscopic salt films to condense liquid water out of humid air when dew-point conditions are

not reached (Folmann 1967; Rundel 1978). Calcium has also been shown to be an important ion in these environments (Fletcher 1976). Hence, thalli of *X. parietina*, a common species of the submesic zone of the supralittoral (Fletcher 1976) and many nutrient-enriched sites inland (Brodo 1973), degenerate when transplanted to nutrient-poor inland sites (Armstrong 1990b). Transplanted thalli, however, grow successfully inland when supplied with calcium carbonate added as a paste to the thalli at intervals over a year. Adaptation to a relatively constant supply of calcium may therefore be necessary for this species. This hypothesis is also supported by experiments showing that *X. parietina* thalli lose potassium ions when treated with distilled water or a saline solution (Matos et al. 2011), and an application of a 0.250 mM solution of calcium to the medium prevents this loss in the light (Fletcher 1976; Beckett 1996). The maritime environment may also influence lichens some distance from the sea. Hence, in *Ramalina canariensis* J Steiner, there is a logarithmic decrease in extracellular ions including chloride, sodium, and magnesium with distance from the coast (Figueira et al. 1999). The intracellular fraction of these ions was relatively independent of the surface and wall-bound fractions reflecting physiological control by the organism and a likely adaptive mechanism in coastal environments (Figueira et al. 1999). In addition, many coastal lichens can maintain nPS at very low water potentials when moistened by salt spray (Rundel 1988).

Despite the reinvasion of many urban sites by lichens in the last 20 years, sites subject to SO_2 air pollution have significantly lower lichen diversity than rural sites, a testament to the powerful effect of air pollution on growth. In addition, SO_2-tolerant species such as *Lecanora conizaeoides* Nyl. Ex Cromb. have declined in the UK since the 1960s as a result of the reduction in pollution over this period (Massara et al. 2009). Lichens exhibited several adaptations to these conditions. First, surface hydrophobicity is a feature of lichens tolerant to SO_2 (Hauk et al. 2008), and *L. conizaeoides* appears to be 'superhydrophobic' as a result of the presence of hydrophobic compounds and a rougher thallus surface which sheds water (Shirtcliffe et al. 2006). Gas channels are also present to allow photosynthesis resulting in essentially a 'breathable' surface (Shirtcliffe et al. 2006). Second, fluctuations in stress ethylene concentration have been observed in some lichens including *Hypogymnia physodes* (l.) Nyl., when exposed to sulphur at low pH, a response which correlates with their degree of tolerance (Garty et al. 1995). Third, the presence of secondary lichen substances such as fumarprotocetraric acid may be associated with tolerance to acidic air pollution (Hauck et al. 2009).

Lichens may accumulate heavy metals under various conditions including from metal-enriched rocks, industrially polluted sites, and near metallurgic plants and waste dumps. There are three heavy metal uptake mechanisms in lichens: (1) extracellular via ion exchange, (2) intracellular accumulation, or (3) trapping metal-rich particles (Richardson 1995). Metal accumulation is often selective with lichens preferentially accumulating zinc at various sites (Glenn et al. 1991, 1995). Uptake via ion exchange is assumed to occur at anionic sites in association with the surface of cell walls (Puckett et al. 1973). Hence, potentially toxic metals taken up by this mechanism may not influence lichen metabolism as they may not enter fungal or algal cells. Nevertheless, metals may be capable of penetrating cells and accumulating to toxic