1 Introduction

Lichens are composite organisms comprised of a fungus and one or more algae living together in symbiotic association in which the algal partner produces essential nutrients for the fungal partner through photosynthesis, while the fungal partner provides mechanical support to the algal partner. Development and establishment of lichen on a substratum is achieved by fruiting bodies (apothecia) produced by the fungal partner, which must germinate and find an algal partner before they can form a new lichen thallus or may produce minute fragments (as finger-like outgrowths, isidia or sugar-like granules, soredia) containing both partners, which can disperse quickly and colonise available habitats.

Being pioneers on rock surface lichens are important component of the ecosystem that establishes life on rock and barren disturbed sites. As lichens colonise rocks, they trap dust, silt and water which leads to biogeophysical and biogeochemical weathering of the rock surface leading to soil formation.

Lichens occur in all available substrata and in all possible climatic conditions, but the lichen diversity of an area of interest or substratum is highly dependent on prevalent microclimatic conditions. Apart from morphology and anatomy of lichens, the high success of lichens in extreme climates has been attributed to the secondary metabolites produced by the fungal partner to protect the algal partner.

This chapter discusses the unique characteristics about lichens which facilitate their survival in extreme climates and makes them an ideal organism for ecosystem monitoring.

1.1 Introduction

The word lichen has a Greek origin, which denotes the superficial growth on the bark of tree, rock as well as soil. Theophrastus, the father of botany, introduced the term 'lichen' and this group of plants to the world. Lichen species collectively called as 'stone flower' in English, 'Patthar ka phool' in Hindi, 'Dagad phool' in Marathi, 'Kalachu' in Karnataka, 'Kalpasi' in Tamil, 'Richamkamari' in Urdu and 'Shilapushpa' in Sanskrit.

Lichen is a stable self-supporting association of a mycobiont (fungus) and a photobiont (alga) in which the mycobiont is the exhabitat (Hawksworth 1988). The plant body of lichen is called 'thallus', and it had been considered a single plant till 1867 when Schwendener (Swiss botanist) demonstrated the lichen thallus to be a composite body made up of fungus and an alga, and he propounded his well-known dual hypothesis for this body. This view was not accepted by the prominent lichenologist of the time, but later the composite nature of lichen thallus was universally accepted, and the two components were considered to be in a symbiotic association. The mycobiont predominates and the gross morphology of lichen thallus is generally determined by mass, nature and modifications of the fungal hyphae. The photobiont (Fig. 1.1), on the other

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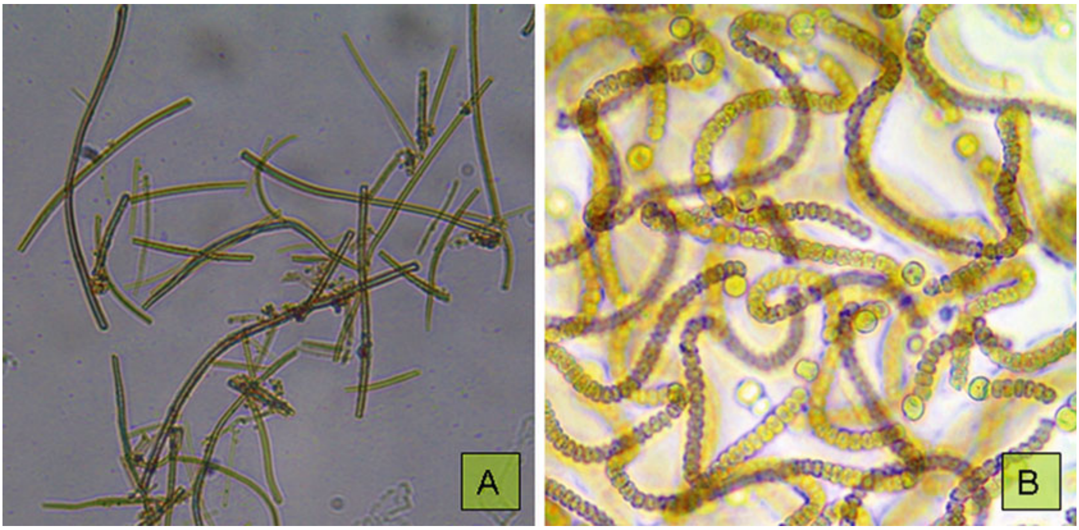

Fig. 1.1 Common photobionts which facilitate lichenisation with compatible fungal partner resulting in formation of lichen thallus. (**a**) *Trentepohlia* and (**b**) *Nostoc*

hand, also plays an important role in the development of the thallus. The resultant thallus is unlike the two symbionts in morphological appearance and physiologically behaving as a single autonomous biological unit (Awasthi 2000). About 85 % of lichens have green algae as symbionts, approximately 10 % have blue-green algae and/or cyanobacteria, and less than 5 % of lichens have both green algae as primary symbionts and blue-green algae as secondary symbionts. The lichen fungus is typically a member of the Ascomycota or rarely Basidiomycota and hence termed as ascolichens and basidiolichens, respectively. The hyphae of mycobiont are septate, branched and thin or thick walled and possess either a single or three septate through which the cytoplasmic contents of the adjoining cells are connected by plasmodesmata; rarely, the septum may be multiperforate (Honegger 2008).

Repeated septation, branching and different degree of compactness, coalescence or conglutination result in the formation of diverse type of tissue. The development of such tissues is also necessary for a durable and proper functioning of the symbiotic relationship in a lichen thallus. It is necessary that the photobiont, which is basically and essentially aquatic in nature, remains protected from desiccation in a lichenised terrestrial condition.

Most of the cyanobacterial photobiont possess a mucilaginous sheath, which protects them from desiccation to some extent, but no such protective sheath is present in the green-algal photobiont, which predominate in lichen taxa. The protection, however, is provided by the mycobiont through the development of specialised hyphal tissues in the form of a cortex over the stratum of the photobiont (Ahmadjian 1993).

Lichens have a poikilohydric nature to survive in various climatic conditions as they have no mechanism to prevent desiccation; they desiccate and remain dormant when their environment dries out but can rehydrate when water becomes available again. Lichens usually absorb water directly through their body surface by aerosol, mist and water vapours; due to this nature, lichens live long in dry areas even on stones and rocks used for construction of monuments and other building artefacts.

The role of alga in lichen partnership is that of producing food for themselves and their partner, the fungus. The fungus (mycobiont) in a lichen partnership cannot live independently. The fungus partner is able to obtain and hold water, which is essential for alga. The mycobiont attached firmly to the algal cell (photobiont) cannot be easily washed away by water or blown by wind. Due to this type of relationship, lichens are eminently successful and enjoy worldwide distribution and occur in every conceivable habitat, growing on a variety of substrata, including most natural substrata as well a host of human-manipulated or manufactured substrata. The common natural substrata on which lichens can colonise and grow successfully include all categories of rock (saxicolous), trees (corticolous), soil (terricolous) wood (lignicolous) and leaves (foliicolous), while man-made substrata include rubber, plastic, glass, stonework, concrete, plaster, ceramic, tiles and brick.

1.2 About Lichens

Lichens are perennial plants with very slow growth rate which is mainly attributed to the growth of the mycobiont. There is no supply of nutrients from the central part to the growing part, and the food produced by the photobiont at the growth site is used by the mycobiont. The pattern of growth in general is centrifugal, apical and marginal. In crustose and foliose lichen radical growth occurs, while in fruticose lichens there is an increase in length. The annual radial increase has been found to be 0.2–1.0 mm in crustose and 1.0–2.5 mm in foliose, while in fruticose lichens 2.0–6.0 mm growth can be seen in a year (Awasthi 2000).

1.2.1 Thallus Morphology and Anatomy

Growth forms (Fig. 1.2) are categorised mainly on the basis of morphology without direct reference to ecological adaptations, yet distribution of growth form primarily reflects competition and adaptation to abiotic environmental conditions, mainly water relations (frequency and intensity of periods of water shortage). Based on the external morphology (growth form), lichen thalli exhibit three major growth forms: crustose, foliose and fruticose. Crustose lichens are tightly attached to the substrate with their lower surface, which cannot be removed without destruction. Water loss is restricted primarily to the upper, exposed surface only. Crustose lichens may be subdivided as leprose, endolithic, endophloeodic, squamulose, peltate, pulvinate, lobate, effigurate and suffruticose crusts. Majority of crustose lichens grows directly on the surface of the substrate and is referred to as episubstratic, while a small minority grows inside the substratum called endosubstratic. The episubstratic thallus consists of a crust-like growth adherent or attached to the substratum throughout its underside by hyphae and cannot be detached without destruction (Büdel and Scheidegger 2008).

The leprose thallus is effuse and consists of a thin layer of uniformly and loosely disposed photobiont cells intermixed with hyphae forming a yellow, greyish-white or reddish powdery mass on the surface of the substratum. In terms of complexity, the powdery crust, as found in lichen genus *Lepraria*, is the simplest and lacks an organised thalline structure. Algal structure is embedded in the loose fungal hyphae, having no distinct fungal or algal layer.

Endolithic (growing inside the rock) and endophloeodic (growing underneath the cuticle of leaves or stems) are more organised as compared to leprose lichens. In most cases, an upper cortex is developed. The upper cortex can consist of densely conglutinated hyphae forming a dense layer named 'lithocortex' as seen in *Verrucaria* species.

In some crustose lichens as in genus *Rhizocarpon*, there is a prothallus which is a photobiont-free, white or dark brown to black zone, visible between the areolate and at the growing margins of the thallus.

A thallus is effigurate when the marginal lobes are prolonged and are radially arranged, as in genus *Caloplaca*, *Dimelaena* and *Acarospora*.

The squamulose thallus is an intermediate form between crustose and foliose forms. It generally has rounded to oblong minute lobules or squamules distinct from each other as they develop individually. The squamules are dorsiventral, attached to the substratum along an edge or by rhizoidal hyphae from the lower surface as in genera *Peltula*, *Psora* and *Toninia*. The flat scaled squamulose thalli, with more or less central attachment area on the lower surface, are called peltate as in *Peltula euploca*. Extremely inflated squamules in the lichen genus *Mobergia* are called bullate, while in some genera coralloid

Fig. 1.2 External morphology of the lichen thallus can be categorised into (**a**) fruticose, (**b**) foliose, (**c**) crustose and (**d**) dimorphic growth forms

tufted cushions termed as subfruticose are formed. In some species of *Caloplaca* and *Lecanora*, a thallus becomes radially striated with marginal partially raised lobes termed as lobate thallus.

The foliose or leafy thallus of lichens is typically flattened, dorsiventral, spreading and expanding horizontally outwards and usually attached to the substratum by rhizines arising from the lower surface. Foliose lichens develop a great range of thallus size and diversity.

Lacinate lichens are typical foliose lichens. They are lobate and vary considerably in size, which may be gelatinous–homoiomerous (e.g. *Collema*, *Leptogium*) or heteromerous. The lobes may be radially arranged (*Parmelia*) or overlapping like tiles on a roof (*Peltigera*). Sometimes thallus lobes can become inflated, having a hollow medullary centre (*Menegazzia* species). These foliose lichens are cosmopolitan in distribution.

Umbilicate foliose lichens have circular thalli, consisting either of one single, unbranched lobe or multilobate thalli with limited branching patterns, attached to the substrate by a central umbilicus from lower surface.

An ecologically interesting group of foliose lichens are vagrant lichens such as *Xanthomaculina convolute*, which do not remain adhered to the substratum and have hygroscopic movement.

In dry conditions, the thalli roll up and expose lower cortices. When they take up water, thalli unroll and expose their upper surface to the sunlight. In rolled condition they can be blown with the wind to longer distances.

Fruticose type of lichen is either erect or pendent shrubby growth attached to the substratum at the base by basal disc or holdfast (formed by mycobiont hyphae). Some groups have dorsiventrally arranged thalli (*Sphaerophorus melanocarpus*, *Evernia prunastri*) but majority possess radial symmetric thalli (*Usnea* species and *Ramalina* species).

Genera like *Baeomyces* or *Cladonia* develop a twofold, dimorphic thallus that is differentiated into a fruticose thallus verticalis and a crustose–squamulose to foliose thallus horizontalis.

Another peculiar type of anatomy is that of the thread-like growing genus *Usnea*; *Usnea longissima* is the world's longest lichen, which has a strong central strand of periclinally arranged, conglutinated hyphae that provide mechanical strength along the longitudinal axis.

Highly branched fruticose lichens have a high surface to volume ratio that results in more rapid drying and wetting pattern compared with lichens having lower surface to volume ratio. This phenomenon seems to be the main reason for attributing high sensitivity to this class of lichens towards slight change in the microenvironment. Fruticose growth forms can preferentially occur either in very wet, humid climates and in the dry urban climates its distribution is restricted.

Among the different growth forms of lichens in the evolutionary series, leprose are considered pioneers followed by crustose, placodioid, squamulose and foliose, dimorphic and fruticose being the latest. Leprose, crustose, some placodioid and squamulose lichens are called microlichens as they are smaller in size and mostly require a compound microscope for identification. Foliose, fruticose and dimorphic lichens on the other hand are called macrolichens. Macrolichens have a comparatively larger thallus and a hand lens and stereozoom microscope are sufficient for identification.

1.2.2 Anatomical Organisation of Algal and Hyphal Layer

1.2.2.1 Homoiomerous and Heteromerous (Stratified) Thallus

In homoiomerous thalli mycobiont and photobiont are evenly distributed, while in majority of lichens including many crustose species, internally stratified (heteromerous) thalli are found. The main subdivisions are into upper cortex, photobiont layer, medulla and lower cortex. These layers may include various tissue types, and their terminology follows the general mycological literature. Pseudoparenchymatous and/or prosoplectenchymatous tissue types are present where hyphae are conglutinated to the extent that single hyphae are indistinguishable.

1.2.2.2 Cortex, Epicortex and Epinecral Layer

In most of the lichens, the algal layer is covered by a cortical layer ranging from a few microns to several hundred microns. In many dark lichens, pigmentation (which is due to secondary metabolites' UV protective nature) is confined to fungal cell walls of cortical hyphae (Esslinger 1977; Timdal 1991) or the epinecral layer. In gelatinous lichens the secondary metabolites are primarily confined to the outer wall layers of the mycobiont (Büdel 1990). Pseudoparenchymatous or a prosoplectenchymatous fungal tissue mainly forms the cortex in foliose and fruticose lichens. Usually living or dead photobiont cells are completely excluded from the cortex, but in the so-called phenocortex collapsed photobiont cells are included (e.g. *Lecanora muralis*). In Parmeliaceae some species have a 0.6–1 mm thick epicortex, which is a noncellular layer secreted by the cortical hyphae. This epicortex can have pores, as in *Parmelina*, or have no pores, as in *Cetraria*. In a broad range of foliose to crustose lichens, an epinecral layer of variable thickness is often developed which is composed of dead, collapsed and often gelatinised hyphae and photobiont cells. Thalli often have a whitish, flour-like surface covering, the so-called pruina that consists primarily of superficial deposits, of which calcium oxalate is the most common as in *Dirinaria applanata*. The amount of calcium oxalate is probably dependent on ecological parameters, such as calcium content of the substrate and the aridity of the microhabitat (Syers et al. 1964).

Functions of the upper cortex and/or its pruina include mechanical protection, modification of energy budgets, antiherbivore defence and protection of the photobiont against excessive light (Büdel 1987). Light- and shade-adapted thalli of several species differ considerably in the anatomical organisation of their upper cortical strata (e.g. *Peltigera rufescens*). In a nearby fully sun-exposed habitat, the thickness of the cortex is reduced, but a thick, epinecral layer with numerous air spaces is formed giving the thallus a greyish-white surface due to a high percentage of light reflection (Dietz et al. 2000). This cortical organisation results in decreased transmission of incident light by 40 % in the sun-adapted thallus measured at the upper boundary of the algal layer. Epinecral layers of *Peltula* species are also known to contain airspaces that may also act as CO_2 diffusion paths under supersaturated conditions (Büdel and Lange 1991).

1.2.2.3 Photobiont Layer and Medulla

In most foliose and fruticose thalli, the medullary layer occupies the major part of the internal thalline volume. Usually it consists of long-celled, loosely interwoven hyphae forming a cottony layer with high intercellular spaces. The upper part of the medulla forms the photobiont layer. In many lichens, the hyphae of the photobiont layer are anticlinally arranged and may sometimes form short or globose cells. The hyphal cell walls of the algal and medullary layer are often encrusted with crystalline secondary products which make medullary hyphae hydrophobic (Honegger 1991).

1.2.2.4 Lower Cortex

In some foliose lichens such as *Heterodermia*, the medulla directly forms the outer, lower layer of the thallus. However, typical foliose lichens of the Parmeliaceae and many other groups have a well-developed lower cortex. As is the case with the upper cortex, it is either formed by pseudoparenchymatous or a prosoplectenchymatous tissue. But unlike the upper cortex, the lower cortex is often strongly pigmented. Its ability to absorb water directly is well documented. Only low water conductance has been found thus far. However, it may play a major role in retaining extrathalline, capillary water (Jahns 1984).

1.2.2.5 Attachment Organs and Appendages

In order to provide strong hold of the substratum for lichenisation, lichen develops a variety of attachment organs from the lower cortex and also occasionally from the thallus margin or the upper cortex to establish tight contacts to the substrate.

In foliose lichens attachment is mainly by simple to richly branched rhizines, mostly consisting of strongly conglutinated prosoplectenchymatous hyphae. Umbilicate lichens as well as *Usnea* and similarly structured fruticose lichens are attached to the substrate with a holdfast, from which hyphae may slightly penetrate into the substrate. Deeply penetrating rhizine strands are found in some squamulose, crustose or fruticose lichens growing in rock fissures, over loose sand.

In crustose lichens a prosoplectenchymatous prothallus is often formed around and below the lichenised thallus. It establishes contact with the substrate from where bundles of hyphae penetrate among soil particles. Members of various growth forms produce a loose web of deeply penetrating hyphae, growing outwards from the noncorticate lower surface of the thalli.

Cilia are fibrillar outgrowths from the margins or from the upper surface of the thallus. A velvety tomentum consisting of densely arranged short, hair-like hyphae may be formed on the upper or lower cortex. Tomentose surfaces are mainly reported from broad-lobed genera such as *Pseudocyphellaria*, *Lobaria*, and *Sticta* and few *Peltigera* species.

1.2.2.6 Cyphellae and Pseudocyphellae

Upper or lower cortical layers often bear regularly arranged pores or cracks. Pseudocyphellae, as found on the upper cortex of *Parmelia sulcata* or on the lower side of *Pseudocyphellaria*, are pores through the cortex with loosely packed medullary hyphae occurring to the interior. Cyphellae are bigger and anatomically more complex than pseudocyphellae and are only known from the genus *Sticta*. In the interior portions of the cyphellae, hyphae form conglutinated, globular terminal cells, and this is the main difference from pseudocyphellae.

Pseudocyphellae and young cyphellae are the regions in the cortex having lower gas diffusion resistance. The pseudocyphellae and cyphellae are hydrophobic structures of lichens and may act as pathways for gas diffusion into thalli only when there is drying of the thallus (Lange et al. 1993).

1.2.2.7 Cephalodia (Photosymbiodemes)

Representatives of the foliose Peltigerales with green algae as the primary photobiont, and members of such genera as *Stereocaulon*, *Chaenotheca*, and *Placopsis* usually possess an additional cyanobacterial photobiont. In *Solorina*, the secondary photobiont may be formed as a second photobiont layer underneath the green-algal layer, but usually it is restricted to minute to several millimetres wide cephalodia. Cephalodial morphology is often characteristic on a species level and ranges from internal verrucae to external warty, globose, squamulose or shrubby structures on the upper or lower thallus surfaces. Cephalodial morphology usually differs completely from the green-algal thallus, and this emphasises the potential morphogenetical influence of the photobiont on the growth form of the mycobiont–photobiont association. Because many cyanobacterial photobionts are nitrogen-fixing, these lichens may considerably benefit from cephalodia, especially in extremely oligotrophic habitats.

1.2.2.8 Differentiating Lichens from Other Groups of Plants

Along with lichens, non-lichenised fungi, algae, moss, liverworts (bryophytes) are the plants which grow on rocks, bark and soil and may create confusion for beginners in the field. However, lichens can be easily be differentiated from these group of plants as lichens are never green as algae, liverworts and mosses. Foliose lichens growing in moist places or in wet condition may look greener but have thick, leathery thallus, while in contrast liverworts have non-leathery and slimy thallus. The dimorphic forms of lichens such as *Cladonia* may be confused with the leaf liverworts and mosses in the field. Leafy liverworts and mosses have dense small leaf-like structures throughout the central axis of the plant, while in the case of dimorphic lichens, the squamules of semicircular shape usually present at the base of the central axis or sparse throughout. Dried algal mat on rocks and bark may look like lichens, but it may be checked by spraying some water on these mats as upon hydration algae regain its colour and texture which may be distinguished clearly.

The non-lichenised fungi are the most confusing ones with crustose lichens in the field. Such fungus usually forms patches with loosely woven hyphae, while lichens form smooth, perfect thallus which can be distinguished under the microscope. The fungus are usually whitish in colour and lichens are usually greyish, off-white, but sometimes yellowish, yellowish-green or bright yellow or yellow-orange in colour which is attributed to the presence of lichen substances in the cortex of the thallus as in the case of *Xanthoria parietina* (orange) due to the presence of parietin. The greenish colour of the thallus is mainly due to the presence of algal cells in the thallus. The lichen thallus usually bears cup-shaped structures called apothecia or bulged, globular structures called perithecia. Some crustose lichens belonging to family Graphidaceae bear worm-like structures, lerielle, which are modified apothecia (Fig. 1.3). Asexually reproducing fruiting bodies present on the thallus surface may be finger-like projections called isidia or granular, powder-like structure called soredia (Fig. 1.4). While collecting lichens, it is necessary to look for such structures with the help of the hand lens. When a lichen thallus does not have any such structures, it makes it difficult to differentiate it from fungus.

In any case it is observed that a beginner usually collects fungus and other plants in place of lichens. Usually fungus of various colour (mostly appearing like mushrooms) are confused for lichens and collected by beginners. Such specimens can be identified by taking a thin section of the thallus and studying them under a

Fig. 1.3 Sexually reproducing fruiting bodies, (**a**) apothecia, (**b**) perithecia and (**c**) lerielle, which are exclusively produced by fungal partner

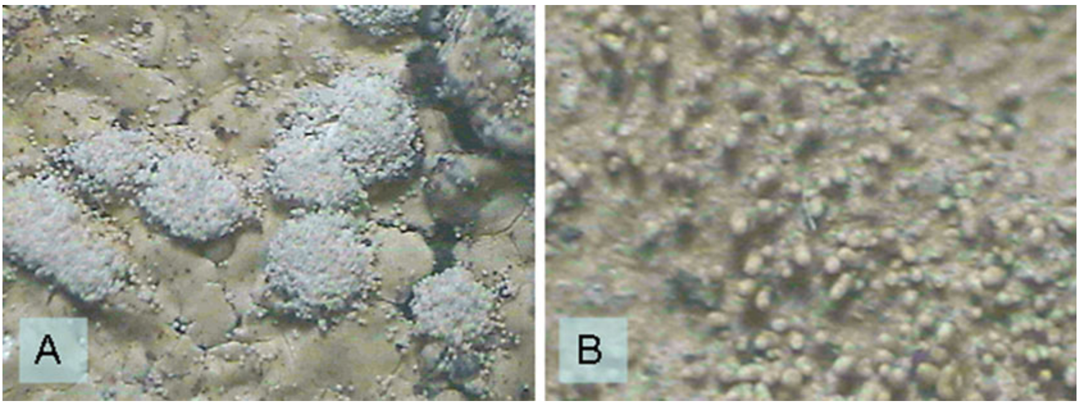

Fig. 1.4 Asexually reproducing bodies. (**a**) Soredia. (**b**) Isidia containing both fungal hyphae and algal cells

microscope. If the section contains both fungal tissue and algal cells, then the specimen is lichen; otherwise, it may be some other plant group. In India basidiolichens (looking like mushrooms) are rare or absent (Nayaka 2011).

1.3 Development and Establishment

Development and establishment of lichen thallus, termed as morphogenesis, involves the process of lichenisation (spore/propagule dispersal), acquisition of compatible partners, competition and growth of lichen thallus resulting in its establishment on the substratum.

Lichen-forming fungi express their symbiotic phenotype (produce thalli with species-specific features) only in association with a compatible photobiont. About 85 % of lichen mycobionts are symbiotic with green algae, about 10 % with cyanobacteria ('blue-green algae') and about 3–4 %, the so-called cephalodiate species, simultaneously with both green algae and cyanobacteria (Tschermak-Woess 1988; Peršoh 2004).

Majority of lichen-forming fungi reproduce sexually and thus have to re-establish the symbiotic state at each reproductive cycle. Compatible photobiont cells are not normally dispersed together with ascospores; exceptions are found in a few species of Verrucariales with hymenial photobionts (e.g. *Endocarpon pusillum*). Many tropical lichen-forming fungi associate with green-algal taxa that are widespread and common in the free-living state (e.g. *Cephaleuros*, *Phycopeltis*, *Trentepohlia*) (Honegger 2008).

1.3.1 Colonisation

The ability of lichens as primary colonisers on barren rock is evident by distribution of *Rhizocarpon geographicum* on rocks and moraines exposed by glacier retreat phenomenon and is used worldwide in lichenometric studies to study paleoclimatic condition. Resistance to drought condition and extreme temperatures and presence of lichen substances enable lichens to colonise on rock surface.

Colonisation on bark surface is governed by water relation, pH, light and nutrient status which determine lichen diversity on the bark surface, while on soil surface colonisation by lichens is limited by their poor competitive abilities compared to the higher plants, and because of their small structures, they are more prone to trampling and trekking activities. Most of the soil-inhabiting lichens fix atmospheric nitrogen like species of *Stereocaulon*, *Peltigera* and *Collema* due to the presence of cyanobacteria *Nostoc*. The ability to accumulate nutrients from rain or runoff (in which nutrients are present in small quantities) enables them to colonise on varied substratum (Brodo 1973).

1.3.2 Growth

Growth rate has a pronounced effect on colonisation and competitive ability of the new thalli resulting in establishment of the thalli. The balance between growth rate and reproductive activity varies with environmental changes (Seaward 1976). Growth varies over the geographical range of a species, and the size ratio of equal-aged thalli of two species may differ in different regions. Rainfall is important for many species as in *Xanthoria elegans* growth rate correlated linearly with the annual rainfall (Beschel 1961).

In species *Parmelia caperata* occurring in colder climate shows frost damage, while alternations in regimes of incident light and humidity are essential for growth of *Parmelia sulcata* and *Hypogymnia physodes*.

Nutrient enrichment also affects growth rate; moderate levels of nutrients are found to favour growth, while excessive levels of nutrients (pollutants) result in slow growth rate depending on the species.

Lichens colonising on non-vertical surfaces of the substratum show good growth rate in comparison to the vertical surfaced substratum, as non-vertical surface retains moisture content for longer periods of time.

Growth rate also depends on the age of the thalli. The life cycle of fruticose lichen *Cladonia* has been divided into three periods: generation, renovation and decline. In generation, phase growth is continuous (5–25 years); in the second podetia decay from below, while growth continues at the tips (80–100 years); and in the final period (20 years) decay predominates. But in the case of crustose lichen especially *Rhizocarpon geographicum*, growth rate is approximately constant with time and this feature is exploited in lichenometric studies. Growth rate affects biomass, i.e. productivity and carbon assimilation potential of the species (Seaward 1976).

1.3.3 Succession

Replacement of one growth form or community structure with another in the course of colonisation and establishment refers to succession. Succession, in general, begins with crustose continuing with foliose and concluding with fruticose. But in the case of epiphytic lichens, foliose lichens may colonise first on tree bases and on twigs (Kalgutkar and Bird 1969).

In successions on soil, colonising species vary; it has been observed that after forest fires *Lecidea* species colonises first; same is the case in the Arctic where *Stereocaulon*, *Cetraria* and *Peltigera* are primary successors. Many successions, especially in mesic or humid environments, do not involve lichens and in xeric environments, mosses compete with lichens by colonising on similar niches. In several studies conducted involving rock substratum like granite, rock ledges and sloping cliffs, mosses are found to be the primary coloniser (Topham 1977).

The prominent role of lichens in succession indicates their contribution to community structure. Lichens increase the intrabiotic fraction of inorganic nutrients, as corticolous species trap nutrients from the phorophytes and from rainwater, while saxicolous species mobilise and extract mineral nutrients from substrates, rainwater and airborne dust.

In the process of succession, lichen diversity increases as do the vascular plants. Species diversity is found to increase in early stages of succession until a closed community is formed (Degelius 1964).

Pioneer species in diverse habitat are morphologically adapted with reduced thalli and abundant production of small ascospores which are soon replaced by taller growing life-forms with larger reproductive bodies with spore, soredia, isidia, thalline lobule and fragments. In general as the community becomes closed and ecosystem more matured, diaspore size increases, few in number with longer time to reproduce.

Reindeer lichens and Lobarion lichens show the trend of increasing thallus size in climax communities. Thus, succession by lichens is highly influenced by generation time, diaspore size and thallus size, which ultimately decide its position in the developing ecosystem.

1.3.4 Competition

Being pioneers lichens usually lack competitive ability in comparison to other plants especially vascular plants. In the process of succession, an organism competes successfully with its immediate predecessors and succumbs to its immediate successor. In general crustose lichens are less competitive than foliose, which are less aggressive than fruticose ones (Brightman and Seaward 1977). Competitive ability corresponds to stages in succession.

Allelopathic nature of lichen substances also enables certain species to predominate in the area by the creation of an 'inhibition zone'. The 'inhibition zones' are zones of 1–5 cm where concentrations of lichen substances produced by lichens are maximum. This phenomenon is quite pronounced in *Rhizocarpon* species.

The study of competition is also closely linked to autecology of the individual species, since successful species in a competitive condition is usually best adapted to its environment (Topham 1977).

1.4 Role of Lichens in Biodeterioration and Soil Establishment

There is no distinct demarcation between the terms biodeterioration and soil formation (pedogenesis), and they may be treated as two distinct phases of a process in which primarily physical and chemical weathering results in loosening of rock and later 'windblown material' soil is formed (Joffe 1949). Biodeterioration (rock weathering) may be defined as any undesirable change in the properties of a material caused by vital activities of living organisms (Saiz-Jimenez 1995, 2001, 1994; Wilson et al. 1981). The development of specific biological species on a particular stone surface is determined by the nature and properties of the stone. Many building materials are prone to colonisation by living organisms. The invasion results in changes in colour and in the chemical or physical properties of the materials (Saiz-Jimenez 1981). In order to assess the impact of colonisation on the material, 'bioreceptivity' of the material is estimated. Bioreceptivity is defined as the overall properties of the material that contribute to the establishment, anchorage and development of flora and or fauna (Guillitte 1995). Other than bioreceptivity of the material, the response of living organisms to a potentially colonisable surface depends on the ecological and physiological requirements of the biological species involved (Fig. 1.5) (Caneva and Salvadori 1988; Seaward and Giacobini 1991). The predominant role of lichens as pedogenetic agent is also related to physical and chemical characteristics which makes them potential biodeteriorating agents. Pedogenesis (soil formation) is thus defined as the transformation of rock material into soil. Linnaeus in 1762 first discussed the ability of crustose lichens to colonise on unweathered rocks and its role in soil formation and plant succession (Bajpai 2009).

1.4.1 Biodeterioration (Rock Weathering)

Lichens are known to occur on various substrates including rocks, which is mainly due to their resistance to desiccation in extreme temperature and efficiency in accumulating nutrients (Martin 1985; Chaffer 1972; Seaward 1979, 1988). Anchoring structures present in lichens which facilitate attachment to the rock substrate are rhizoids and hyphae (Chen et al. 2000). The

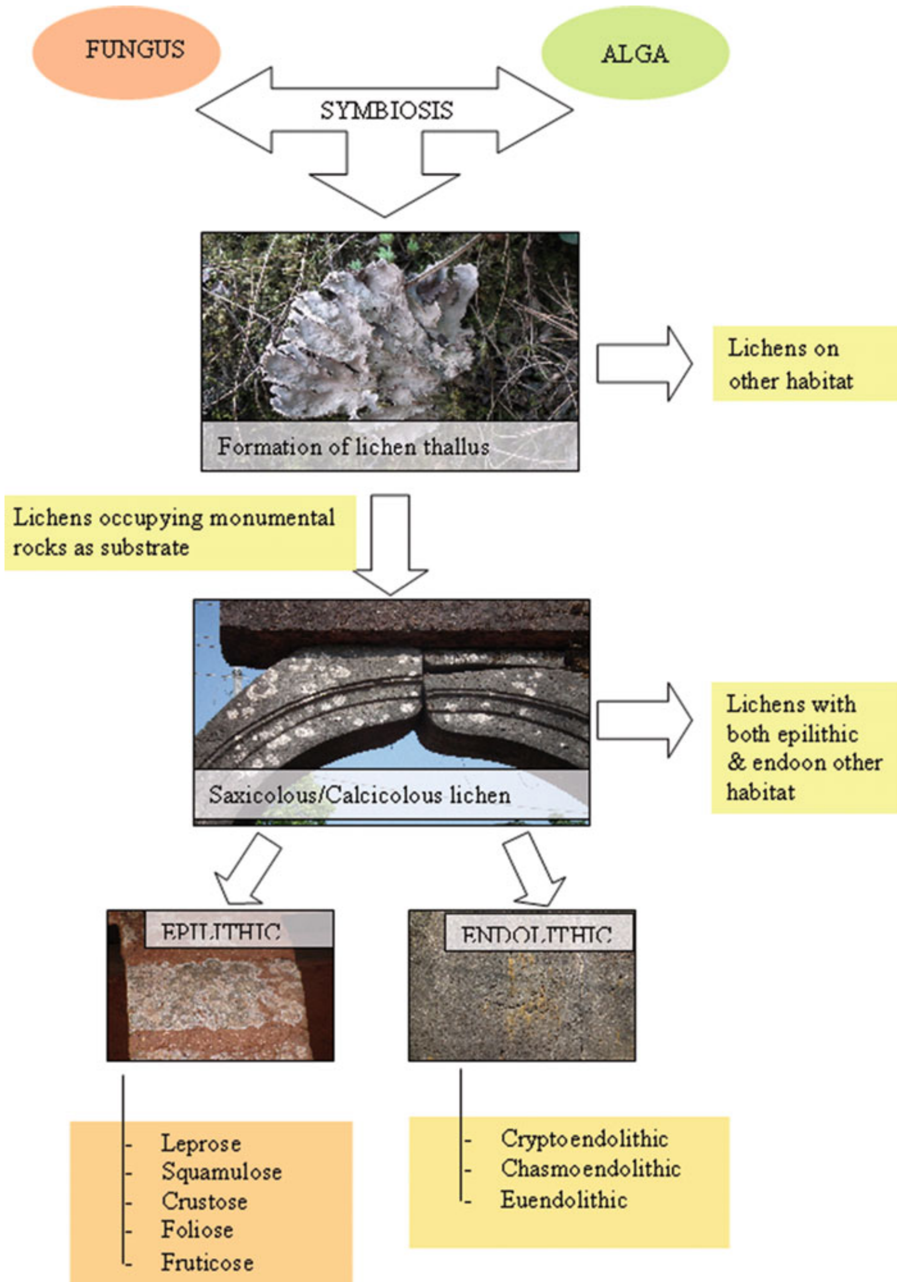

Fig. 1.5 Lichens and their classification based on habitat variation (After Chen et al. 2000)

growth of lichens may either be over the rock surface, epilithic, or it may be entirely living beneath a stone surface, endolithic (Danin et al. 1982, 1983).

Various factors (Table 1.1) are responsible for the establishment of lichens on rock which include pH range, humidity, incident light and nitrogen supply (Erick et al. 1996). Lichens which establish and survive in very narrow range of factors are stenoic, while other species which grow over a wider interval of conditions are euroic. pH plays a predominant role in the development and estab-

Table 1.1 Factors influencing colonisation of lichens and its biodeterioration potential

	Factors	
1	Environmental factors	Incident light (exposed to Sun or shady), humidity, temperature
2	Inorganic and organic pollutants	As carbon, nitrogen and sulphur source which act as growth inhibitors
3	Surface bioreceptivity	Nature of material, pH range, conservation measures, length of exposition
4	Colonising species	Ecological and physiological requirement of the particular species
5	Treatment	Biocides, surfactants/hydrophobic compounds

Modified from Urzi and Krumbein (1994)

lishment of lichens on rocks. Calcicolous species develop on neutral and alkaline substrates, e.g. Lecanora calcarea grow on basic substrates, while silicicolous species grow on acidic substrate, e.g. Parmelia saxatilis (Lisci et al. 2003).

Lichen establishes more readily on a substrate after it has been partly transformed by chemical substances in the air and then by bacteria. This fact is evident from the findings that lichens grow more readily on archaeological ruins, on which mould and porous surfaces facilitate bacterial growth. Biodeterioration caused by lichens has been reviewed by several workers (Hale 1983; Seaward 1988; Monte 1991; Clair and Seaward 2004).

1.4.1.1 Biogeophysical Deterioration

Physical weathering of the rock by saxicolous lichens is mainly brought about by rhizinae penetration and thallus expansion/contraction. Mechanical damage is mainly due to penetration of rhizinae deep into the substrate. The depth to which thallus penetrates depends on the lichen species and nature of the substrate. According to Syers (1964) penetration ranges from 0.3 to 16 mm. Frequent dying and saturation events of the thallus result in loss of cohesion. Porous and calcareous sedimentary rocks have been found particularly susceptible to physical rhizinae penetration by lichens. Among the different growth forms of lichens, foliose and crustose lichens are the most harmful biodeteriogens (Singh and Upreti 1991).

Expansion and contraction of the lichen thallus result in formation of cleavages on the rock surface. Epilithic crustose lichens growing on rocks have a medullary zone that is attached directly to the substratum, and when the cortical tissue at the marginal fringe of the thallus contracts during drying, it creates a pulling strain which may tear the thallus and leave the extreme margins attached to the substratum. In species with thicker thalli, the hyphal tissue may be torn from the substratum detaching rock fragments (Syers and Iskandar 1973; Fry 1922, 1924, 1927).

The squamulose form of lichens has peculiar thallus morphology as they have slightly upward curled margins in dry conditions. Numerous soil particles of the substratum adhered on their lower surface. The curling of margins in dry season thus seems to be the result of the well-documented pulling action of lichen thallus when it dries up. On receiving moisture it expands and squamules margins flatten to attach themselves to the substratum once more; these conditions may accelerate the physical deterioration of monuments (Griffin et al. 1991).

The extent of biogeophysical weathering inhabited by lichens is influenced mainly by the nature of the thallus and by chemical and physical composition of the rock substratum. Because of the nature of attachment, foliose species are probably more effective in biogeophysical weathering. As rhizinae and haptera are more abundant in peripheral region of the thallus, therefore damage caused by expansion and contraction of the thallus is more pronounced in the rocks covering peripheral region (Fry 1924).

These biogeophysical processes result in increase of the surface area of the mineral or rock, making it more susceptible to biogeochemical weathering. The mechanical disruption of crystals due to penetration of the rhizinae accelerates chemical decomposition.

1.4.1.2 Biogeochemical Weathering

The biocorrosive activity by lichens is mainly due to the presence of substances like carbonic acid, lichenic acid and oxalic acid which by acidolysis release proton capable of corroding the material via proton exchange phenomenon (Salter 1856; Salvadori and Zittelli 1981). These weak acidic lichen substances cause chemical degradation of the substrate (Warscheid and Braams 2000; Jackson and Keller 1970).

Water is an essential component in any chemical reaction (being the source of –OH and –H). Lichens, especially crustose lichens, have a tendency to absorb water up to 100–300 % of the dry weight in order to withstand extreme conditions of desiccation. Water is absorbed in the medulla of the thallus, and since the medulla of crustose lichens is in direct contact with the rock surface, the substratum becomes more prone to chemical weathering in the presence of a proton donor (from water).

CO_2, produced during the metabolic process in the thallus, in presence of water forms carbonic acid which being unstable dissociates into H^+ and HCO_3^-. The ability of H+ to accelerate chemical decomposition is a well-established fact (Keller and Frederickson 1957).

Oxalic acid has significant contribution in rock weathering process (Beeh-Andersen 1986). Salter (1856) first observed the role of oxalic acid produced by lichens in disintegration of rocks. Affinity of oxalic acid for calcium (limestone as substratum) may be attributed to their electronic configuration, because of which they form insoluble calcium oxalate. The insoluble calcium oxalate usually deposits on the outer surface of the fungal hyphae in the lichen thallus or on the surface of the upper cortex (Smith 1962). Concentration of calcium oxalate varies from species to species; it may range up to 66 % of the thallus dry weight as in the case of Lecanora esculenta (Euler 1939).

Biocorrosive activity of lichens is mainly characterised by the excretion of organic acids complexation. These acids are capable of chelating cations such as calcium and magnesium from mineral forming stable complexes. It has been shown that biogenic organic acids are considerably more effective in mineral mobilisation than inorganic acids and are considered as one of the major damaging agents affecting monument deterioration. The higher concentration of calcium and magnesium is reported in crustose forms of lichens (*Caloplaca subsoluta*, *Diploschistes candidissimum*) followed by squamulose forms (*Peltula euploca*, *Phylliscum indicum*). The lichen taxa tightly adpressed to the substratum exhibit higher concentration of Ca and Mg than the lichen having loose thallus with free lobe margins.

As secondary substances of lichens including various organic acids, which actively chelate substrate cations and thus modify the chemical and physical structure of mineral substrata. The corrosion of rocks in the study area cannot be ruled out as it has drier and warmer climate coupled with luxuriant growth of oxalic acids and chelating substance producing lichens. Thus, enumeration of lichens and their type of biodeterioration capacity data will be helpful in conducting future biomonitoring studies and to the conservators for adopting conservation practices for the monuments (Bravery 1981; Charola 1993; Koestler et al. 1994, 1997).

Lichen species growing on the monuments produce different secondary metabolites. These chemicals secreted by the mycobiont of many lichens are commonly considered to play a crucially important role in the chemical weathering of monuments (Pinna 1993). In the present study, out of 95 species, 65 have the capability to produce secondary substances. A total of 26 different secondary metabolites are reported, of which atranorin, zeorin, parietin and norstictic, lecanoric and usnic acid are the most common.

Metal chelation ability of the lichen substances is another aspect which contributes towards rock weathering by formation of complexes of the mineral component of the rock with electron-rich lichen substances (Neaman et al. 2005). Lichen substances frequently contain polar donor groups in ortho position which favour the complex formation of cations (Syers 1969). According to Culberson (1969), apart from the presence of electron-rich moieties, water-soluble phenolic groups have an important role to play in metal chelation.

The effect of biogeochemical weathering is pronounced in limestone inhabited by lichens due to the slight solubility of calcium carbonate in water. Many calcicolous species are known to immerse in substratum and form endolithic thallus. Formation of perithecial pits (foveolae) is an evidence of the effect of chemical weathering by lichens on the substratum. When the perithecium dies, a hemispherical pit is left exposed to further weathering. Jackson and Keller (1970) found that lichen-covered rock surface weathered more in comparison to the uncovered surface.

The formation of primitive or lithomorphic soil below saxicolous lichens is well documented (Emerson 1947). Microorganisms and insects feed on living and dead lichen thallus, and organic acids produced by the microorganisms probably decompose minerals of the substratum, thus accelerating biogeochemical weathering (Golubic et al. 1981; Lewis et al. 1985). Due to the thallus morphology, lichens not only accumulate nutrients but also trap dust particle. The trapped dust particle gets mixed with the organic matter produced by the decomposing thalli and with detached particles of the underlying rock altered by weathering processes. Polynov (1945) first discussed the formation of organomineral particle below lichens, which may be considered the first manifestation of the unique and most characteristic feature of soil formation, i.e. lithomorphic soil (Ascaso et al. 1976, 1982).

The formation of lithomorphic soil is significant in plant succession as nutrients particularly P, S, Mg, Ca and K which are essential for plant growth are potentially present in bioavailable form in lichens. Together with cyanobacteria, the lichens play an important role as pioneer organisms in colonising rocks as few cyanolichens have an ability of nitrogen fixation. Water-holding capacity increases with the accumulation of organomineral material which provides favourable habitat for the development of plants especially mosses. Lichens provide habitat for a group of oligonitrophile microorganisms involved in the nitrogen cycle in primitive soils (Evdokimova 1957; Stebaev 1963). Lichens are known to convert the primary calcium phosphate, apatite, into bioavailable form for the growth of species growing in succession (Bobritskaya 1950; Syers and Iskandar 1973; Schatz 1962, 1963).

As lichens have slow growth rate, soil formation induced by lichens is a rather slow process which restricts its predominant role in soil formation, but on plane rock surfaces, lichens are undoubted pioneers (Hale 1961). Slow growth rate in no way hinders the role of lichens as biodeteriorating agents (both physical and chemical), being reservoir of nutrients necessary for plant succession and precursors of organomineral material which results in formation of lithomorphic soil.

Thus, the knowledge of the type of lichen growth form, frequency, density and abundance of lichens and the type of lichen substance produced together with the extent of mycobiont penetration into the rock can provide information about the kind of damage caused by lichens.

Environmental pollution plays a significant role in eliminating a large number of lichen species as they cannot tolerate soot and sulphate and thus have no chance to invade monuments in such areas. A few resistant species that perhaps could not compete with other lichens in earlier unpolluted atmospheric condition find a competition-free field to thrive, or even some species get metabolic stimulation by certain pollutants; they thus spread rapidly. Such lichens are highly virulent as monument biodeteriorating agents (Ayub 2005). Some poliotolerant species, like *Phaeophyscia hispidula*, *Phylliscum indicum*, *Rinodina* sp. and *Buellia* sp. that exhibited aggressive behaviour, spreading rapidly, covering a variety of substrates replacing the disappearing harmless or less harmful species that are susceptible to air pollution, have been reported. Under these conditions, it becomes necessary to determine the interaction between species of lichens and monument stone surface. Such increased lichen activity coupled with direct action of pollutants clearly explains why the monuments apparently unchanged for centuries in the past appear now vulnerable to deterioration by lichen attacks (Singh and Upreti 1991).

Association of lichens and monuments in atmospherically unpolluted areas is a common sight throughout the world (Fig. 1.6). The growth of lichens on monuments and buildings is variously

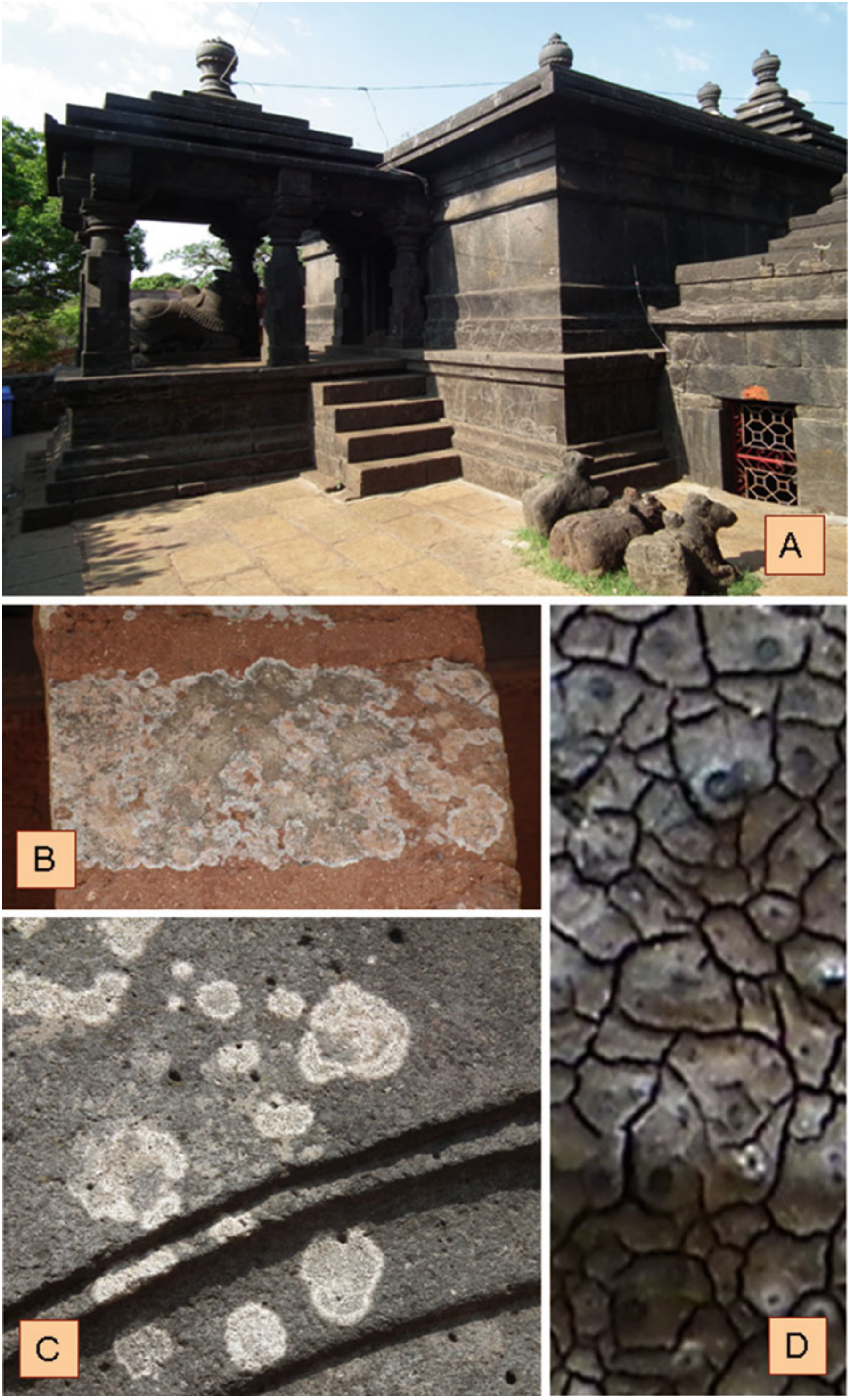

Fig. 1.6 An ancient monument (**a**) Panch Ganga Temple in Old Mahabaleshwar (**b**) Lichen species growing luxuriantly on the pillar colonised by lichens (**c**) *Dirinaria* species and (**d**) *Diploschistis* species

interpreted. Some lay greater emphasis to the protective role of lichens, while others consider them as harmful agents. The multicoloured mosaic lichens on monuments' surface has an aesthetic appeal to the viewers, and it also forms a protective cover against external weathering agents. The lichens' cover provides a protective plastering over the substrate. After the removal of lichens, the rock surface under lichen thallus may be more prone to abiotic and biotic factors such as wind and moisture and insects, respectively (Hawksworth 2001; Hyvert 1978).

Damage caused by lichens to monuments has drawn worldwide attention. The extent of damage caused by lichens varies with species (Gayathri 1980; Tiano 1993). Some species are highly corrosive to rocks due to chemical substances widely known as lichen substances. In a study carried out by Chatterjee et al. (1996), different monuments in culturally rich heritage of Karnataka, Orrisa and Uttar Pradesh were studied (Upreti 2002; Upreti et al. 2004; Jain 2001). It was observed that architectural patterns creating many microclimatic conditions also seem to control the distribution and frequency of different lichen species, at different niches. In Karnataka monuments are generally topped by flat roof covered with plaster of lime. It accumulates dust, dirt and plant remains and is exposed to direct sun rays during greater part of the day, producing xeric conditions. In such habitats, *Endocarpon*, *Peltula* and *Phylliscum* are common, while in vertical walls lichen taxa occupy different niches of walls depending upon light exposure and moisture content of the wall. Basal portions of walls are more shady and humid which is preferred by *Lepraria* species, while higher locations are occupied by *Caloplaca*, *Buellia* and *Lecanora* species. Higher and more lightened walls are inhabited by *Pyxine cocoes*, *P. petricola* and *Candelaria concolor*; other species are *Physcia, Dirinaria, Heterodermia, Leptogium, Coccocarpia* and *Parmelia* (Singh and Dhawan 1991; Singh et al. 1999). The taxonomic identification and ecological properties of each species growing on monuments are necessary since different species contribute to the process of degradation in a different way. Lichen communities growing on rocks undergo regular patterns of successional change; one assemble of species may occupy a given rock surface for several years, steadily altering the substratum in ways that eventually better accommodate a new combination of species. Thus, over time, the changing lichen community relentlessly changes the rock surfaces. The correct determination of lichens species together with their frequency, abundance and density can provide a clue to the conservators to know the nature of the damage caused by lichens (Singh and Upreti 1991). In order to understand the growth and activity of lichens on different monuments, monuments and rocks representing seven districts of Madhya Pradesh exhibited occurrence of a total number of 95 species belonging 34 genera and 17 families of lichens. Most of the species were recorded from monuments of Raisen district followed by Hoshangabad, Dhar and Anuppur district as 43, 36, 29 and 28 species, respectively. Among these lichen families, Physciaceae, Peltulaceae and Verrucariaceae were the most common in most of the monuments, while Collemataceae, Teloschistaceae and Bacidiaceae were restricted in some localities. Among the different substrates, the sandstone bears the occurrence of maximum species followed by calcareous and bauxite rocks. The reason for more growth of lichens on cement plaster and sandstone is due to their excellent water-holding capacity, while siliceous and bauxite rocks are less porous and exhibit poor growth of lichens (Bajpai 2007).

All the recorded species of lichens from the study area can be grouped into four growth forms. Among the different growth forms, the crustose forms exhibit the dominance of 67 species followed by foliose, squamulose and leprose as 54, 44 and 7 species, respectively, in all the 7 districts. Hoshangabad district exhibits the maximum diversity of crustose form, while Anuppur district is dominated by foliose form of lichens. Dhar district showed luxuriant growth of leprose lichens on the monuments, while Raisen has the dominance of squamulose forms.

The negative role of lichens on monuments has greater acceptance. The monuments of the state of Madhya Pradesh bear luxuriant growth of both more effective biodeteriorating and less effective biodeteriorating species. The information presented about the lichens, substrata and chemical substances will be helpful to the conservators of the monuments to clearly distinguish between the aggressive and less harmful groups and to form appropriate strategies for conservation of monuments in the different states of the country.

1.5 Effect of Microclimatic Condition on Lichen Diversity

The microclimate plays an important role in colonisation of lichens on the substrata. Environmental factors including precipitation, light and shady conditions, humidity and dryness, air quality and wind currents show pronounced impact on the lichen diversity of an area.

Light is a vital ecological factor for a lichen-forming fungus being dependent on a close symbiotic association with its autotrophic photobiont partner. The amount of light received by the photobiont during periods of thallus hydration may determine lichen growth (Dahlman and Palmqvist 2003).

Variation in the incident sunlight gives rise to light and shady conditions. Bright sunlight and high temperature have an inhibiting effect on the lichen growth. In order to protect the thallus especially the algal partner from high irradiance, lichens develop cortical pigments such as parietin or melanin which act as UV filters. Such conditions are quite prevalent in alpine cold deserts and urban centres.

The most suitable temperature for the growth of lichens is 20–25 °C, which is evident by the high diversity in the temperate regions of the world. Many lichens are able to withstand high temperatures of the tropics because of high moisture content due to heavy rainfall. Lichen diversity in tropical areas is mostly corticolous. Certain alpine lichens such as *Rhizocarpon* and *Acarospora* can tolerate very low temperature in high altitudes in the Arctic and Antarctic regions. Lichen species which withstand high temperature are termed as thermophilous lichens.

Moisture content reflected by humidity and dryness affects lichen diversity. Semi-moist tropical areas which have seasonal rains provide favourable conditions for members of Lichniaceae which retain moisture for longer periods of time. In temperate regions, rains are intermittent, so foliose and fruticose lichens grow luxuriantly, while in desert conditions having no rains and dry conditions, they exhibit poor growth of lichens. Only crustose species and some vagrant lichen species compose the flora of the area.

Assessment of air quality is an important parameter for lichen diversity studies. Lichen diversity has been found to be highly influenced by the air quality of an area as lichens are sensitive to phytotoxic gases especially sulphur dioxide which impairs the photosynthetic apparatus by irreversible conversion of chlorophyll a in phaeophytin. For details of the effect of air quality on lichen diversity, see section on Ecosystem Monitoring.

The intensity of wind currents influences lichen diversity. Areas with intense wind have dominance of crustose lichens as they tightly adhered to the substratum. Species of *Usnea* and *Ramalina*, having thin strands, aerodynamically allow wind to pass through the strands without being uprooted by the strong wind current.

Hence, changes in the biotic factors contribute towards varying lichen diversity across the globe. Lichen diversity under natural conditions is dependent on the microclimatic condition and changes in the lichen community structure clearly indicates the changes in the surrounding environment.

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