

# Chapter 18

## Physiology of Photosynthetic Organisms Within Biological Soil Crusts: Their Adaptation, Flexibility, and Plasticity

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### 18.1 Introduction

All photoautotrophic organisms (called “plants” for the purpose of this chapter) in biological soil crusts (abbreviated to biocrusts for this chapter) are small and *poikilohydric* in that their hydration status tends to equilibrate with the water status of their environment. Unlike vascular plants, they lack adaptations to maintain a quasi-constant internal water content by regulating water loss, coupled with water uptake from the soil. However, that does not mean that the water content of *their cells* fluctuates continuously with the changing availability of water in the atmosphere, which is for most of the time far below the range of water potentials at which metabolism is possible. The photosynthetic cells in biocrusts are generally intimately associated with greater or lesser amounts of external capillary water at near-zero water potential, so if liquid water is present at all in their surroundings, they are at full turgor (when wall pressure is numerically equal to osmotic potential) and to some extent buffered against immediate changes in environmental water status. There is a complex interaction between photosynthesis and water storage, and many features of shoot and leaf architecture in bryophytes, and thallus form in lichens, act through surface tension to store and to regulate the distribution and movement of this extracellular water, maintaining cell turgor while minimizing interference with gas exchange (Buch 1945, 1947; Dilks and Proctor 1979; Green

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et al. 1985; Proctor 1979a, 2000a, 2009). The extracellular gelatinous material secreted by many cyanobacteria and algae probably performs a similar function. As long as any extracellular liquid water remains in contact with them, the photosynthetic cells remain fully turgid. When evaporation exhausts the extracellular water, the cells themselves quickly dry out and cease metabolism (Proctor 2002). Most terrestrial biocrust organisms are desiccation tolerant (DT)—able to lose the greater part of the cell water (down to 5–10 % RWC)—suspend metabolism when dry, and recover within an hour or two upon rewetting (Proctor and Tuba 2002). When dry, they often need and are able to withstand high temperatures and intense photosynthetically active radiation (PAR) and UVB. Despite their apparent simplicity, there is growing evidence of physiological agility with acclimation to environmental factors such as light, UV, and temperature being reported.

In this chapter we look at the response of biocrust photosynthetic organisms to the main factors of light, temperature, CO<sub>2</sub>, and thallus water content, but we emphasize the special features of the poikilohydric lifestyle and the biocrust environment; that means that these organisms cannot be treated as small higher plants but show important differences in their physiology and ecology.

## 18.2 The Importance of Scale

Scale is of paramount importance. Area is proportional to the square and volume to the cube of linear dimension. Surface tension acts on *linear* interfaces. Gas exchange and interception of radiation are proportional to *area*, mass, and with it metabolic capacity (and demand) and weight are proportional to *volume*. The consequence is that gravity, a limiting factor for mammals or trees, is trivial at a scale of millimeters, while surface tension, which is a trivial force for us, is among the most powerful forces to which a small organism is exposed. A consequence of scale relationships is that most plants larger than about 10 cm are vascular plants and most smaller than about 1 cm are a varied collection of “lower plants” including cyanobacteria, various “algae,” mosses, liverworts, and lichens. There is a “window” between about 1 cm and 10 cm in which both strategies are viable and coexist. All plant organs (and organelles) have a minimum size, and there would simply not be the space to pack the necessary complexity of a vascular plant in a plant body less than about 1 cm (all gardeners know the vulnerability of small seedlings). Conversely, the poikilohydric plant is limited beyond ~10 cm by water supply and support.

## 18.3 Climate and Microclimate

### 18.3.1 Boundary Layers

Scale enters also into relations with the atmospheric environment. The ground or any other solid object in contact with the atmosphere influences the airflow around it. Trees, buildings, crops, and shelter belts all have their effect (intended or otherwise) on airflow. This region of interaction between air and ground is the *boundary layer*. Close to the ground (or any object), the streamlines are parallel with the surface—the airflow is *laminar*. Farther from the surface, the airflow breaks up into eddies—the airflow becomes *turbulent*. The importance of this is that, within the laminar boundary layer, diffusion of heat, water vapor, CO<sub>2</sub>, etc. takes place by the slow process of molecular diffusion, whereas away from the laminar boundary layer, turbulent mixing becomes dominant, which may be orders of magnitude faster. The laminar boundary layer has no sharp upper limit, but gradually gives way to the turbulence of the surrounding air. Roughly, the laminar boundary layer at the scale of a biocrust, at a wind speed of 1 m s<sup>-1</sup>, is around 1–2 mm. At 0.1 m s<sup>-1</sup> (conventionally taken as “still air”), the thickness of the laminar boundary layer will be ~3–6 mm. Even if conditions are such, that turbulence is being generated, there will always be a laminar sub-layer close to the surface (Monteith and Unsworth 1990). The figures imply that biocrust organisms exist largely within the laminar boundary layer in all but windy weather. In vascular plants, the stomata mark the transition between the predominantly turbulent air outside the leaf and the predominant molecular diffusion in the mesophyll; the diffusion path in the mesophyll is typically around 0.5 mm.

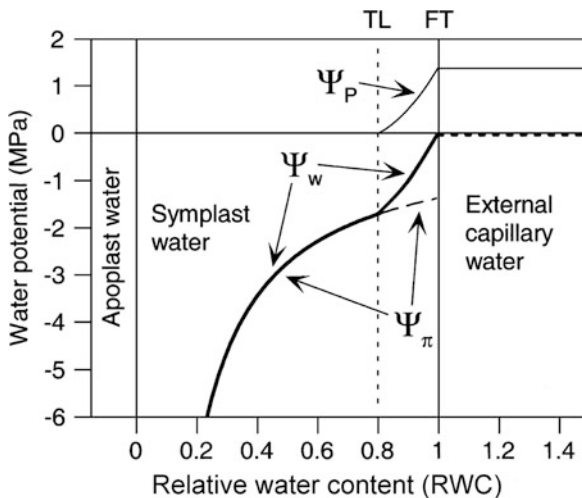
### 18.3.2 Microclimate

“Climate” is in the perception, and on the scale, of the organism that experiences it. Many climatic and environmental variables, such as temperature, humidity, CO<sub>2</sub> concentration, and wind speed, show more or less steep gradients near the ground. Standard meteorological air temperature and humidity measurements are taken about 1.5 m above the ground, with the instruments freely exposed to the air but shaded from direct sun, as in a louvered Stevenson screen. That gives air (“shade”) temperatures appropriate to our own scale or to the scale of our farm livestock and tall crops or trees. We measure “grass minimum” temperature because many crops (and grasslands) are low growing, and “ground frosts” can occur, while the air temperature is still several degrees above freezing. Were we to measure our climate parameters on the scale of biocrust organisms, we should get an entirely different picture; the average might be almost the same but the extremes would be very different. This is reflected by the much wider latitudinal distributions of mosses and lichens, which can productively use the temperature maxima near the ground,

compared with forest trees, which are constrained by air temperature. For example, the moss *Bryum argenteum* (a common constituent of biocrusts) occurs from the Arctic to the Antarctic and at all latitudes in between. For more on climate and microclimate, and plant responses thereto, see Geiger (1950, a classic, still worth consulting), Gates (1980), Campbell (1977), Monteith and Unsworth (1990), Jones (1992), and Barry and Chorley (2003). An outline on bryophytes is given by Proctor (2011).

## 18.4 Water Relations of Poikilohydric Plants

The water relations of poikilohydric plants are basically the same as those of vascular plants, but with two crucial differences. In the Höfler diagram of Fig. 18.1, the cells of homoiohydric vascular plants function between *full turgor* (100 % RWC and 30 % RWC) (0 to  $-5$  MPa). If the cell water content drops below



**Fig. 18.1** Höfler diagram for a typical bryophyte, based on thermocouple psychrometer measurements on the leafy liverwort *Porella platyphylla* (Proctor 1999). The body of the diagram shows the relation of *relative water content* to water potential ( $\Psi$ ) and its components:  $\Psi_w$  = water potential of the cell,  $\Psi_\pi$  = osmotic potential of the cell sap, and  $\Psi_p$  = turgor pressure. The water potential of the cell ( $\Psi_w$ ) is zero at full turgor (FT); the cell is in equilibrium with liquid water in its environment. As the cell loses water, turgor pressure ( $\Psi_p$ ) falls and becomes zero at the point of turgor loss (TL). The tissue then becomes flaccid, and  $\Psi_w$  becomes equal to  $\Psi_\pi$ . Bryophytes share this much of the diagram with vascular plants. But in addition to water inside the cell, turgid metabolically active bryophytes (or lichens) have *external capillary water* held in spaces at near-zero water potential outside the cells, and this water is physiologically important, too. The external capillary water is physically continuous with the *apoplast water* in the cell walls (which needs a diagram to itself), spanning a range of water potentials from zero to negative values far outside the limits of metabolism

about 30 % RWC, the cell dies. The regions of interest in cells of poikilohydric plants extend far beyond these limits. Vascular plants are basically *endohydric*; all the physiologically important water is inside the plant. Poikilohydric plants are *ectohydric*; much of the water associated with plant is held in capillary spaces outside the plant, and this water too is physiologically important to the functioning of the plant. This externally held water can vary widely in quantity, but while it is present, the photosynthetic cells remain fully turgid. Whereas the full-turgor water content of a vascular plant is easily established by weighing a fully turgid leaf, and weighing the same leaf after oven drying, it is not so easy to obtain for poikilohydric plants because of the external capillary water. Full-turgor water content of a poikilohydric plant is difficult to measure without recourse to thermocouple psychrometry, but acceptable approximations can often be obtained (at least for bryophytes and lichens) by careful blotting with soft absorbent paper (Beckett 1995, 1996, 1997; Green et al. 1985; Proctor et al. 1998; Proctor 1999; Nardini et al. 2013; Merinero et al. 2014). Saturation (maximal) water content is an entirely different thing from full-turgor water content, with the latter being *essential* for physiological work. “Relative water contents” based on “saturated” water content are meaningless. The only easily reproducible datum is oven-dry weight.

Because of their impermeable cuticularized epidermis, vascular plants operate between full turgor and ~30 % RWC; if the soil is dry or saline, the plant is water stressed. For a poikilohydric plant, all habitats are mesic when the cells are fully turgid, and all habitats are arid when the cells are desiccated. Water stress is confined to (relatively brief) intervals between the two states, and the difference between mesic and xeric habitats is a matter of the time spent in the two states (Proctor 2000b).

## 18.5 Desiccation Tolerance (DT)

Desiccation tolerance in bryophytes and lichens has been defined as the ability to equilibrate its internal water potential with that of moderately dry air and then resume normal function when rehydrated (Alpert 2000). This means equilibration with 50 % relative humidity at 20 °C, which leads to a thallus water content (WC) around 10 % and a water potential of –100 MPa. This threshold of 10 % WC seems to have physiological meaning and to correspond to the point at which there is no longer enough water to form a monolayer around macromolecules thus stopping enzymatic reactions and metabolism (Billi and Potts 2002). In the laboratory, much lower hydrations, less than 1 %, can be achieved by drying over P<sub>2</sub>O<sub>5</sub>, and levels almost as low, around 2 %, can occur in the field when dry lichens are heated by the sun to temperatures that can reach 70 °C. Desiccation tolerance is shown by bacteria (including Cyanobacteria), many “algae,” mosses, liverworts, and lichens and among animals by many “infusoria,” rotifers, nematodes, tardigrades, etc. What is it that enables them to do this? Several mechanisms seem to be required to achieve DT. There is evidence of the importance of vitrification (glass

formation) of the cell contents to DT (Crowe et al. 1992, 1998; Buitink et al. 2002). Solutes, such as sucrose, oligosaccharides, fructans, polyols, and trehalose; protective proteins, LEA (late embryogenesis abundant) proteins and HSPs (heat-shock proteins); and amphiphilic metabolites, are important in membrane stabilization; antioxidants are important against accumulation of reactive oxygen species (ROS) that can occur during dehydration and rehydration (Smirnov 1993; Asada 2006; Green et al. 2011a; Proctor and Smirnov 2011).

Some bryophytes of frequently desiccated habitats (and lichens in general) are constitutively DT (CDT). *Syntrichia ruralis* (formerly *Tortula ruralis*), *Grimmia pulvinata*, and *Schistidium apocarpum* (s.l.) can withstand drying from full turgor to a water content of 5%–10% of their dry mass in half an hour or less, and on remoistening after a few hours or days of desiccation, recover positive net assimilation within a few minutes, and return to a positive net carbon balance within an hour or less. Most molecular work has been done on *Syntrichia ruralis*, which does not need a transcriptional activation of a distinct set of “tolerance genes,” but rather relies heavily on the more rapid response afforded by translational controls (Oliver and Bewley 1997; Oliver 2009). The response is certainly not as rapid in all bryophytes. Abel (1956) screened detached leaves of 66 mosses and found that they formed a nearly perfect continuum from *Schistostega pennata*, *Sphagnum* sp., and *Bryum schleicheri*, killed by 24 h exposure to 96 % RH, to *Syntrichia ruralis* and *Grimmia* sp., whose leaf cells would still plasmolyze even after 24 h over concentrated sulfuric acid. Over half the species tested showed a dramatic increase in tolerance following pre-desiccation at 96 % RH, a phenomenon also demonstrated for biocrust mosses in the Mojave Desert (Stark et al. 2005, 2011, 2012). Stark and Brinda (2015) emphasize the continuum that exists between CDT plants and plants in which desiccation tolerance is induced by slow drying (induced drought tolerant: IDT). Many small mosses important in biocrusts in seasonal climates are IDT. The relationship between the normal habitat conditions of a bryophyte or lichen and degree of survival following drying and desiccation is important and should be taken into account at all times. The CDT mosses and lichens represent one extreme in desiccation tolerance, while, at the other extreme, there are examples of species that have almost zero tolerance of dehydration, let alone desiccation. For lichens, *Pseudocyphellaria dissimilis* cannot survive even 20 h equilibration at 12 % relative humidity (Green et al. 1991), while species of the moss order Hookeriales and many (not all) thalloid liverworts are also desiccation intolerant (Proctor and Pence 2002). It is important to remember that most bryophytes and lichens fall between these extremes of desiccation tolerance, but, because of the open environments of most biocrusts and the wide range of climatic (and often seasonal) conditions to which they are exposed, their component species span a wide range of the DT spectrum. Both CDT and IDT species occur in the Mojave Desert (and in the UK). Smaller seasonal gregarious species seem to be predominantly IDT, but larger perennial mosses of dry places are CDT.

### 18.5.1 Recovery from Desiccation

The general pattern of recovery from desiccation after rewetting is similar in both lichens and bryophytes although generally more rapid (and less studied) in lichens (Ried 1960; Hinshiri and Proctor 1971; Farrar 1976a, b; Farrar and Smith 1976; Bewley 1979; Bewley and Krochko 1982; Oliver 1991; Oliver and Bewley 1997; Tuba et al. 1996; Proctor et al. 2007a, b; Proctor 2009, 2010). Respiration, protein synthesis, and the activity of the photosystems begin immediately on rewetting. The enzymes of the “dark reactions” of photosynthesis take a few minutes to be fully functional. Gas exchange measurements immediately on rewetting show enhanced respiration. This “resaturation respiration” is different from basal respiration; it is cyanide sensitive in the lichen *Hypogymnia physodes* (and perhaps generally), which basal (dark) respiration is not, and decays in a comparable time that it takes for the fine structural changes to be completed (Farrar and Smith 1976; Proctor et al. 2007a). Recovery from desiccation takes place regardless of the presence of protein synthesis inhibitors (Proctor and Smirnov 2000; Proctor et al. 2007a, b; Pressel et al. 2009). The pattern of protein synthesis alters dramatically in the first hours following rewetting, and the sequence of events during recovery is complex (Oliver 2009). Morphological change at the subcellular level is most active in the first few hours of rehydration, but full return of organelles to their pre-desiccation form and disposition, and reassembly of the cytoskeleton may take 24–48 h (Pressel et al. 2006, 2009). This is essential for active translocation (Ligrone and Duckett 1994; Pressel et al. 2006) and for the cell cycle, cell division, and cell growth (Mansour and Hallet 1981), but apparently not for photosynthesis or carbon fixation (Pressel et al. 2009).

Recovery follows much the same course for liverworts, although data are available for only a few species. The “oil bodies” of liverworts appear to play a crucial role in recovery of *Southbya nigrella* and probably other species (Pressel et al. 2009; Proctor 2010). Some species of liverworts, particularly small Marchantiales (*Corsinia*, *Exormotheca*, *Mannia*, *Oxymitra*, *Plagiochasma*, and *Riccia* spp.), are DT and are prominent in biocrusts in the Mediterranean region with cool wet winters and summer drought and in comparable climates elsewhere.

In general there is a positive and not unexpected link between time to achieve recovery and length of time active once rehydrated. Lichens recover rapidly but then remain active only briefly, while, at the other extreme, many mosses recover slowly but then remain active longer (Green et al. 2011a; Kappen and Valladares 2007; Proctor 2004; Zotz et al. 2000; Zotz and Rottenberger 2001). The greater time and thallus water content required by mosses to recover full activity, plus the enhanced respiratory activity after rehydration (Dilks and Proctor 1976; Farrar and Smith 1976; Schlenz et al. 2004) means that partial hydration followed by rapid drying, as found in hot desert environments, can lead to damage and death (Coe et al. 2012, 2014; Barker et al. 2005; Stark et al. 2011). In view of the longer recovery times and ability to utilize heavier rainfall events, it is also not unexpected

that bryophyte biomass in biocrusts will be positively linked to overall precipitation and they show a greater representation in wetter habitats (Wu et al. 2015).

## 18.6 Sources of Water to Biocrust Plants

Poikilohydric organisms such as lichens and mosses can become hydrated from rain, humid air, dew, and fog, with only the first being usually available to homoiohydric plants. The rate and extent of hydration differs between the different sources, and the actual effectiveness depends on the individual organisms.

### 18.6.1 *Rainfall*

Rain is the most obvious and the easiest to deal with; rainfall records are among the most widely available of meteorological data. At the Tabernas Desert, Almeria, rainfall greater than 0.1 mm fell on 23 occasions in 2013, and all events would have hydrated the lichens enough for activity to start and all but two to reach the WC optimal for photosynthesis ( $WC_{opt}$ ; see Table 18.1). Sixteen of the events would have fully saturated the lichens and mosses. Biocrust organisms can remain active for long periods after hydration by rain, but the actual carbon gain depends on the photosynthetic response at high WC (see Sect. 18.8.1).

### 18.6.2 *Humid Air*

Laboratory studies (e.g., Bertsch 1966; Lange et al. 1988) have often shown that lichens with green algal photobionts can become active from humid air alone and that lichens with cyanobacterial primary photobionts do not. As hydration by humid air is not a rapid process, at 97 % relative humidity the majority of green algal lichens need 6 h or longer to reach 60 % WC, it seems improbable that moistening by humid air alone can be significant in practice for most biocrusts and almost certainly not for those with cyanobacteria. A small number of examples are known where positive net photosynthesis occurs by late afternoon high humidity although the ecological significance is questionable (Lange et al. 2008). There could, however, be an important indirect effect through the water content gain from humidity lowering the amount of water required for full activity from other sources such as dew or impaction of water droplets from mist. This could be important for both lichens and bryophytes. There are also a few examples where some green algal lichens in arid areas do not show activation by high humidity (Del-Prado and Sancho 2000; Colesie et al. 2014a; Hovenden and Seppelt 1995).



**Table 18.1** LMA (mass per unit area), thallus water contents in % dry weight, and mm rain equivalent

Species	LMA g m <sup>-2</sup>	Thallus water content				Depression		Dew fall required		Maximal net photosynthetic rate		Dark respiration		Chlorophyll	
		% dry weight		mm		%	MCP	Opt	MCP	Opt	μmol m <sup>-2</sup> s <sup>-1</sup>	nmol g <sup>-1</sup> s <sup>-1</sup>	μmol m <sup>-2</sup> s <sup>-1</sup>	QE	mg m <sup>-2</sup>
		MCP	Opt	Max	MCP										
<i>Collema cristatum</i> <sup>1</sup>	310	42	500	1700	0.16	1.52	5.2	80	10	95	2.8	9.03	0.95	0.015	43
<i>Fulgensia fulgens</i> <sup>2</sup>	440	11	56	270	0.05	0.25	1.2	100	3.1	15.6	5.2	11.82	1.25	0.026	450
<i>Lecanora muralis</i> <sup>3</sup>	510	29	106	310	0.15	0.55	1.6	100	9.4	34.4	6.5	12.75	1.6	0.025	564
<i>Cladonia convoluta</i> <sup>4</sup>	630	38	150	500	0.24	0.95	3.2	0	15	59.4	5.4	8.57	1.8		280
<i>Squammarina lentigera</i> <sup>5</sup>	684	10	53	120	0.08	0.4	0.9	30	5	25	4	5.85	1.5	0.024	227
<i>Collema tenax</i> <sup>6</sup>	1190	18	84	210	0.22	1	2.5	85	13.8	62.5	3.9	3.28	1.8	0.015	170
<i>Diploschistes diacapsis</i> <sup>7</sup>	2000	3	25	60	0.06	0.5	1.2	60	3.8	31.3	5	2.5	1.5	0.011	1350

Source of data: <sup>1</sup>Lange (2000), <sup>2</sup>Lange et al. (1995), <sup>3</sup>Lange (2002), <sup>4</sup>Lange and Green (2003), <sup>5</sup>Lange and Green (2004), <sup>6</sup>Lange et al. (1998), <sup>7</sup>Pintado et al. (2005)

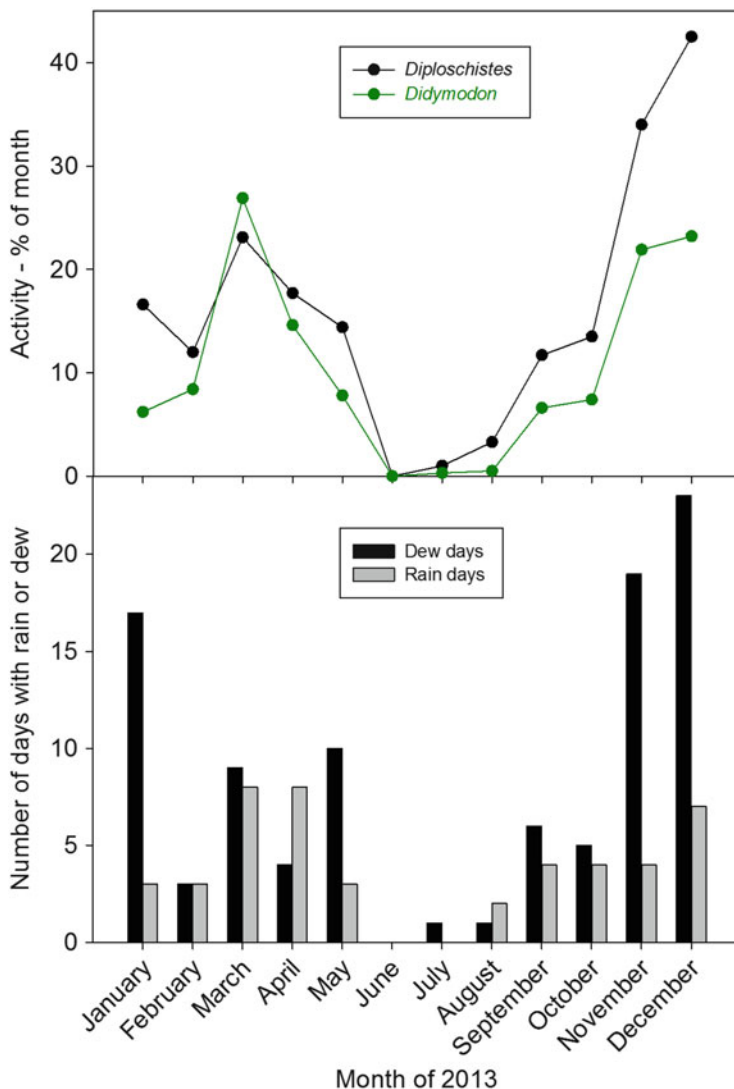
MCP moisture compensation point for NP; Opt water content at maximal NP; Max maximal measured water content; depression—NP at maximal water content as % maximal NP; dewfall required in mm to achieve MCP and Opt; maximal net photosynthetic rates on area (μmol m<sup>-2</sup> s<sup>-1</sup>) and dry weight (nmol g<sup>-1</sup> s<sup>-1</sup>) basis; dark respiration on area basis (μmol m<sup>-2</sup> s<sup>-1</sup>); QE quantum efficiency (initial slope of NP response to PPFD); and chlorophyll content (mg m<sup>-2</sup>) for seven BSC lichen species

### 18.6.3 Dew

Hydration by dew is well known for lichens and less so for mosses (Lange 1969, 2001; Csintalan et al. 2000) and produces the so-called “gulp” effect in which the organism activates during clear radiation nights, giving a brief period of positive net photosynthesis when the sun rises, before the temperature increases and the lichen or moss dries rapidly and photosynthesis ceases. The length of the active period and the total carbon gain will depend on two main factors, the amount of dew fall that has occurred during the night and the degree of hydration required by the individual species to achieve positive net photosynthesis (NP). Dew fall occurs commonly in desert areas because of the clear skies and the consequent radiative cooling of the soil surface. The number of nights with dew fall can be very large, for instance, 78 % of nights in a coastal arid zone near Almeria, Spain (Uclés et al. 2014; Fig. 18.2). Quantity of dew fall is normally not high, and a summary by Uclés et al. (2014) suggests that amounts up to 0.17 mm (precipitation equivalent) are normal, while occasional falls up to 0.3 mm can occur. The amount of dew fall appears to be strongly linked to the length of time that the surface is below the dew point. A rate of  $0.014 \text{ mm h}^{-1}$  was demonstrated by direct measurement for El Cautivo, Tabernas Desert, Spain, by Uclés et al. (2015), with dew fall lasting for up to 15 h in winter. Dew fall appears to be slower at most other sites (Zhang et al. 2014). Lichens are best studied, and species differ considerably in the amount of dew fall needed to become active. The moisture compensation point (MCP) is reached at 0.05 mm (about  $3\frac{1}{2}$  h dew fall) by *Fulgensia fulgens* (Table 18.1), while 0.24 mm (17 h dew fall) are needed by *Cladonia convoluta*; so this species does not benefit from dew.

### 18.6.4 Interception of Fog and Cloud Water Droplets

Higher hydration levels can be achieved by interception and capture of droplets of water from fog or clouds. This is a dynamic process, which depends on the mass of the water droplets and the diameter of the target; it is most effective with a heavy mist and target of negligible diameter, as spiders’ webs are on misty autumn mornings (Monteith and Unsworth 1990). *Teloschistes capensis* in the Namibian coastal lichen fields reaches optimal levels of hydration from fog, which can occur on more than 250 days a year (Lange et al. 2006). Rundel (1978) gives details of lichen communities that are supported by fog. Although there are few studies, fog or clouds are also important for alpine biocrusts both for rehydration and extending activity in the light (Reiter et al. 2008). Growth forms in biocrusts, such as those of *Racomitrium* and *Teloschistes*, appear well adapted to the interception of droplets of water from mist or clouds.



**Fig. 18.2** Activity (% of each month) for the lichen *Diploschistes diacapsis* and the moss *Didymodon rigidulus* in the Tabernas Desert in 2013. The number of days in each month when there was dew or rain is shown in the lower part of the figure. The lichen shows higher activity especially in the three winter months (November to January) when dew occurrence is particularly common

## 18.7 Mass per Unit Area and Thallus Water Content

In almost all studies of lichens and mosses, plant water content is expressed as percentage of dry weight (% dw = [wet weight – dry weight]\*100/dry weight). For biocrusts it is more common to use millimeter precipitation equivalent, because this

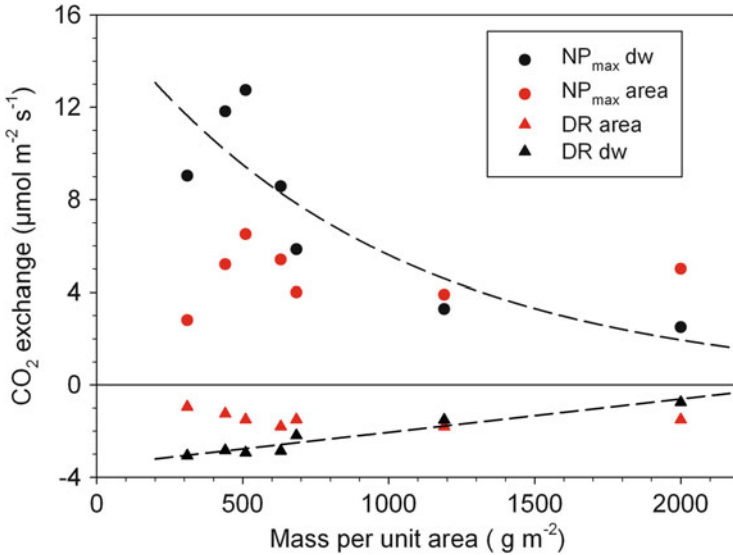
is not only how the inputs, rain or dew, are measured, but also there is often great difficulty to separate individual organisms from the crust.

There is a wide range in leaf mass of biocrust lichens per square meter (mass per area: LMA) from 310 g for *Collema cristatum* to 2000 g for *Diploschistes diacapsis* (Table 18.1). Biocrust lichens are heavy in comparison to foliose lichens from forests. Merinero et al. (2014) report that *Lobaria scrobiculata* and *Lobaria pulmonaria* range from 50 to 200 g m<sup>-2</sup> (mean 86 and 97 g m<sup>-2</sup>, respectively), while *Pseudocyphellaria crocata* ranges from 40 to 100 g m<sup>-2</sup> (mean 73 g m<sup>-2</sup>); Snelgar and Green (1981) give *Pseudocyphellaria dissimilis* from inside a New Zealand rain forest as 59 to 91 g m<sup>-2</sup>. Similar LMA is shown by a wide range of lichens summarized in Green and Lange (1994). Merinero et al. (2014) link the changes in dry mass per unit area with habitat; the wetter the habitat, the lower is the lichen mass per unit area. Lichens in biocrusts fit with this suggestion as they grow in extremely dry habitats and have the highest LMA. In comparison, normal C3 leaves average about 110 g m<sup>-2</sup> (Vile et al. 2005), but the leaf area index is commonly around 5.

For lichens and bryophytes, LMA provides the link between water inputs in millimeters and thallus water content in % dry weight. A precipitation equivalent of 0.1 mm corresponds to 100 g m<sup>-2</sup>, so a lichen or bryophyte with 100 g m<sup>-2</sup> would be hydrated to a water content of 100 % dw (assuming all incoming water is taken up by the organisms). It might be expected that the lower the LMA then the less water (in mm) would be needed to achieve a WC high enough to activate the lichens. However, this depends on the species. In Table 18.1, *Collema cristatum* has the lowest mass per square meter but the highest MCP and WC<sub>opt</sub>. In contrast *Diploschistes diacapsis* has the highest LMA and lowest MCP and WC<sub>opt</sub>. Although the input rate of water is not under the control of biocrusts, it appears that the response to the input is determined by the species.

Net photosynthesis increases with relative water content (full turgor = 1.0) and maximal rates are not reached until full turgor (Proctor 2009). The water content needed to reach maximal net photosynthesis also depends, therefore, on the cell structure and interactions with water location. An unusual form is the gelatinous homoiomerous lichens such as *Collema* and *Leptogium* species. Here, a very small mass of (high molecular weight) gelling agent is used to capture a large amount of “internal” water that actually lies outside the outer cell membrane. However, again, optimum net photosynthesis will not be reached until full turgor (near-zero water potential) is reached for the whole system.

Maximum net photosynthesis (NP<sub>max</sub>) on an area basis is independent of LMA which, as a consequence, means that biocrusts with low LMA will have higher NP<sub>max</sub> on a dw basis (Fig. 18.3,  $P = 0.0004$ ,  $R^2 = 0.92$ ). There is a similar situation for dark respiration (DR), which also shows no significant changes on an area basis, but which shows a linear decline with increasing LMA on a dw basis ( $P = 0.016$ ,  $R^2 = 0.66$ ). These relationships suggest that there is an increase in metabolically inactive mass at higher LMA. The manipulation of water-holding capacity by differential mass allocation appears to offer a method for lichens and mosses to adapt their water relations to the local environment.



**Fig. 18.3** Relationship between maximal net photosynthesis ( $NP_{\max}$ , circles) and dark respiration (DR, triangles) on an area basis (red symbols,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and dry weight basis (black symbols,  $\text{nmol g}^{-1} \text{s}^{-1}$ ) for the seven biocrust lichens in Table 18.1. The fitted curves for the dry weight basis data are significant,  $P = 0.0004$ ,  $R^2 = 0.92$ , for DR, and  $P = 0.016$ ,  $R^2 = 0.66$  for  $NP_{\max}$ .

### 18.7.1 Chlorophyll Content and Photosynthetic Rates

Lange (2001) gives a summary of the then available maximal net photosynthetic rates under optimal conditions ( $NP_{\max}$ ) for a wide variety of soil crusts, and these span over two orders of magnitude between around 0.1 and 11.5  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , the latter being for a green algal lichen-dominated biocrust in Germany.  $NP_{\max}$  is mainly between 2 and 5  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , which are high rates compared to the more typical 1–2  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for rain forest lichens (Lange et al. 1993). The rates are comparable to the leaves of phanerogamic vegetation at the biocrust sites (Lange 2001); however, the annual carbon uptake per surface area will certainly be much lower, because the poikilohydric nature of biocrusts means that they are often dry and they are often active under nonoptimal conditions (see later Sect. 18.9.1) and also because phanerogamic plants can build canopies, i.e., have a higher leaf area index.

Chlorophyll contents of biocrust lichens span a wide range from a low 42.7  $\text{mg m}^{-2}$  for *Collema cristatum* to an exceptional 1350  $\text{mg m}^{-2}$  for *Diploschistes diacapsis* (Table 18.1; Lange 2001). Other soil crusts can have even lower contents, such as 20.7, 29.0, and 38.1  $\text{mg m}^{-2}$  for algal, mixed, and moss-dominated biocrusts from Tengger Desert in China (Zhao et al. 2014), and 16.7 to 43.4  $\text{mg m}^{-2}$  for cyanobacterial biocrusts, and 53.2  $\text{mg m}^{-2}$  for moss-dominated biocrusts in the Negev Desert (Kidron et al. 2012). Lan et al. (2012), for

the Qubqi Desert, Mongolia, found a large increase in chlorophyll content with biocrust development from  $30 \text{ mg m}^{-2}$  in cyanobacteria-dominated early crusts to  $210 \text{ mg m}^{-2}$  for fully developed moss-dominated crusts. The chlorophyll contents for lichen-dominated biocrusts can, therefore, be comparable with those of average C3 leaves, which require  $500\text{--}700 \text{ mg chl m}^{-2}$  to achieve maximal quantum yield of  $\text{CO}_2$  uptake (Lange 2001). Utilizing the data from Table 18.1 and from Lange et al. (1997), there appears to be no significant link between biocrust chlorophyll content ( $\text{mg m}^{-2}$ ) and maximal NP ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ). The two cyanobacterial *Collema* species (Table 18.1) have the lowest chlorophyll contents and  $\text{NP}_{\text{max}}$ , which is a little unexpected as cyanobacterial lichens often have high NP (Lange 2001) and also higher nitrogen availability through their nitrogen fixation. *Diploschistes diacapsis* presents an interesting situation, as the same  $\text{NP}_{\text{max}}$  is supported by  $210 \text{ mg Chl m}^{-2}$  in Utah but requires  $1350 \text{ mg Chl m}^{-2}$  in Almeria (Pintado et al. 2005). This suggests that two different strategies are in use by the same species.

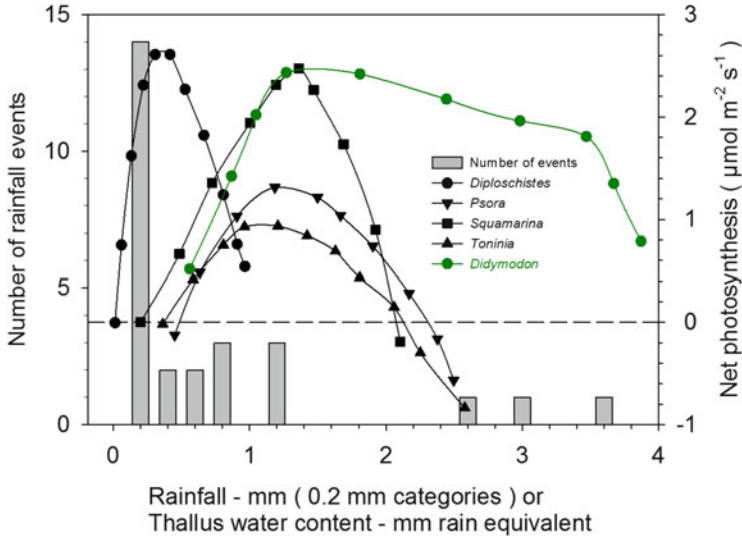
Overall, the higher LMA and  $\text{NP}_{\text{max}}$  in comparison with other lichens conform with trends in other plants that are adapted to high light conditions.

## 18.8 Responses of Biocrust Plants When Active

### 18.8.1 Responses to Hydration

Fundamentally, poikilohydric plants have similar responses to vascular plants in their cell water relations below full turgor. What makes the difference is the external capillary water. Consequently, poikilohydric plants that are fully turgid in the field carry variable amounts of this external water. On an RWC scale, setting full turgor as 100 %, poikilohydric plants can be carrying water equivalent to 200–300 % RWC (or more). The presence of this external water can have a large effect on the photosynthetic rate. The diffusion coefficient of  $\text{CO}_2$  in water is about 10,000 times less than in air, so superincumbent water increases resistance to  $\text{CO}_2$  uptake at higher (total) water contents. Depressed NP at higher WC has been commonly found for lichens (e.g., Kershaw 1972; Lange et al. 1994) but it is equally true for bryophytes (Stålfelt 1938; Dilks and Proctor 1979; Alpert and Oechel 1987), except that bryophytes commonly have adaptations which minimize the conflict between water storage and gas exchange (Proctor 1979a, 2002, 2009; Fig. 18.4). Cowan et al. (1992) working on *Ramalina maciformis* confirm the greatly increased diffusion resistances at high WC. There is little change in the respiration rate with WC beyond full turgor.

Despite the overall similarity in the response of both NP and DR to WC (below full turgor) for bryophytes and lichens, there is a high level of variability in detailed response and absolute values (Fig. 4 in Lange 2001; Table 18.1). Many green algal lichens have a maximal NP first at about 100 % WC with maximal WC below



**Fig. 18.4** Line graph: response of net photosynthetic rate (right hand axis,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) measured at saturating PFD and  $15^\circ\text{C}$  to thallus water content (mm precipitation equivalent) for four lichens and one moss from Tabernas Desert, Almeria, Spain. Bar graph: distribution of rainfall occurrence with each bar representing the number of occurrences of a rainfall event of a particular size; X axis is rainfall event size in 0.2 mm categories. Note the “plateau” of the moss (green points)

200 % and various levels of depression in NP at high WC. In contrast, many cyanobacterial lichens have both high WC for optimal NP (around 300 %) and a very high maximal WC, reaching 1200 %. Mosses often reach maximal NP at WC around 100 %, but thalloid liverworts (and some mosses, e.g., Hookeriaceae, Sphagnaceae) can have very high maximal WC, reaching 2000 %, with a less pronounced depression in NP. In general, there is a positive linkage between a high WC for maximal NP and maximal WC.

The difference between mosses and lichens is usually explained as resulting from the greater ability of mosses to separate stored extracellular water from photosynthetic exchange surfaces (Green and Lange 1994). How the external water is controlled in bryophytes is well understood (Buch 1945, 1947; Dilks and Proctor 1979; Proctor 1979a; Proctor and Tuba 2002). A lot of the detailed architecture of bryophyte shoots and ornamentation of their surfaces reflects adaptations to provide capillary spaces for water storage while at the same time leaving surface clear for gas exchange (Buch 1945, 1947; Dilks and Proctor 1979; Proctor 1979a, b, 2009). For lichens, some of the same principles apply. The medulla has wide airspaces, to which the algal cells in the gonidial layer have free access—an efficient “pseudo-mesophyll.” The interior of the thallus is water repellent and protected against waterlogging (like the mesophyll of higher plants); connection to the atmosphere at large probably varies with the species between upper and lower cortex. Storage of water is probably partly internal, and partly in the immediate

environment, depending on species and habitat. At present, there are few morphological explanations for the differences between lichens in the level of depression of NP at high WC, although such changes in structures will be difficult to discover as even a fully active lichen at optimal WC for NP needs a very small proportion of its surface to be air-filled pores for CO<sub>2</sub> exchange. The most robust estimate is 0.2 % for *Ramalina maciformis* (Cowan et al. 1992).

An important result of the depressed NP at high WC is that heavy rain may not lead to increased carbon gain and this effect is clearly shown by *Lecanora muralis* (Lange 2003). When this lichen was thoroughly wetted by heavy rain for 74 days of its active time, the heavily depressed NP and unaffected respiration meant that these days contributed only 4.2 % of its net annual carbon gain compared to the 40.0 % contributed by the 105 days with dew. This contrasts with *Cladonia convoluta* (= *foliacea*), which has no depression at high WC and makes most of its carbon gain following wetting by heavy rain (Lange and Green 2003). Most bryophytes would be expected to behave like *Cladonia convoluta*, as they usually show efficient adaptations, tending to keep surfaces free of water for gas exchange, and only small depressions (up to ~50 %) in NP at high WC (Dilks and Proctor 1979; Alpert and Oechel 1987). Bryophytes are more prominent in wetter and shadier habitats and in more oceanic areas, and lichens are more prominent in drier and more brightly lit places and in continental regions, but there is a great deal of overlap between the two groups.

Bryophytes are suggested to be particularly vulnerable to the effects of partial hydration, probably because they need longer to reactivate photosynthesis than lichens. Stark (2005) found that to fully hydrate patches of dry *Crossidium crassinerve* in the Mojave Desert, a rain event of at least 2 mm was required, and that lesser amounts, together with the rapid drying after rain, can contribute to substantial carbon losses and death (Barker et al. 2005). It is often noticeable that dry bryophytes are water repellent when first wetted; this could be interpreted as insuring that recovery is not started by trivial amounts of rain. The influence of rain on biocrust productivity depends, therefore, not only on the amount of rain but also on the rate of recovery and the quantity of water needed to achieve saturation.

In terms of contribution to overall productivity, the minimum water potential, at which photosynthesis is detectable, is only of academic interest. Respiration is rather different. Even a modest level of carbon loss over weeks could negate a brief period of carbon gain. This is one reason why, once a poikilohydric plant is dry, it needs to be dry enough to stop metabolism altogether. Dryness also prevents fungal attack.

### **18.8.2 CO<sub>2</sub> Concentration**

Biocrusts show the typical and expected saturation curve relationship between NP and CO<sub>2</sub> concentration, but Glime (2007) points out that there is a major difference between lichens and bryophytes for the CO<sub>2</sub> concentration required to saturate

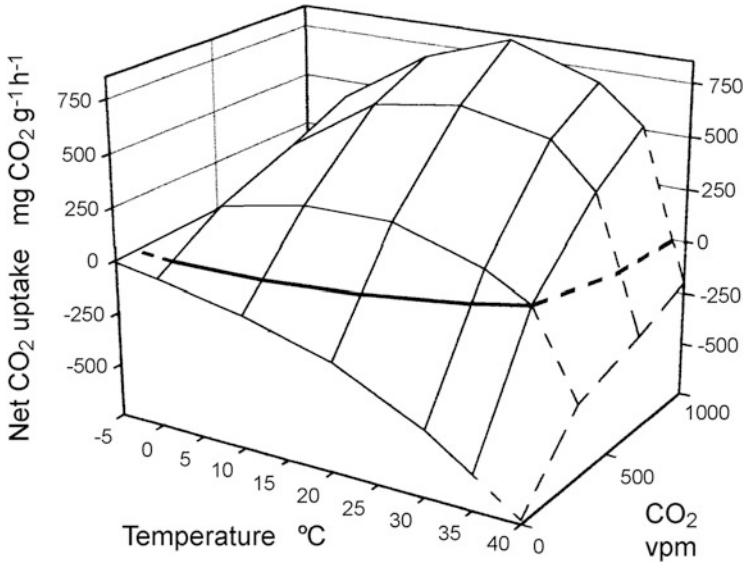


NP. Many lichens studied have their NP at optimal water content saturated with CO<sub>2</sub> at close to present ambient levels (400 ppm; Green and Snelgar 1981), whereas NP of bryophytes is typically not saturated at 1000 ppm CO<sub>2</sub> (Pannewitz et al. 2005; Glime 2007). The compensating CO<sub>2</sub> concentration (the value when NP matches respiratory loss) is around 100 ppm for most bryophytes as might be expected for typical C3 plants. Hornworts (Anthocerotae) have a CCM (see below). Lichens show more variability, and all cyanobacterial species and many green algal species possess CO<sub>2</sub> pumps (CCM; Raven et al. 2008) and can have CO<sub>2</sub> compensation points close to zero ppm (Badger et al. 1993; Palmqvist 2000).

The higher CO<sub>2</sub> requirement by bryophytes appears to be related to the absence of a CO<sub>2</sub> pump and to the liquid-phase diffusion resistance between the wet cell wall and chloroplasts of the leaf cells. This liquid-phase diffusion resistance affects lichens as well, but its effect is moderated by the higher effective “ $A_{mes}/A$ ” (area of mesophyll to surface area of leaf) of the gonidial layer. This is in addition (and quite unrelated) to the superincumbent water, which is usually given as the cause of the strong depression of NP in lichens.

Most bryophytes have unistratose leaves; calculation suggests that at current ambient CO<sub>2</sub> concentrations, and assuming a reasonable value for the liquid-phase diffusion resistance between the moist leaf surface and the chloroplasts, the maximum rate at which CO<sub>2</sub> can diffuse into a single surface could be matched by the energy available from a photon irradiance of  $\sim 250 \mu\text{mol m}^{-2} \text{s}^{-1}$ —around 14 % of full sunlight (Proctor 2005). A unistratose leaf has two surfaces, and leaves generally overlap on bryophyte shoots. However, not all of that area is available for gas exchange, and in practice photosynthesis is saturated below  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  in most mosses (Marschall and Proctor 2004). Many estimates of saturation irradiances are higher, but the actual quantity of light reaching the active centers will also be lowered by filters and refractive surfaces. If CO<sub>2</sub> diffusion limits photosynthesis at high irradiance in many bryophytes, their CO<sub>2</sub> uptake would be expected to respond positively to enhanced CO<sub>2</sub> concentration. The data of Silvola (1985) for mire and forest bryophytes in Finland and Pannewitz et al. (2005) for three Antarctic mosses show that this is indeed so. As Fig. 18.5 shows, temperature and CO<sub>2</sub> concentration interact in their effect on net CO<sub>2</sub> uptake.

Biocrusts are close to the ground by definition, so they exist within the steep gradients of microclimatic factors near the surface. There is some evidence that elevated ambient CO<sub>2</sub> levels can occur in biocrusts, with the highest values observed on moss carpets in the Antarctic, where up to ten times normal ambient CO<sub>2</sub> has been measured (Tarnawski et al. 1992; Green et al. 2000a). Higher levels, 60 % higher than normal ambient concentrations, have also been reported from forest floor moss communities (Tarnawski et al. 1994) meaning that the CO<sub>2</sub> flux is always from the soil to the atmosphere and there is no net CO<sub>2</sub> uptake from the atmosphere by the bryophytes. CO<sub>2</sub> efflux is also reported from biocrust communities and this may be abiotic as it occurs when the surfaces are dry (Rey 2014).



**Fig. 18.5** Diagrammatic response of net CO<sub>2</sub> uptake to temperature and CO<sub>2</sub> concentration, at an irradiance (photon flux) of  $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ , in a boreal forest moss, based on the data of Silvola (1985) for *Dicranum majus*. Broken lines are extrapolated beyond the range of the measurements. The bold line shows the compensation point. Note that the temperature optimum for net CO<sub>2</sub> fixation tends to increase with rising ambient CO<sub>2</sub>

### 18.8.3 Light

The response of net photosynthesis to photosynthetically active photon flux density (PFD) for biocrusts is the typical saturation curve (Lange 2001). The light level required to saturate NP ( $\text{PFD}_{\text{sat}}$ ) of biocrusts is almost always at, or above, about  $700 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  and, because of this, biocrusts have often been referred to as being similar to sun plants (Lange 2001), but they do not reach the  $\text{NP}_{\text{max}}$  associated with such plants although they certainly have higher  $\text{NP}_{\text{max}}$  than species from shadier habitats (Proctor 2014; Robinson and Waterman 2014). It is probable that the high  $\text{PFD}_{\text{sat}}$  (and NPQ) provides protection against occasional high incident PFD. The latter is the situation for lichens in shady rain forests (Green et al. 1997) and is probably also the case for biocrusts (see Sect. 18.9 on activity).  $\text{PFD}_{\text{sat}}$  is dependent on thallus water content, being lower at WC below  $\text{WC}_{\text{opt}}$  and remains constant or occasionally lower at higher WC (Lange 2001). The light compensation point ( $\text{PFD}_{\text{c}}$ ) is correlated with high  $\text{PFD}_{\text{sat}}$ , and, therefore, biocrusts have relatively high values, often 60 to  $100 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ , which are also influenced by temperature, being lower at low temperatures.

The maximal apparent quantum efficiency for CO<sub>2</sub> fixation ( $\Phi$ ) is relatively constant at WC greater than  $\text{WC}_{\text{opt}}$  and declines rapidly at lower WC (Proctor et al. 2007a). It also declines with temperature, indicating a negative effect on

photosynthetic fixation pathways (Lange 2001). In general,  $\Phi$  for biocrusts is around 0.011–0.016 (Table 18.1), which is low compared to higher values for shade lichens (around 0.05) and higher plants, which are around 0.06 and higher.

Overall, the high  $\text{PFD}_{\text{sat}}$  enforces higher compensation points of NP and lower  $\Phi$ , which make biocrusts less efficient at low light. To some extent this is moderated by lower temperatures.

#### 18.8.4 Responses to Excess Light

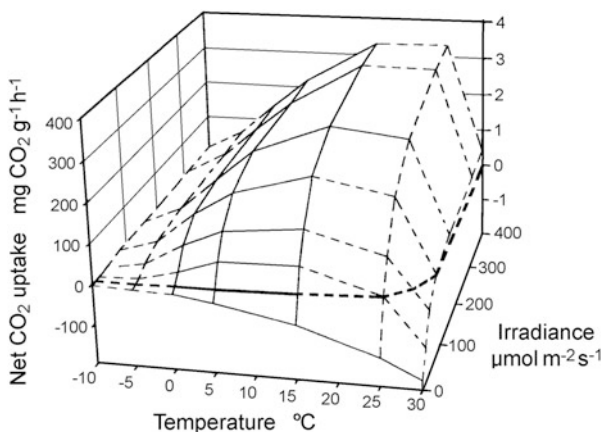
Bryophytes and lichens show excellent protection against possible damage by high UVB and PAR (Büdel et al. 1997; Robinson and Waterman 2014). This protection seems to be constitutive, and when the plants are dry and inactive, chlorophyll fluorescence is near zero. Heber et al. (2006a, 2007) conclude that the incoming solar energy is dissipated harmlessly as heat in the reaction centers and antenna of photosystem II (PSII). Where high light prevails, when the organisms are active, different mechanisms operate (Heber et al. 2006b; Kranner et al. 2002, 2008). The Antarctic lichen *Umbilicaria aprina* showed no negative effects after exposure to full sunlight immediately following the first rehydration after a winter buried under snow (Kapfen et al. 1998). The Antarctic moss *Bryum argenteum* showed no effects of full sunlight, whether a shade or sun form, and always maintained a high level of xanthophyll cycle constituents (Schroeter et al. 2012). Different mechanisms are used by *Bryum argenteum* to protect against UV radiation and high PFD. Samples with low UV protection replaced the protection within days after renewed exposure to UV, and their NP was not negatively impacted during this time (Green et al. 2000b).

Desiccation-tolerant bryophytes and lichens in sun-exposed situations must be exposed while turgid and metabolically active to light greatly in excess of that needed for carbon fixation, at least for short intervals (Heber et al. 2006b; Demmig-Adams and Adams 2006). In many (perhaps all) of these species, photosynthetic electron flow inferred from chlorophyll fluorescence does not saturate, but continues to rise (often near linearly) at high irradiance (Marschall and Proctor 2004; Proctor and Smirnov 2011). Similar non-saturating electron flow has been reported by Pannowitz et al. (2003) for *Hennediella heimii* in the Antarctic. In the species that have been investigated (*Schistidium apocarpum* (s.l.), *Syntrichia ruralis*, *Racomitrium lanuginosum*),  $\text{CO}_2$ , and  $\text{O}_2$  act as interchangeable electron sinks, and the non-saturating component of electron flow is to photoreduction of oxygen. It is always associated with high levels of non-photochemical quenching (Proctor and Smirnov 2011, 2015). Vascular plants and algae prevent reactive oxygen species (ROS) formation by activation of non-photochemical quenching (NPQ), which dissipates excess excitation energy by zeaxanthin-mediated photoprotection harmlessly as heat (Asada 1999, 2006; Niyogi et al. 2005). Although NPQ is found in both algae and plants, these organisms rely on two different proteins for its activation, light-harvesting complex stress-related (LHCSR) protein and

photosystem II subunit S (PsbS). In the moss *Physcomitrella patens*, both proteins are present and active (Gerotto et al. 2012). The algal protein has yet to be demonstrated in other mosses, but the presumption is that it will occur. The presence of alternative quenching systems is also present in lichens, as shown by the constant yield at all incident PFD for many Antarctic lichens (Schlensog and Schroeter 2000). One result of the presence of an alternative electron sink is that electron transport rate (ETR) calculated in fluorescence measurements is a poor indicator of CO<sub>2</sub> fixation, although useful in other ways for interpreting performance.

### 18.8.5 Temperature

Many mosses and lichens maintain modest (sometimes substantial) net CO<sub>2</sub> uptake at or even a few degrees below 0 °C. Limitation of photosynthesis and respiration probably arises mainly from water loss, as ice forms outside the cells. As temperature increases, net CO<sub>2</sub> uptake rises to a maximum at the optimal temperature, before declining again at higher temperatures, ultimately reaching a point where photosynthesis fails to balance respiration, and net CO<sub>2</sub> exchange again becomes negative. Thus, there is an upper temperature compensation point, which sets a limit to the highest temperature at which the bryophyte can grow. As Fig. 18.6 shows, the



**Fig. 18.6** Diagrammatic response of net CO<sub>2</sub> uptake to irradiance and temperature at ambient CO<sub>2</sub> concentration in a common temperate moss, based on the data of Stålfelt (1938) for *Hylocomium splendens*. Irradiances in the original measurements were expressed in kilolux and have been roughly converted to equivalent quantum flux units. *Broken lines* are extrapolated beyond the range of the measurements. The *bold line* shows the compensation point, the line of zero net CO<sub>2</sub> exchange. Note that the temperature optimum for net CO<sub>2</sub> fixation tends to increase with irradiance, and the light saturation level rises with increasing temperature (modified from Proctor 2011)

compensation point is in fact one line varying with irradiance and temperature. Cyanobacterial lichens provide an interesting exception by being unable to carry out positive NP below freezing point (Lange 1965). As a result, they are excluded from the main continent of Antarctica (Green et al. 2011b) and also from high-elevation habitats.

Biocrusts show a wide range of optimal temperatures for net photosynthesis ( $T_{opt}$ ) that show a strong link to the temperatures of their habitats. Optimal temperatures in polar regions are low. Mosses from the Ross Sea region had optima of 6.8 °C for *Ceratodon purpureus*, 9.1 to 15.9 °C for *Bryum argenteum*, and 12.0 °C for *Bryum pseudotriquetrum* (Pannewitz et al. 2003), while green algal lichen biocrusts ranged from 5 °C at Darwin area (80°S latitude) to 17 °C at Homburg (Germany, 50°N; Colesie et al. 2014b). Biocrusts in arid areas range from 21 °C (*Fulgensia fulgens*, *Diploschistes diacapsis*) to 29 to 32 °C, *Collema tenax*, *Cladonia convoluta*, *Squamarina lentigera*, and *Collema cristatum* (Table 18.1). This wide range for temperature optima contrasts with the limited range in PFD required to saturate photosynthesis.

It is known that some soil crust lichens can almost fully acclimate their respiration rates, so that there is no change in DR at mean habitat temperatures (Lange and Green 2005). This ensures that respiration rates do not increase at warmer times of the year, but it also means, because gross photosynthesis will be increasing with temperature, while DR remains relatively constant, that optimal temperatures for NP will also rise (Sun and Friedmann 2005). The means by which the acclimation in respiration occurs is not known, but it also offers a mechanism to adjust the optimal temperature for NP.

## 18.9 Reality: The Duration of Active and Inactive Periods

### 18.9.1 Background

Biocrusts are all poikilohydric and being terrestrial will almost certainly be desiccated on many occasions and for various lengths of time. When desiccated, the biocrusts are dormant and can withstand extremes in temperature (cold and hot) and light. Tolerance to these extremes is adaptive and does not occur in poikilohydric organisms that do not meet these environmental stresses (e.g., Green et al. 1997, 2011a). They represent a different set of adaptations to those utilized when the biocrusts are active when they are under much more moderate conditions (Green et al. 2007). In order to interpret the response of CO<sub>2</sub> exchange of biocrusts to environmental factors, it is necessary to know when biocrusts are active and under what conditions. Knowledge about the times when biocrusts are active can also inform the choice of conditions in laboratory-based investigations and assist interpretations of field manipulations. If the object is simply to record inactive and active periods, electrical resistance with a suitable data logger is an obvious choice

(Proctor 2004); it can be employed at various levels of sophistication (Weber et al. 2016). Some bryophytes look strikingly different wet and dry (e.g., *Syntrichia ruralis* and related species); for these a visual system can be used, based on a web camera (Graham et al. 2006). Hamerlynck et al. (2000) used changes in albedo to follow the hydration state of *Syntrichia ruralis*. Monitoring of environmental conditions such as air temperature, thallus temperature, incident PFD, wet/dry, and relative humidity is now a routine matter with data loggers coupled with sensors with response times that match environmental changes.

Two main forms of monitoring have been used to track photosynthetic activity, CO<sub>2</sub> exchange and chlorophyll fluorescence. Gas exchange is the gold standard to monitor biocrusts. The significant advantage is that, because actual CO<sub>2</sub> exchange is measured, it is possible to calculate carbon budgets with accuracy only limited by the capabilities (and errors!) of the system. Modern portable CO<sub>2</sub> infrared gas analyzer (IRGA) systems require only minutes to make measurements on samples, and, provided such measurements are made at suitable time intervals, then information about diurnal or daily activity patterns can be obtained (e.g., Lange et al. 1990, 1994). Automatic systems have been produced, with which measurements for periods up to 16 months have been made, and allow calculation of annual carbon budgets for biocrust plants. The major limitation with gas exchange-based systems is that only one sample can be measured, and, as with the manual systems, the sample has to be enclosed to make the measurement, leading to uncertainties about whether microclimate is representative.

The major advantage of chlorophyll fluorescence (Maxwell and Johnson 2000; Baker 2008) is that it is noncontact and noninvasive, so that samples can be measured in situ without disturbance or harm, and is also quick and easy. Of the commonly calculated parameters,  $F_v/F_m$ , which measures the maximum quantum yield, is often used in vascular plant physiology as a measure of “stress” and recovery. Effective quantum yield ( $\Phi_{PSII}$ ) is the fraction of excitation energy flowing through photosystem II, and with some crop plants, it is a reasonable (and much more easily measured) surrogate for photosynthesis. Non-photochemical quenching (NPQ) is largely a measure of the harmless dissipation of excitation energy as heat. These three measures are dimensionless ratios and are not influenced by, for instance, distance of measuring probe from the sample. Automatic systems have been developed, which allow measurements at suitable intervals for long periods, sometimes years (Pintado et al. 2010; Raggio et al. 2014; Barták and Váczi 2014).

Measurements of chlorophyll fluorescence in vascular plants are an unreliable guide to its use to best effect with poikilohydric plants. The use of maximal quantum efficiency,  $F_v/F_m$ , as a stress-and-recovery measure presupposes that  $F_m$  remains constant. A higher plant leaf is a population of cells, all of the same age, functioning as an integrated whole; a moss shoot is a population of cells of different ages. It is reasonable to expect the cells of the leaf to behave in more or less the same way. In the moss shoot, the older cells may die and the younger recover; it only takes a small proportion of tissue to survive to create a wholly misleading impression of the response of the tissue as whole. That makes changes in  $F_m$

important, too. Similarly, ETR (relative electron transport rate) is not a good indicator of net photosynthesis for biocrust photosynthetic organisms because some of the electron flow (sometimes the majority at high irradiance) through PSII is related to photoprotection rather than to carbon fixation (Green et al. 1997; Proctor and Smirnov 2011). However, the presence of a chlorophyll fluorescence signal for  $\Phi_{\text{PSII}}$  is an excellent indicator that the studied photosynthetic organism is hydrated and has active photosystems, and from this, the active time and relationships between activity and concurrent environmental conditions can be determined.

Considerable confusion exists because some authors specifically report chlorophyll fluorescence studies as photosynthesis (Hui et al. 2014 among others) or have incorrectly utilized  $\Phi_{\text{PSII}}$  as an indicator of photosynthetic capacity (e.g., Wertin et al. 2012). Chlorophyll fluorescence is at its most powerful when used in conjunction with gas exchange.

### 18.9.2 Dry (Inactive) Periods

Long periods of continuous dryness are surprisingly rare. The longest “rainless” (<0.2 mm of rain) period recorded in the British Isles in the twentieth century was 59 days, from August to October 1959; there were five other “rainless” periods of 45 days or more, all between April and October, and all in the second half of the century (Dukes and Eden 1997). In two years’ recording of *Grimmia pulvinata* cushions on a wall top in Devon, UK (Proctor 2004), the longest dry periods recorded were 367 h (15.3 days) in April–June 1989 and 268 h (11.2 days) in October–December the same year (Table 18.2).

**Table 18.2** *Grimmia pulvinata*

Time interval	Quartile 1	Median	Quartile 3	Maximum	Midpoint of logistic fit
Dry					
Jan–Mar 1989	1.8	5.5	12.0	123.5	4.76
Apr–June 1989	2.3	5.5	29.1	367.0	7.30
Jul–Sep 1989	6.5	25	104.5	255.0	52.94
Oct–Dec 1989	2.8	9.8	27.1	267.5	9.48
Wet					
Jan–Mar 1989	2.1	14.5	37.3	161	26.59
Apr–June 1989	1.5	6.5	17.0	72.0	13.83
Jul–Sep 1989	1.5	10.0	17.5	152.5	10.91
Oct–Dec 1989	0.9	11.0	103.8	669.0	17.66

Length of moss-wet and moss-dry intervals recorded at Morchard Bishop, Devon, UK, during 1989: descriptive parameters (hours). The logistic fit tends to be truncated at its upper end for wet periods in winter and for dry periods in summer; its midpoint (representing the steepest point on the fitted curve and the mode of the fitted distribution) is then substantially greater than the (nonparametric) median value of the raw data



Rainless periods in more arid climates can be much longer, but may be punctuated by summer thunderstorms and by nighttime dew deposition. Stark (2005) monitoring the moss species *Crossidium crassinerve* in the Mojave Desert reported dry periods generally being <25 days, but with one or two periods from 26 to 150 days and one exceptional period of 191 days in 2002. In Tabernas Desert the longest period without activity was 48 days but dry periods longer than 16 days occurred only twice in the year.

Survival for very long periods of desiccation (tens of years) have been reported (Bristol 1916; Malta 1921; Maheu 1922; Keever 1957; Breuil-Sée 1993), but are probably of little ecological relevance. That is subject to the qualification that biocrust organisms pass a substantial fraction of the time at temperatures up to 60 °C; Hearnshaw and Proctor (1982) found that survival time of dry bryophytes declined steeply with temperature, while Lange (1955) showed that dry mosses showed an annual cycle in the lethal temperature (30 min treatment) being around 15 °C higher in summer at around 93 to 105 °C. Surprisingly, lichens seem to show a lower ability to tolerate long periods of desiccation than bryophytes and even DT vascular plants (Green et al. 2011a).

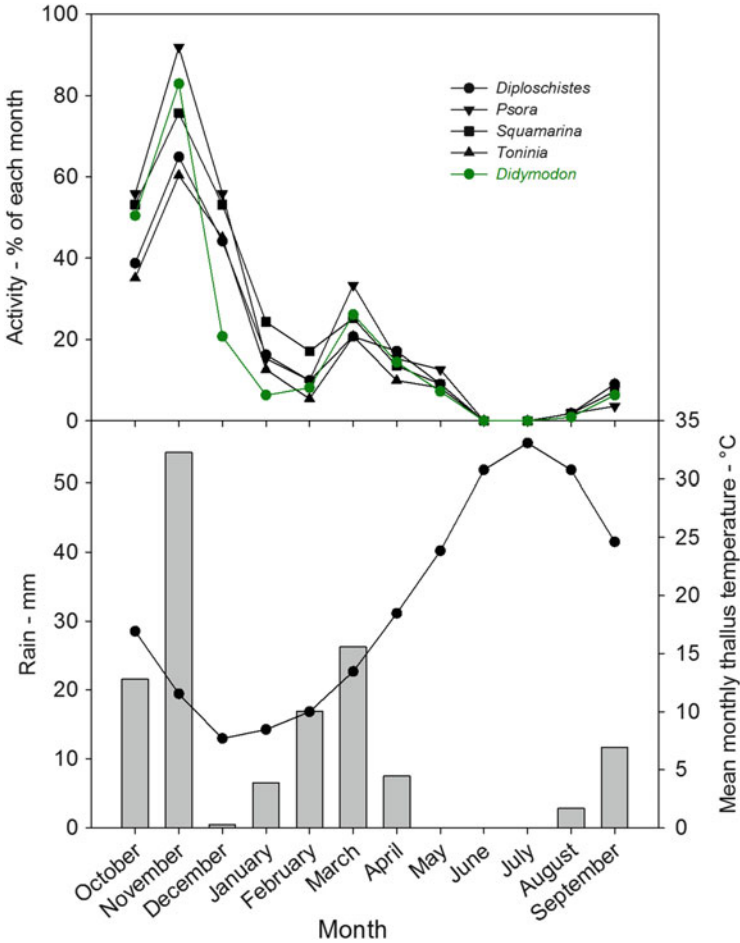
### 18.9.3 Wet (Active) Periods

On a wall top in Devon (UK), the longest “moss-wet” period in 1989 was 669 h (27.9 days, Table 18.2). This accords well with expectation and with autumn as the season when mosses grow the most. But the medians of the data and the estimates derived from the logistic fits tell a different story, which is, there is surprisingly little difference between the length of the moss-wet periods between the summer and winter seasons of the year. Stark (2005) found in the Mojave Desert that longest continuous hydration was 17 and 14 days and that most of wet periods were 4 days or shorter. In Tabernas Desert the longest period in which activity occurred during each day (i.e., could be a dew event) was 33 days. However, for biocrusts at more temperate sites, active periods in winter can last several months, up to around 140 days. At alpine sites, the active period could be most of the year depending on snow coverage and also on the activity state of biocrusts under snow.

Desiccation-tolerant bryophytes (and lichens) are preeminently organisms adapted to frequent, and often short, dry–wet cycles, but it is also clear that in wetter, temperate, or alpine sites, the wet periods are definitely not short.

Considering data obtained from monitoring periods of around 1 year or longer, annual activity varies over a large range from 4.6 % for the lichen *Umbilicaria aprina* at Botany Bay, 77°S; in Antarctica through 46 to 55 % for *Usnea aurantiaco-atra* at Livingston Island, 62°S; and to 65.6 % for *Cladonia convoluta* in Germany, 52°S (Schroeter et al. 2000, 2010; Lange and Green 2003). In the Tabernas Desert, the driest area of Europe, *Diploschistes diacapsis* was active for only 20 % of the year (Pintado et al. 2010). The differences in the length of the active periods in these examples certainly reflect the different severity of the





**Fig. 18.7** Upper panel: monthly activity (% of month) for four lichens and one moss at Tabernas Desert, Almeria, Spain, from October 2012 to September 2013 (modified from Raggio et al. 2014). Lower panel: monthly rainfall (mm) and mean thallus temperature (°C, mean of all species) for the same period

habitats, particularly in terms of available water for hydration. Belnap and Lange (2005) give the activity periods for six lichens, which were all monitored at the same location. Annual activity varies from 34.4 % for *Fulgensia fulgens* to 65.6 % for *Cladonia convoluta* and this must reflect different hydration strategies by the species.

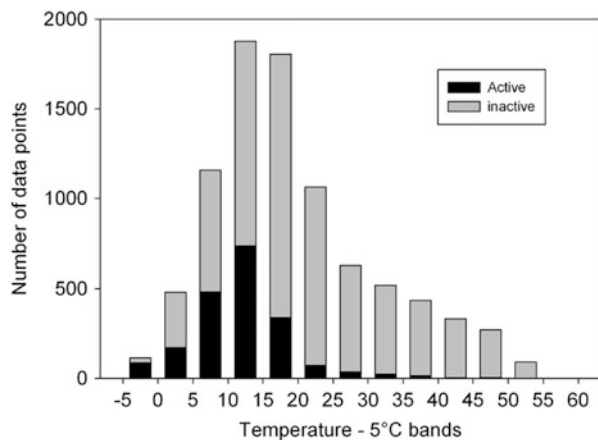
Activity also varies through the year, as can be clearly seen in the data for four lichens and a moss in the Tabernas Desert, Almeria, southern Spain (Fig. 18.7, modified from Raggio et al. 2014). Monthly activity is zero for the two dry months June and July, but reaches around 80 % in November. The activities of the lichens

and moss all follow a similar general pattern, tracking rain and dew events, suggesting that activation by humid air, only reported for lichens, is not significant.

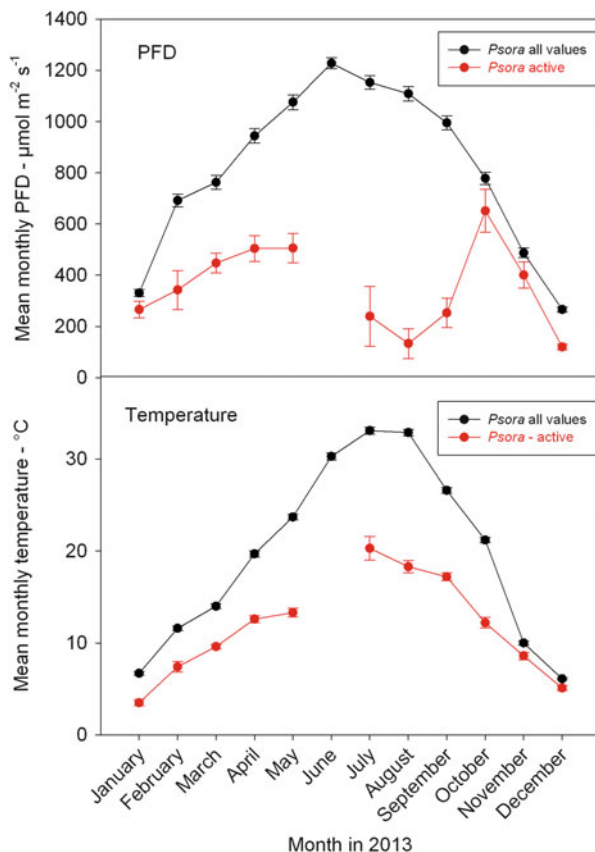
### 18.9.4 Activity, Light, and Temperature

Because biocrusts will desiccate and become dormant especially under high incident radiation, conditions when they are active may diverge from the overall distribution of an environmental factor. An example is given in Fig. 18.8 for thallus temperature of *Diploschistes diacapsis* in Tabernas Desert. Very high temperatures can occur in summer months, reaching over 50 °C, but the lichen is inactive at these times. Most activity occurs between 10 and 15 °C and only rarely above 20 °C. *Psora decipiens*, also in the Tabernas Desert, also shows this divergence for both thallus temperatures and incident PFD (Fig. 18.9). This deviation has been reported for many species from diverse ecosystems such as temperate steppe vegetation (Lange 2003), Tabernas Desert (Pintado et al. 2010; Raggio et al. 2014), and Antarctica (Schlensog et al. 2013; Green et al. 2007). An impressive example is that of *Umbilicaria aprina*, which had almost identical temperature when active in continental (77°S) and maritime (62°S) Antarctica, despite a difference of around 10 °C in annual mean temperature (Green et al. 2011b). Schlensog et al. (2013) compared the summer activity of lichens and bryophytes at a single site on Leonie Island, Antarctic Peninsula, and showed that the bryophytes in the wetter flush area were much more active than the lichens, which dried regularly, and that species with high activity were more strongly coupled to the general environment than those with low activity. This can be seen in Fig. 18.9, where active and overall conditions of PFD and temperature converge in the winter, the period of higher activity, and most strongly diverge in the autumn and spring.

**Fig. 18.8** Distribution of thallus temperatures of *Diploschistes diacapsis* for the year 2013. The x-axis is thallus temperature in 5 °C categories; and the y-axis is the number of data points (reading taken every 30 min) with these temperatures. The height of the bar is the total number of times that temperatures in a particular band occurred and each bar is divided into the active (*dark portion*) and inactive (*gray portion*) periods



**Fig. 18.9** Mean monthly values for incident photon flux density (PFD, *upper panel*) and thallus temperature (*lower panel*) for the lichen *Psora decipiens* for the year 2013 at Tabernas Desert, Almeria, Spain. In each panel, the *black symbols* represent the mean of all values (in the case of PFD, zero values are excluded) and the *red symbols* are when the lichen is active. The lichen was not active in June



## 18.10 Conclusion: Adaptation, Flexibility, and Plasticity

By necessity of their lifestyle, all biocrust organisms are small, and, because of this, the organisms making up biocrusts are often regarded as being “simple” in contrast to vascular plants. Ever since their origin in the Paleozoic, cells of vascular plants have been subject to entirely different selection pressures from those of poikilohydric plants. Vascular plant cells have a (quasi)-constant water supply, and water potential is constrained within narrow limits, thanks to a combination of roots, a conducting system, an impermeable cuticle, and stomata. Poikilohydric plant cells have, by contrast, to live with whatever diverse conditions their environments throw at them. This arises partly as a result of the difference in scale and partly from the difference in life strategy (Proctor and Tuba 2002; Proctor 2014). Neither does small size mean simple metabolic ability, there is growing evidence that lichens and mosses, in particular, are metabolically versatile and show a large

range of acclimation to environmental factors. We should not, therefore, be surprised when we find evidence for such adaptive changes or acclimation. The scale of the changes and ability to adapt or acclimate will, of course, be species dependent and can be expected to vary between organisms, even within a single habitat. It follows that while some species can span many environments, with the moss *Bryum argenteum* being one of the better examples (Longton 1981), in most cases a change in environment will bring about a change in species. For example, strong relationship between water regime and lichen, moss and hepatic diversity is present across the latitudinal gradient of Antarctica (Green et al. 2011b). Major changes with climate will result in alterations in biodiversity due to the arrival of better-adapted species and the inability of existing species to sufficiently adapt and remain competitive.

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