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Cryptogamic crust metabolism in response to temperature, water vapor, and liquid water

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Abstract

Cryptogamic crusts are communities composed of lichens, cyanobacteria, algae, mosses, and fungi. These integrated biological soil crusts are susceptible to disturbance, but if intact, appear to play a role in providing nutrients, especially nitrogen, to higher plants. Crust samples from the Colorado Plateau and the Great Basin were brought to the laboratory and exposed to atmospheres of different humidity and different amounts of liquid water. Metabolic heat rate (R_q) and carbon dioxide evolution rate (R_{CO_2}) were measured in microcalorimeters at temperatures from 5 to 40 °C. Exposure to water vapor alone had little effect, but addition of liquid water caused a marked increase in metabolic rate and a switch from anaerobic to aerobic metabolism. Crusts from both sites had maximum growth rates around 30 °C. Colorado Plateau crusts had much higher metabolic and growth rates than Great Basin crusts.
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Keywords: Cryptogamic crust; Metabolic heat rate; Respiration rate; Temperature; Water

1. Introduction

Cryptogamic soil crusts cover as much as 40–60% of desert surfaces in the intermountain western USA [1]. These microbiotic crusts are a mixture of lichens, mosses, cyanobacteria, and green algae that retain soil moisture, fix nitrogen, and protect the desert ecosystem by preceding vascular plant growth and preventing erosion [2]. Trampling by grazing cattle is most destructive in spring and summer months, but even in the winter there is a 50% reduction in crusted area compared to an ungrazed control plot [3]. Crusts are also vulnerable to destruction by hikers [4]. Crusts play an important role in nitrogen fixation [5], and may be important for making other essential elements available to higher plants [6].

Given their importance, more needs to be learned about recovery of disturbed crusts [7]. Our research explores conditions of temperature and moisture for optimal growth of microbiotic crust communities. Such information could help land managers protect microbiotic crusts during critical growth periods. In addition, the findings could help establish better inoculation techniques for reestablishing degraded crusts.

Poikilohydric organisms, such as those found in biological soil crusts, respond quickly to moisture in

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terms of physiological function. Equilibration of water content by crust organisms has been suggested to occur with atmospheric humidity as well as precipitation [8].

Aerobic respiration has two aspects: catabolism and anabolism. In catabolism, organic substrates are oxidized to produce CO_2 and energy. Part of the energy produced by oxidation is used to convert ADP and inorganic phosphate (Pi) to ATP, the rest is lost as heat.

$$\text{substrate} + O_2 + x\text{ADP} + x\text{Pi} \rightarrow CO_2 + H_2O + x\text{ATP} + \text{heat} \quad (1)$$

ATP produced in catabolism is transient, but is used for cellular work, including anabolism as shown below:

$$\text{substrate} + y\text{ATP} \rightarrow \text{growth} + y\text{ADP} + y\text{Pi} + \text{heat} \quad (2)$$

In anabolism, heat and new plant tissue are produced and ATP is hydrolyzed back to ADP and phosphate. A calorimeter measures the rate of heat loss (R_q) from both catabolism and anabolism. The rate of CO_2 production (R_{CO_2}) measures the rate of catabolism. With carbohydrate as the substrate, the growth rate or rate of anabolism (R_{SG}) is related to two measurable variables and two constants as

$$R_{SG}\Delta H_B = 455R_{CO_2} - R_q \quad (3)$$

where ΔH_B is the enthalpy change of the formation of biomass from photosynthate and Thornton's constant ($455 \pm 15\,\text{kJ mol}^{-1}$ of O_2) and is incorporated to calculate the rate of energy generated by catabolism. Thus, growth rate in terms of energy (i.e. $R_{SG}\Delta H_B$) is proportional to the difference between the measured values of R_{CO_2} and R_q. The temperature dependencies of R_{CO_2} and R_q are different [9]. The difference between $455R_{CO_2}$ and R_q therefore changes with temperature and this difference can be used to predict growth rate changes with temperature [10].

Growth rate may also be expressed as a function of the substrate carbon conversion efficiency (ε) and respiration rate (R_{CO_2}).

$$R_{SG} = R_{CO_2}\left[\frac{\varepsilon}{(1-\varepsilon)}\right] \quad (4)$$

Combining Eqs. (3) and (4) to eliminate R_{SG} gives Eq. (5)

$$\frac{R_q}{R_{CO_2}} = \left(1 - \frac{\gamma P}{4}\right)455 - \left[\frac{\varepsilon}{1-\varepsilon}\right]\Delta H_B \quad (5)$$

which relates the ratio of R_q/R_{CO_2} to ε and the substrate oxidation state, γ_P. Values of R_q/R_{CO_2} measured as a function of temperature can thus provide information on substrate carbon conversion efficiency and the oxidation state of the substrate carbon [11].

Because oxidation reactions yield so much energy (Thornton's constant), most organisms use oxidative metabolism whenever possible. In the absence of oxygen or other oxidants, anaerobic metabolism can occur, but usually at a much lower rate. Measurement of R_q and R_{CO_2} allows immediate recognition of anaerobic metabolism as it produces CO_2 but little heat compared with aerobic respiration.

In this study, calorespirometry was used to determine the high and low stress temperatures for desert crust under controlled conditions. When the metabolic heat rate exceeds energy made available through catabolism of carbohydrate, the crust is considered to be stressed [12].

2. Materials and methods

In the Great Basin, samples of biological soil crust were collected between shrubs in a stand of basin big sagebrush (*Artemisia tridentata* Nutt. ssp. *tridentata*) in Salt Creek canyon near Nephi, UT during the fall and winter of 1999. Samples were collected at an elevation of 1775 m in an area occasionally grazed by cattle.

Samples of crust were also taken from the Colorado Plateau at Little Valley near Fruita, CO at an elevation of 1500 m. In both cases the collected crusts were approximately 2 cm thick and 15 cm in diameter. They were collected in Petri dishes so the integrity of the crust could be maintained. No moisture was added at the time of collection. Samples were subdivided into two sets, one to measure the effects of humidity and the other to measure the effects of different amounts of liquid water.

Saturated salt solutions and water were used to control the relative humidity of the air surrounding crust samples in sealed jars at 31, 52, 79, and 100%, for 30

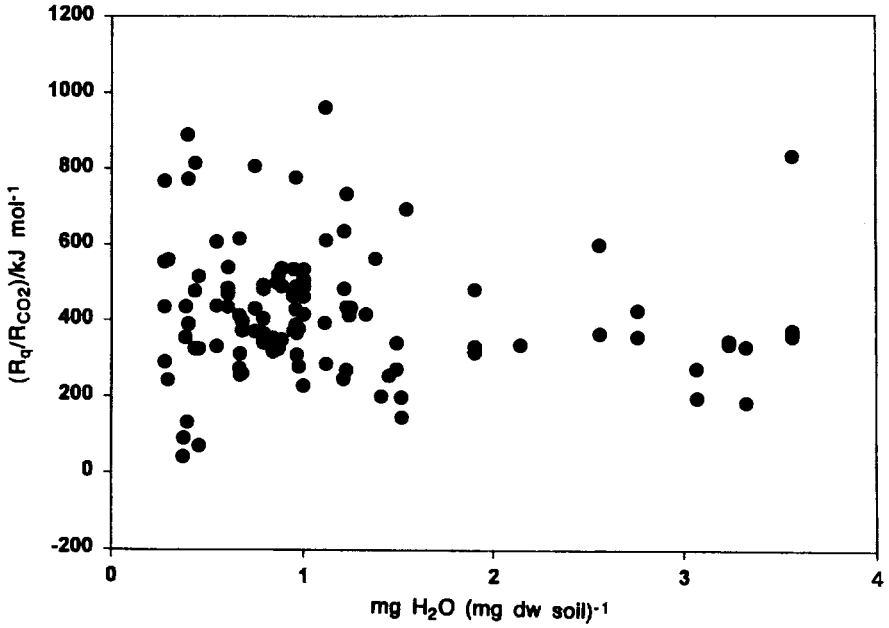

Fig. 1. Cryptogamic crust metabolic efficiency, R_q/R_{CO_2} (kJ mol^{-1}), in response to addition of liquid water (mg H_2O per mg dry weight of soil).

days of equilibration. A sample with no water or solution added to the jar was labeled 0% humidity and used as a control. The amount of water taken up was measured by weighing the crust before and after the equilibration period. Following equilibration, samples were cut off at the base of the mat and excess soil removed. Approximately 500 mg of visually equivalent crust was added to each calorimeter ampoule. Measurements of metabolic heat rate (R_q) and the rate of carbon dioxide evolution (R_{CO_2}) were taken in the isothermal mode in a Calorimetry Sciences Corporation Model 4100 calorimeter at 20, 15, 10 and 5 °C or

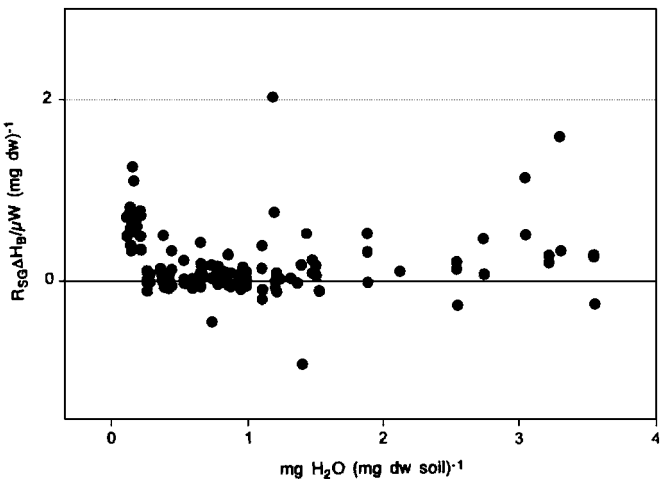

Fig. 2. Cryptogamic crust predicted growth rate, $R_{SG}\Delta H_B$ (μW per mg dry weight), in response to addition of liquid water (mg H_2O per mg dry weight of soil).

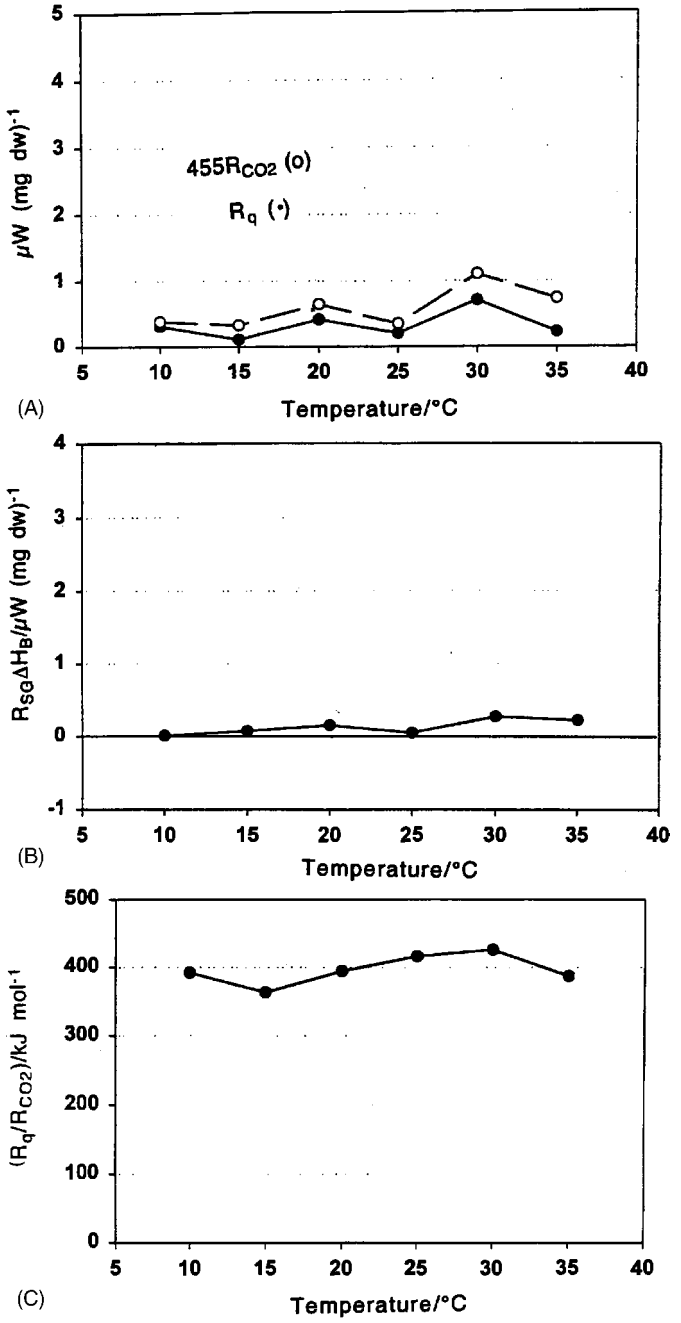

Fig. 3. Cryptogamic crust from the Great Basin (Nephi, UT). (A) Metabolic heat rate (R_q) (●) and respiration rate ($455R_{CO_2}$) (○), as microwatts (μW) per mg dry weight, measured at different temperatures. (B) Predicted growth rate, $R_{SG}\Delta H_B$ in μW per mg dry weight, at different temperatures. $R_{SG}\Delta H_B$ values less than zero mean no growth. (C) Metabolic efficiency, R_q/R_{CO_2} in kJ mol^{-1}, at different temperatures.

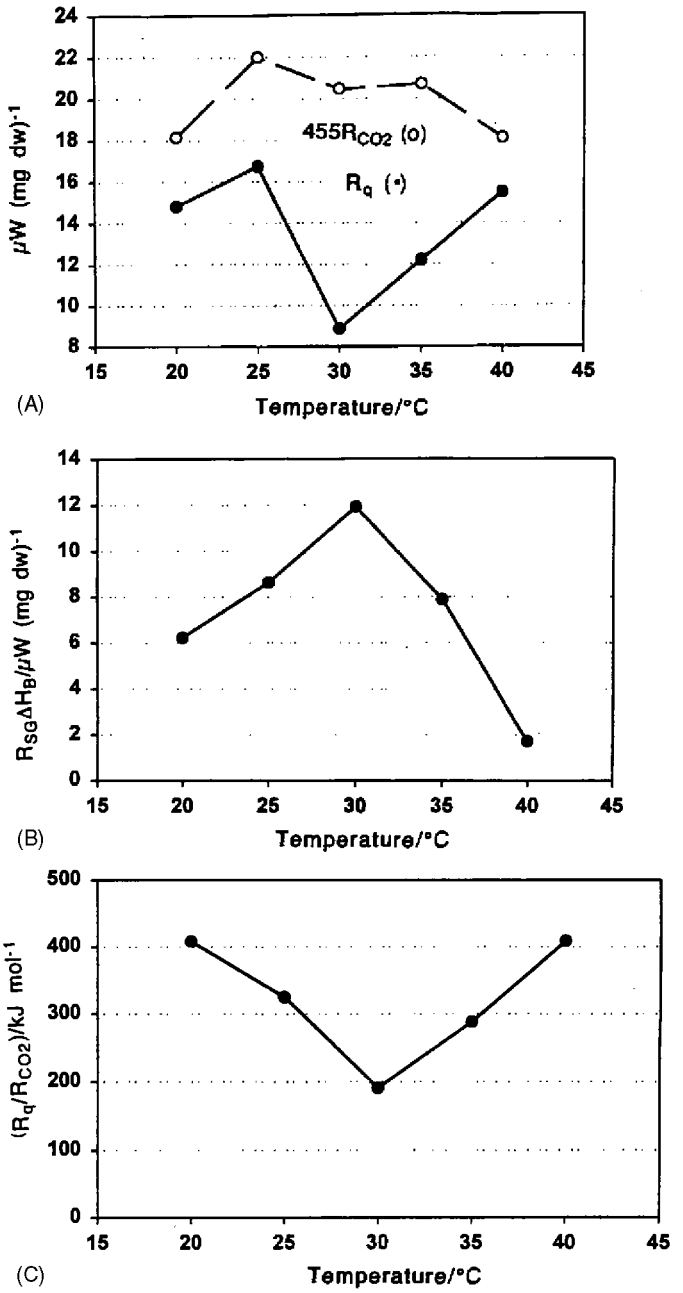

Fig. 4. Cryptogamic crust from the Colorado Plateau (Fruita, CO) as in Fig. 3. (A) Metabolic heat rate (R_q) (●) and respiration rate ($455R_{CO_2}$) (○). (B) Predicted growth rate ($R_{SG}\Delta H_B$). (C) Metabolic efficiency (R_q/R_{CO_2}).

at 25, 30, 35 and 40 °C [11]. There were six replicates for each measurement. The uncertainty for measuring R_q was +5% and for R_{CO_2} ±20%. Following calorimetry, the soil crust was dried overnight at 65 °C in a vacuum oven and the dry weight obtained. The sample was then combusted in a muffle furnace at 400 °C and the weight was obtained again. About 10% of the dry weight of the crust was lost in the muffle furnace, and thus considered to be organic matter.

In a separate experiment, different amounts of distilled water were added to dry crust samples 2 h preceding calorimetric measurements. Samples were then prepared and analyzed as described above.

3. Results

Increasing relative humidity up to 100% had no effect on crust metabolism. Heat rates (R_q) ranged from +0.068 to −0.045 μW and CO_2 rates (expressed as $455R_{CO_2}$) from 0.614 to 0.031 μW. The ratio of R_q/R_{CO_2} ranged from +50 to −50 kJ mol^{-1} with an average near zero. These data demonstrated that anaerobic respiration was the major process in crusts exposed to atmospheric humidity. However, addition of even small amounts of liquid water switched the R_q/R_{CO_2} ratio to values around 400 kJ mol^{-1} (Fig. 1), very typical of aerobic respiration [10,11]. Liquid water thus promotes growth of the crust (Fig. 2).

Cryptogamic crusts from the Great Basin with added liquid water showed an excess of catabolism ($455R_{CO_2}$) over heat loss (R_q) at all temperatures from 15 to 35 °C (Fig. 3A), predicting growth (Fig. 3B). Efficiency changed little with temperature (Fig. 3C).

Biological soil crusts from the Colorado Plateau showed much higher (10–20-fold higher) metabolic rates. Note the different scales in Figs. 3 and 4. We conclude that crusts at both locations grow best at temperatures around 30 °C, and probably not much above 40 °C (Fig. 4B).

4. Discussion

Changes in the relative humidity of the air had no effect on metabolism indicating that, contrary to earlier reports [8], biological crusts do not respond to water vapor. Addition of liquid water gave an immediate metabolic response. Liquid water thus promoted growth of the crust (Fig. 2). This probably relates to the central role of blue-green algae in metabolism of the desert crust community [13,14]. Lange et al. [13] have shown that lichens with green algal photobionts respond to water vapor, while lichens with blue-green photobionts respond only to liquid water. Microtopography of crust growth may orient the community to maximize water retention [15]. The filamentous blue-green algae has a gelatinous coating which, in the absence of liquid water, may prevent oxygen uptake and carbon dioxide production, and thus inhibit oxidative metabolism [14].

Biological soil crusts from the Great Basin site and the Colorado Plateau site were from similar elevations but about 270 km apart. Both sites are cold desert sites. Nevertheless the metabolic response of the moistened crust to temperature was slightly different for the two populations. This suggests adaptation to different climates. Most precipitation at the Great Basin site near Nephi comes as snow in the winter with only 28% of the annual precipitation arriving between July and October. On the other hand the Colorado Plateau receives much summer monsoonal moisture with 43% of the annual precipitation received in the months July through October. The dark color of samples from both locations may serve to raise the crust temperature above the air temperature, allowing growth earlier in the spring. It has been suggested that different rainfall patterns change the species composition of biological crusts [8].

Future research will include biological soil crusts from a variety of sites and conditions which may help us understand better the interactions between metabolism and microclimate.

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