

Calorimetric Studies of Cryptogamic Crust Metabolism in Response to Temperature, Water Vapor, and Liquid Water

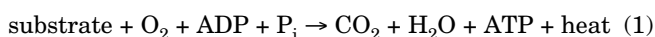
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Abstract—Cryptogamic crusts are communities composed of lichens, cyanobacteria, algae, mosses, and fungi. These integrated soil crusts are susceptible to disturbance, but if intact, appear to play a role in providing nutrients, especially nitrogen, to higher plants. It is not known how or under what conditions desert crusts can grow. Crust samples from localities on the Colorado Plateau and the Great Basin were brought to the laboratory and exposed to atmospheres of different humidity and different levels of liquid water. Both metabolic heat rate (q) and carbon dioxide evolution rate (R_{CO_2}) were measured in microcalorimeters at temperatures from 10 to 35 °C. While exposure to water vapor alone had little effect, addition of liquid water caused a marked increase in metabolic rate and a switch from anaerobic to aerobic metabolism.

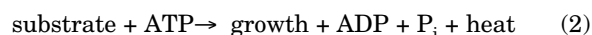
Cryptogamic soil crusts cover as much as 40 to 60 percent of desert surfaces in the Intermountain Western U.S.A. (Evans and Johansen 1999). These microbiotic crusts are a mixture of lichens, mosses, cyanobacteria, and green algae that retain soil moisture, fix nitrogen, and protect the desert ecosystem by preceding vascular plant growth and preventing erosion (Brotherson and Rushforth 1983). Grazing by cattle is most destructive in spring and summer months, but even in the winter there is a 50 percent reduction in crusted area compared to a control plot (Memmott and others 1998). Crusts are vulnerable to destruction by roaming cattle and hikers (Anderson and others 1982). Crusts play an important role in nitrogen fixation (Evans and Belnap 1999). They may also be important for making other essential elements available to higher plants (Harper and Pendleton 1993).

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 to ATP, the rest is lost as heat.



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



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 (q) from both catabolism and anabolism. The rate of CO_2 production (R_{CO_2}) measures the rate of catabolism. With carbohydrate as the specific substrate, predicted growth rate of structural biomass or rate of anabolism (R_{SG}) is related to three measurable variables and one constant as in equation 3.

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

ΔH_B is the enthalpy change for the formation of biomass from photosynthate and Thornton's constant ($455 \pm 15 \text{ kJ mol}^{-1}$ of O_2) is incorporated to calculate the rate of energy generated by catabolism. Thus, growth rate in terms of energy (in other words, $R_{SG}\Delta H_B$) is proportional to the difference between the measured values of R_{CO_2} and q . The temperature dependencies of R_{CO_2} and q are different (Taylor and others 1998). The difference between $455R_{CO_2}$ and q therefore changes with temperature and this difference can be used to predict growth rate changes with temperature (Criddle and others 1997).

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

$$R_{SG} = R_{CO_2}[\epsilon/(1-\epsilon)] \quad (4)$$

Combining equations 3 and 4 to eliminate R_{SG} gives equation 5

$$q/R_{CO_2} = (1-\gamma_P/4)455 - [\epsilon/(1-\epsilon)]\Delta H_B \quad (5)$$

which relates the ratio of q/R_{CO_2} to ϵ . Values of q/R_{CO_2} measured as a function of temperature can thus provide information on substrate carbon conversion efficiency (ϵ) and the oxidation state of the substrate carbon, γ_P (Hansen and others 1994).

Anaerobic respiration by definition does not involve oxygen uptake and conserves much less of the available energy

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than does aerobic catabolism. For this reason, most organisms use oxidative metabolism whenever possible. Anaerobic respiration is immediately recognizable from measurements of q and R_{CO_2} because it produces CO_2 but little or no heat compared to aerobic respiration.

In this study, calorimetry 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 plant is considered to be stressed (Smith and others 2000).

Given their importance, more needs to be learned about recovery of disturbed crusts (Belnap 1993). Our research explores conditions of temperature and moisture for optimal growth of microbiotic crust communities. Such information could help land managers protect the crusts during critical growth periods. In addition, the findings could help establish better inoculation techniques.

Materials and Methods

Samples were collected near Nephi, Utah, during the fall and winter of 1999. The cryptogams grew in a sagebrush community occasionally grazed by cattle. 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 were used to adjust the relative humidity of the air surrounding crust samples in sealed jars to 31, 52, 79, and 100 percent, followed by 30 days of equilibration. A sample with no water or solution added to the jar was labeled 0 percent humidity and used as a control. The amount of water taken up was measured by weighing the crust before and after the equilibration period. In a separate experiment, different amounts of distilled water were added to the crust samples two hours preceding the calorimetric measurements. Following this preparation, the 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 ampule. Measurements of metabolic heat rate and the rate of carbon dioxide evolution were taken in the isothermal mode in a Calorimetry Sciences Corp. Model 4100 calorimeter at 10, 15, 20, 25, and 30 °C.

Results and Discussion

Increasing relative humidity up to 100 percent had no effect on crusts. Heat rates (q) ranged from +0.068 to -0.045 and CO_2 rates from 0.614 to 0.031. The ratio of q/R_{CO_2} ranged from +50 to -50 $kJ\ mole^{-1}$ with an average near zero. These data demonstrate that anaerobic respiration is the only important process in crusts exposed to water vapor. However, addition of even small amounts of liquid water switches the q/R_{CO_2} ratio to values around 400 $kJ\ mole^{-1}$, very typical of aerobic respiration (Criddle and others 1997; Hansen and others 1994). Liquid water thus promotes growth of the crust (fig. 1). This probably relates to the central role of blue-green algae in metabolism of the desert

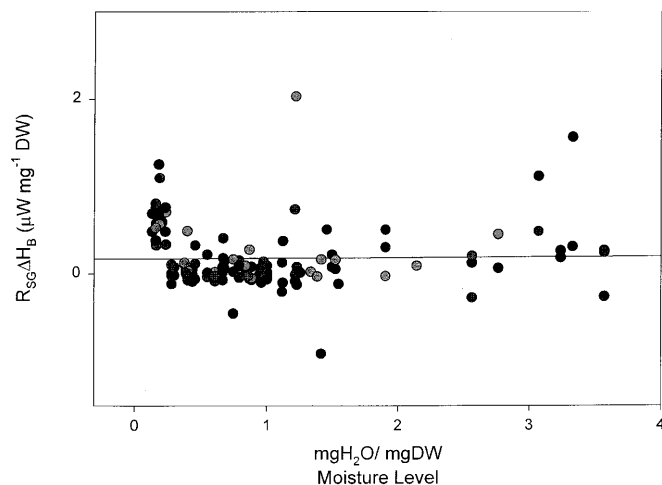


Figure 1—Cryptogamic crust predicted growth rate, $R_{sg}\Delta H_B$ ($\mu W/mg$ dry weight), in response to addition of liquid water ($mg\ H_2O/mg$ dry weight).

crust community. Lange and others (1988) 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 (George and others 2000). The filamentous blue-green algae have a gelatinous coating which, in the absence of liquid water, may prevent oxygen uptake and carbon dioxide production, and thus inhibit oxidative catabolism (Lange and others 1998).

Cryptogamic crusts with added liquid water had a slight, but not significant, decrease in metabolic efficiency with increasing temperatures (fig. 2). Thus rather than growing at a certain season of the year, cryptogamic crusts may show an opportunistic growth response to a significant rainfall event at any temperature from 10 to 35 °C.

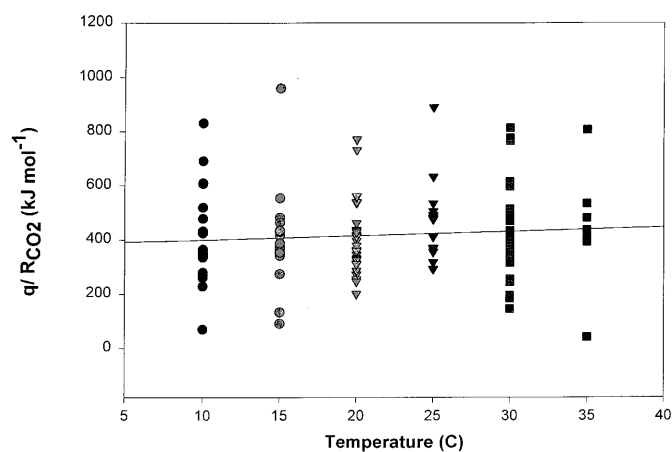


Figure 2—Cryptogamic crust metabolic efficiency of carbon conversion, q/R_{CO_2} ($kJ\ mol^{-1}$), in response to temperature, °C.

Conclusions

- Changing the relative humidity of the air does not affect metabolism.
- Liquid water is a necessity for cryptogamic crusts to grow.
- Temperature seems to have no effect on either carbon conversion efficiency or growth rates.
- Growth of cryptogamic crusts is regulated by availability of liquid water rather than by temperature.

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