1

The lichen environment: temperature

Standard meteorological temperature data are always measured under well-ventilated, diffuse radiation conditions, at approximately 1 m above the ground. Consequently the values obtained have little relevance to the actual temperature experienced by a lichen on the ground, although they may approximate to the thallus temperatures of pendulous arboreal lichens. To appreciate the operating temperature environment, particularly of crustaceous or adpressed soil and rock lichens, it is essential to understand the continuous energy exchange processes and the control of these processes, which take place at all surfaces.

1.1   Surface energy balance

Natural surfaces are never flat and always have some degree of roughness, but for most purposes it is convenient to take a 'principal plane' or 'active surface' to describe, for example, a soil surface with its numerous small irregularities. During the daytime, solar energy arrives at this surface usually at a rate which exceeds the output, resulting in an accumulation of energy. This in turn causes the temperature at the surface to rise. At night the converse is true with the soil surface being the site of radiant emission and hence energy deficit, leading to the development of lowered surface temperatures. This continuous diurnal temperature change at the air/soil interface diminishes with distance away from the interface, resulting in a vertical temperature profile both above and below the soil surface (Fig. 1). The temperature profile below the soil does not concern us here although it has considerable implications for the physiological environment of the roots of higher plants. What are of importance, however, are the values of the surface temperature maxima and minima and the actual temperature gradient above the surface. It is evident from Fig. 1 that the gradient immediately above the surface is extremely steep and it is this environment which is largely utilised by crustaceous as well as many foliose and fruticose lichens.

The steepness of this gradient is due to the presence of a thin layer of air adhering to the surface within which any motion is parallel to the surface
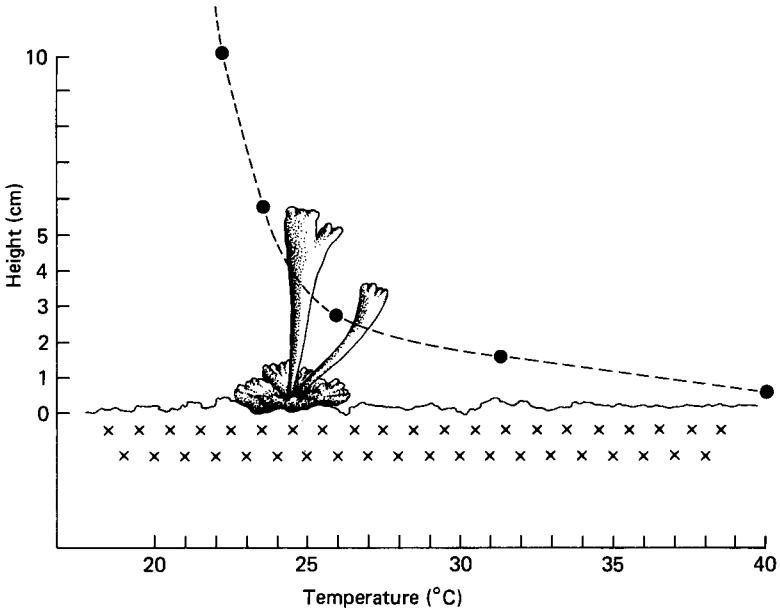
Fig. 1. Diagrammatic representation of the steep temperature gradient adjacent to the soil surface.

(Fig. 2). This layer is called the laminar boundary layer. Its actual thickness is dependent on wind speed and even under still air conditions does not exceed more than a few millimetres. However, because of the laminar flow within the boundary layer the only energy transfer processes across this layer are by radiation and molecular diffusion. As a direct result of the low molecular diffusivity of air, the steep temperature gradient within and adjacent to the boundary layer develops. Above the boundary layer the laminar flow breaks down into a complex of swirling eddies, allowing a much more rapid, turbulent transfer of energy with a correspondingly rapid decrease in the temperature gradient.

The magnitude of the surface temperature values is also dependent partially on the thickness of the laminar boundary layer, and thus under still air conditions surface temperatures will be higher than under windy conditions. However, a number of other factors affect surface temperature to a much greater extent. For example, the level of solar radiation is the primary factor controlling the amount of energy arriving at the surface and indeed will determine the net energy available and thus the final limits of surface temperature.

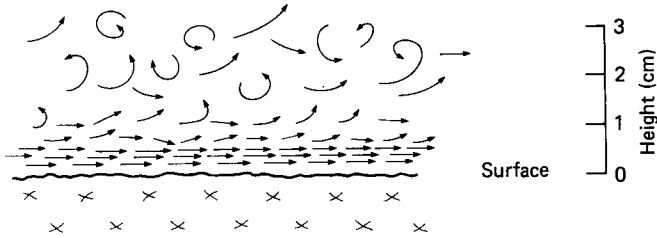The net surface energy is usually termed the net all-wave radiation (Q^*), and during the daytime

Fig. 2. Diagrammatic representation of the laminar flow in the boundary layer adjacent to the soil surface.

$$Q^* = K\downarrow - K\uparrow + L\downarrow - L\uparrow \tag{1}$$

where $K\downarrow$ and $L\downarrow$ are incoming short-wave and long-wave radiation respectively and $K\uparrow$ and $L\uparrow$ are outgoing short-wave and long-wave radiation. At any given location $K\downarrow$ and $L\downarrow$ are both controlled by latitude, the time of day and angle of slope, with maximal values at solar noon, in mid-summer at the equator. Conversely $K\uparrow$ and $L\uparrow$ are controlled by site-specific factors: $K\uparrow$ by albedo (a) and $L\uparrow$ by the surface temperature (T_0). Albedo is a measure of the amount of the incoming short-wave radiation which is reflected by a surface, expressed as a ratio

$$a = \frac{K\uparrow}{K\downarrow} \tag{2}$$

A surface with high reflectivity has a high albedo approaching a value of 1. Thus, fallen snow has an albedo of $c.\,0.95$, in contrast to a wet black soil which has an albedo of $c.\,0.15$. A white surface reflects a large proportion of the incoming short-wave radiation, with resultant surface temperatures potentially cooler than those of an equivalent but dark surface, where most of the incoming radiant energy is available at the surface. However, the net radiation Q^* is partitioned into a number of components, only one of which (H) is responsible for heating the surface and developing a vertical temperature profile above the ground. Thus

$$Q^* = LE + H + G \tag{3}$$

where

Q^* = net all-wave radiation or the total amount of energy available at the surface,

LE = the latent heat flux or the amount of energy which is used to evaporate water,

4   *Physiological ecology of lichens*

H = the sensible heat flux or the amount of energy which is used to heat the active surface and generate a vertical air temperature profile, and

G = the ground heat flux or the amount of energy which is used to heat the soil and generate the vertical soil temperature profile.

The proportion of energy in each component is, in descending order, $LE > H > G$.

There is also a very small component, P, which is the energy used in the photosynthetic activity of a vegetated surface, but it represents such a small proportion of Q^* that it can be conveniently ignored here. The size of H determines the thermal environment of all corticolous, terricolous and epiphyllous lichens on an hour-to-hour basis at the local scale. The local environment is further modified by the position of the lichen in relation to the active surface. This in turn is seasonally and latitudinally modified by variations in $K \downarrow$ and $L \downarrow$ (Equation 1). On the local scale, however, since Equation 3 has always to balance, any increase in LE will automatically mean an equivalent decrease in H and G. Thus, the size of the sensible heat flux is very dependent on the moisture availability at the active surface. If the soil, for example, is at field capacity, water will be freely evaporated, LE will be large and accordingly H will be proportionally much less than for an equivalent but dry soil surface. For a dry soil, with a limited water supply, LE therefore will be small and H, as a direct result, very large. Thus in a sandy desert the radiation budget (Equation 1) has typically a large initial value for incoming radiation as there is little or no water vapour in the atmosphere and cloud cover is totally absent. Since there is no soil moisture at all, $LE = 0$ and all of the energy must be dissipated as sensible and ground heat fluxes. As a result, surface temperatures in extreme deserts can reach 70°C, with more typical values falling in the range 50-60°C, (Lange 1953, 1965). Lange (1954) similarly reports thallus temperatures as high as 54°C for *Cladonia rangiformis* on sandy heaths in Germany. These values are almost certainly due to the very high sensible heat flux over the dry heathland.

In summary, the lichen ground surface environment is considerably more extreme than meteorological air temperature data might indicate. Not only are temperature maxima much higher but the diurnal range is also considerably greater. Although the overall control of surface temperature is a function of latitude and time of day, local values are profoundly modified by both albedo and soil moisture status. (See also Monteith (1973, 1975); and Geiger (1971) for more detailed treatments.) As a result direct measurement of the thallus operating temperature at suitable time
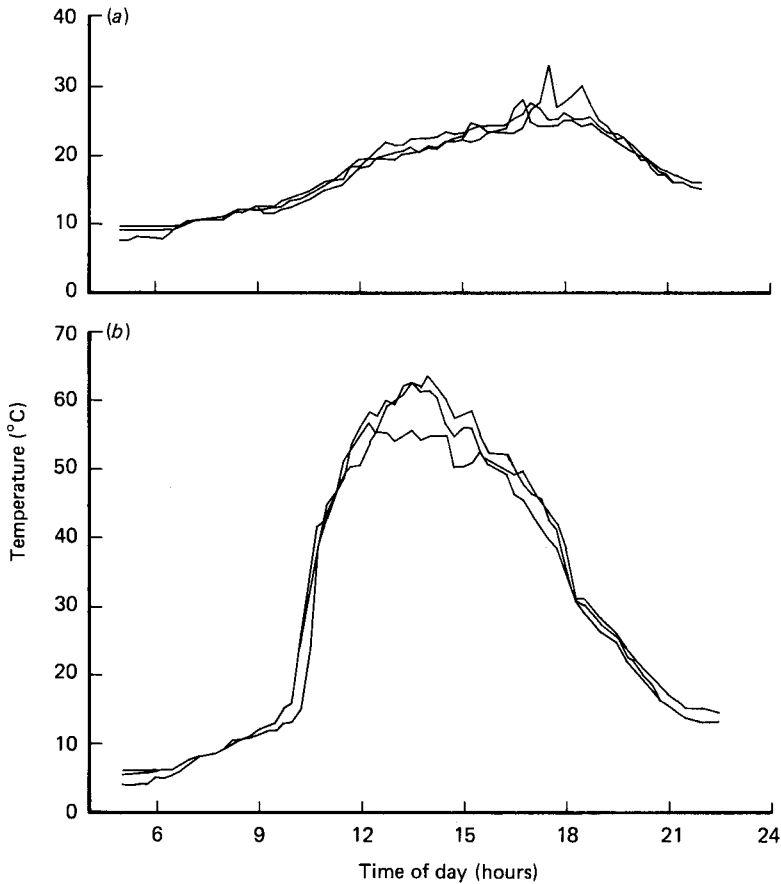
Fig. 3. The time course of thallus temperature *(a)* for *Peltigera praetextata* growing in closed-canopy deciduous woodland, and *(b)* for *P. rufescens* growing on an adjacent exposed roadside. (From MacFarlane and Kershaw 1980*a*.)

periods throughout the year is essential for an understanding of the ecology and the physiological responses of lichens.

1.2   Examples of boundary layer thallus temperatures

MacFarlane and Kershaw (1980*a*) have documented the contrasting thallus temperature environments of two species of *Peltigera* during mid-summer in North Michigan, USA. *P. praetextata* was found in closed-canopy woodland, whilst *P. rufescens* grew 30 m away on an exposed sandy roadside. Under maximal solar radiation conditions, following a rain-free period, thallus temperatures reached 60 °C in the open (Fig. 3), a value which is probably typical for boundary layer conditions on windless days.

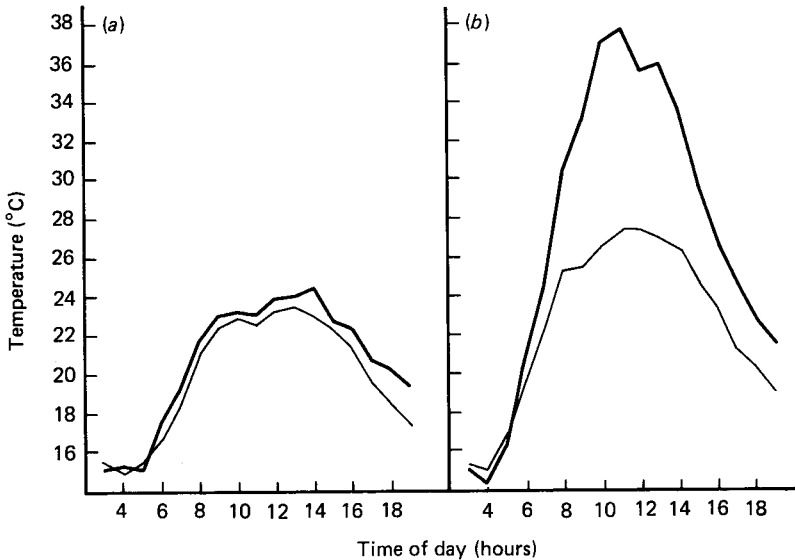6   *Physiological ecology of lichens*

Fig. 4. Thallus (━) and air (—) temperatures for (*a*) the shade Verrucarietum cazzae and (*b*) the open Aspicilietum calcareae associations. (From Kershaw, 1983.)

This contrasted markedly with the adjacent woodland where some soil moisture was still evident and thallus temperatures briefly reached 30 °C during periods of sunfleck activity in late afternoon. Roux (1979) also presents contrasting thallus and surface temperatures for a number of crustaceous lichen associations in France (Fig. 4). In *Verrucaria cazzae*, the dominant species of the Verrucarietum association which is character-istically found on shaded rock surfaces, thallus temperature was close to air temperature throughout the day. However, in *Aspicilia calcarea*, the dominant species of the Aspicilietum association which is always found on open and fully exposed rock surfaces, thallus temperatures in June reached 38 °C even at 430 m elevation and when the air temperature was only 27 °C. Coxson and Kershaw (1983*a*) similarly reported that thallus temperatures for *Rhizocarpon superficiale* at 2500 m in Alberta reached 35 °C under full radiation conditions, and with artificial sheltering from the wind, values rapidly climbed to 44 °C (Fig. 5). Persistent windy conditions – which prevent such high thallus temperatures by reducing the thickness of the boundary layer and hence allowing more rapid transfer of energy from the thallus and rock surface to the surroundings – are among the more impor-tant environmental parameters governing the ecology of this species.

Correspondingly high temperatures for lichen thalli can be expected for
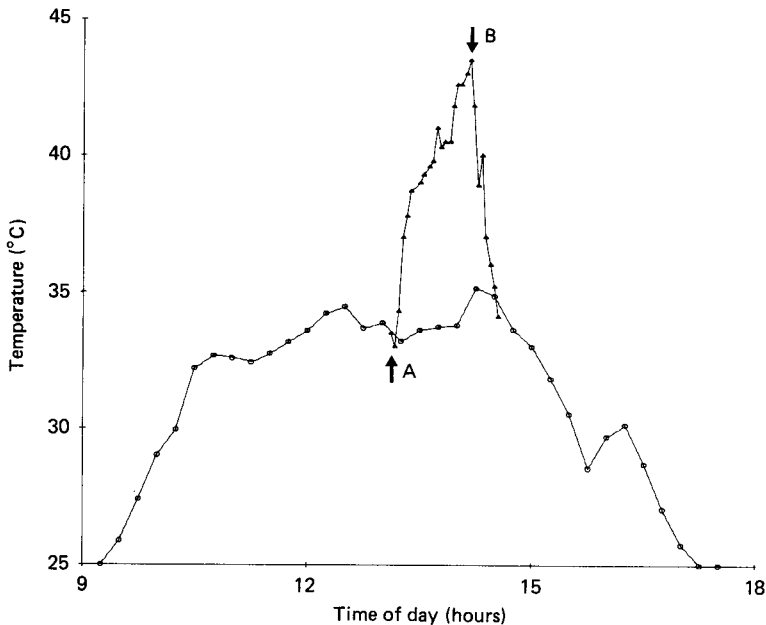
Fig. 5. Normal thallus temperatures in early July for *Rhizocarpon superficiale* under advective cooling (○–○); thallus temperatures screened from the wind for 1 h (A) and after removal of the screen (B). Values are 15 min averages. (From Coxson and Kershaw 1983*a*.)

both arctic and antarctic surfaces: thus, the data of Lewis and Callaghan (1976) for tundra surfaces show that temperatures at the surface exceed 23°C under full radiation conditions with a concurrent maximum air temperature of *c*. 13°C. Similarly Warren Wilson (1957), Bliss (1956, 1962), Mayo, Despain and Van Zinderen Bakker (1973); and Rudolph (1966) have shown that leaf temperatures in the Arctic and Antarctic are closely correlated with radiation levels, aspect and angle of orientation as well as position in relation to the surface boundary layer of the substrate. In general, lichen thallus temperatures, particularly of species growing in the boundary layer, will show similar or even more pronounced correlations with radiation.

For example, *Parmelia disjuncta*, a small adpressed foliose lichen growing on exposed rocks adjacent to Hudson Bay at Churchill, Manitoba, can show considerable elevation of thallus over air temperature (Kershaw and Watson 1983). The diurnal range of thallus temperature on 1 August is given in Fig. 6. The maximum air temperature recorded at 1 m was 9.2°C under good radiation conditions but with a northerly wind. In direct contrast, thallus temperatures reached *c*. 26°C shortly after solar noon
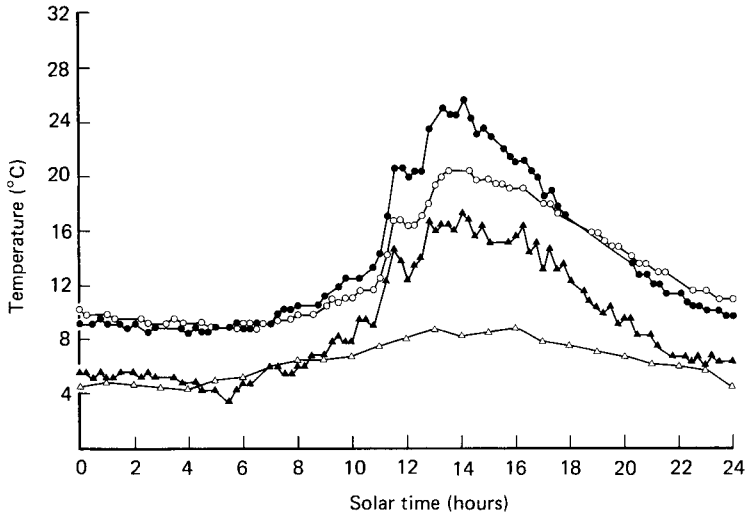
Fig. 6. The diurnal range of thallus temperature for *Parmelia disjuncta* (●–●), temperature at the rock surface (○–○), air temperature at 2 mm (▲–▲) and 1 m (△–△) above the rock surface under good radiation conditions in August. (From Kershaw 1983.)

whilst the temperature at the rock surface was $c.$ 20°C and the air temperature 2 mm above the rock surface was 18°C. During the night, temperatures at the rock surface were consistently warmer than those of the thallus, which gradually cooled to approximately 4°C. Under poor radiation conditions, and particularly on northern aspects, the pattern of thallus temperature is quite different. Under full cloud cover on 2 August and with a maximum recorded air temperature of 7.4°C, thallus temperatures with a south-east exposure were still consistently higher than ambient temperatures, reaching 17.8°C around 1400 hours (Fig. 7). However, replicate thalli with a northerly exposure were some 5 deg C cooler, reaching a maximum of only 12.8°C at 1400 hours. The thermal environment of *Parmelia disjuncta* during the summer months is thus characterised by very modest thallus temperatures during periods of rain. Under average summer radiation conditions temperatures rise to 35°C and probably reach over 45°C under maximum radiation conditions, especially in the absence of the strong prevailing northerly winds. These data are representative of much of the low-Arctic and emphasise the quite specific thermal operating environments that many lichens have irrespective of the latitude of their geographical distribution. Kappen, Friedmann and Garty (1981) similarly document temperature profiles of rocks with contrasting southerly and northerly aspects in Antarctica. Under high radiation conditions, rock
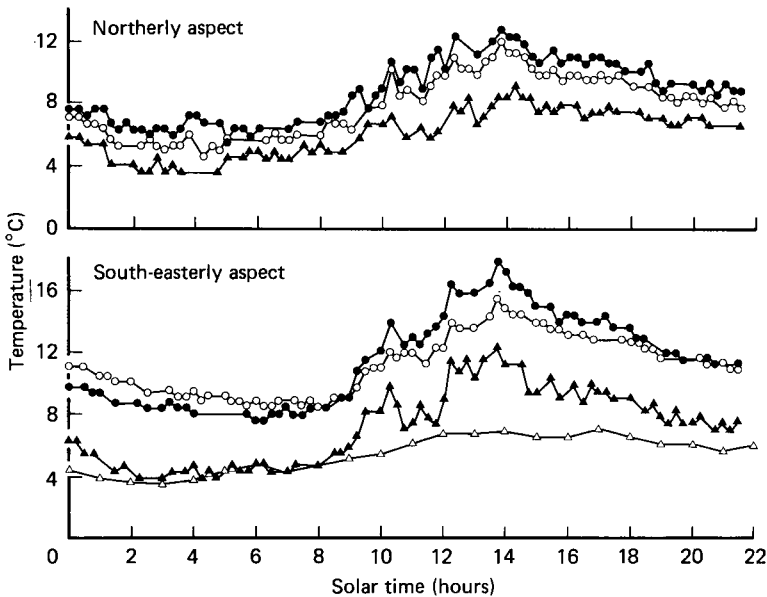
Fig. 7. The diurnal range of thallus, rock surface and air temperatures under poor radiation conditions in August. Symbols as in Fig. 6. (From Kershaw 1983.)

temperatures 15 mm below the surface are 10-15 deg C higher on northerly sunny aspects than the corresponding measurements from rocks with a southerly aspect. It is probable that these higher temperatures in the cryptoendolithic lichen zone are significantly more favourable for metabolism than the temperatures on the rock surface.

1.3 The importance of boundary layer temperatures and energy balances in the recovery succession of lichen woodland following fire

The importance of surface microclimate and its complex interactions with lichen ecology have been examined in detail in relation to the successional sequence following fire in *Stereocaulon* woodland, an extensive vegetation type in the Northwest Territories of Canada (Plate 1; Maikawa and Kershaw 1976). Johnson and Rowe (1975) have examined fire reports prepared by the Northwest Forestry Service for a region of subarctic forest which lies to the east of Great Slave Lake. They show that fire is a frequently occurring but natural event, with almost all of the fires caused by lightning. Four phases of recovery are recognised:

Phase 1, the *Polytrichum* phase with *P. piliferum, Biatora granulosa* and

Plate 1. *Stereocaulon* woodland, a characteristic vegetational type of dry eskers, drumlins and ridges in the Northwest Territories, Canada.