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2.10 Primary Production of the Cryptoendolithic Microbiota from the Antarctic Desert

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Summary: Primary production in the Antarctic cryptoendolithic microbiota can be determined from biomass and photosynthetic $^{14}CO_2$ incorporation measurements. Even though good nanoclimate data are available, it is difficult to determine the amount of time when abiotic conditions permit metabolism. Making appropriate assumptions concerning the metabolism of the cryptoendolithic microbiota during periods of warmth, light and moisture, the primary production of the biota was calculated to be on the order of 0.108 to 4.41 mgC/m^2/yr, with a carbon turnover time from 576 to 23,520 years. These production values are the lowest found on planet Earth.

Zusammenfassung: Die Primärproduktion von antarktischen kryptoendolithischen Mikroorganismen kann aus der Biomasse beziehungsweise aus der photosynthetischen $^{14}Co_2$ Bindung bestimmt werden. Trotz des Vrliegens guter nanoklimatischer Daten ist es noch schwierig, die Zeitabschnitte zu bestimmen, in denen die abiotischen Bedingungen Stoffwechselaktivitäen erlauben. Unter der Annahme bestimmter Zeiträume für den aktiven Stoffwechsel, der sich durch Wärme, Licht und Feuchtgehalt ergibt, kann die Primärproduktion dieser Lebensgemeinschaften in der Größenordnung von 4.41 mg Kohlenstoff pro m^2 und Jahr liegen. Der vorliegende Kohlenstoffumsatz könnte sich innerhalb von 576 bis 23.520 Jahren abspielen. Solche Produktionswerte stellen die niedrigsten der Erde dar.

1. INTRODCUTION

In the Antarctic desert, there exists a microbal ecosystem which lives in the pore spaces of sandstone (FRIEDMANN 1982). This microbiota, termed cryptoendolithic ("hidden within rock"), is dominated by lichens of the genera *Buellia* and *Lecidea* (FRIEDMANN 1982). The primary producers of the ecosystem are the lichen photobiont, occasionally a green alga, *Hemichloris antarctica* (TSCHERMAK-WOESS & FRIEDMANN 1984), and cyanobacteria. The primary decomposers consist of the lichen mycobiont, filamentous fungi, bacteria and yeast (FRIEDMANN 1982). The primitive community lives from 1—5 mm under the surface rock crust where light can penetrate and water, from occasional snow melt (FRIEDMANN 1978), can percolate into the microbial zone. The rocks containing the microbiota are stained on the surface with ferric precipitates which absorb solar heat and warms the upper few mm of rock to as high as 11° C, when conditions permit (FRIEDMANN et al. 1987). The primary research site for the studies reviewed here was Linnaeus Terrace, Upper Wright Valley, Asgard Range, Ross Desert, Antarctica (77° 36' S, 161° 05' E) at an elevation of 1600 m. The mean annual air temperature is –22° C with a mean temperature for January, the warmest month, being –6.7° C (FRIEDMANN et al. 1987).

When one considers the primary production of an ecosystem, it is important to know the standing stock (biomass) and the production rate (in terms of carbon incorporated per unit biomass or area per time period). With these two values, a carbon turnover time can be calculated which gives an estimate of the time it would take for the complete renewal of the carbon in a living ecosystem.

Biomass measurements of the photosynthetic biota can be made in many ways: for crops or forests, the plants can be dried and weighed. For aquatic algae, the biomass is usually measured by determining the amount of chlorophyll a present, followed by correction for phaeopigments. The cryptoendolithic microbiota is such that good extraction of chlorophyll pigments is not achieved, probably due to the tenacious interaction between the lichen phycobiont and mycobiont. In this microbiota, which is composed of algae, fungi, yeasts and bacteria, the biomass can be measured by determining the amount of lipid phosphate (VESTAL 1988b) or ATP (TOUVILA & LAROCK 1987) present. These give actual viable biomass measurements. Also, both measurements show good correlation (VESTAL 1988b).

Determination of production rates is also relatively easy, given the assumption that a laboratory determination can approximate the in situ conditions. Rocks containing the biotic zone are ground to the consistancy of sand, and in vitro experiments are done under controlled conditions. These measure the rates of incorporation of

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^{14}C-bicarbonate into the cells in the presence of light. With this number in mind, and knowing the amount of time the cells metabolize carbon in nature, production rates can be calculated on an annual basis. Then a carbon turnover can be calculated by dividing the production into the biomass.

One of the main problems with the cryptoendolithic microbiota is determining the amoung of time that metabolism can occur under ambient environmental conditions. This is because this ecosystem is so intimately associated with the physical and chemical environment. It is almost impossible to do in situ primary production experiments for this reason. Experiments demonstrating the incorporation of ^{14}C-labelled bicarbonate by intact rocks have been reported (VESTAL 1988a), but in order to do direct primary production measurements, a detailed analysis of the temperature, moisture and light would have to be done during the time of the incubation. The light, temperature and moisture data taken for the calculations presented are too crude for in situ primary production studies. Therefore, it will be the purpose of this review to discuss the physical and chemical conditions which impinge on the primary production during an Austral season, in this unique ecosystem, and to calculate the production and carbon turnover based on logical assumptions about the ecosystem.

2. EFFECT OF LIGHT

NIENOW et al (1988) have shown that light penetration into the biotic zone varies as a function of depth in the rock with about an order of magnitude decrease per mm depth. On a bright, sunny day at Linnaeus Terrace, the maximum ambient light intensity is about 1800—2000 µmoles photons/m^2/s. This means that the amount of light is about 0.02—20 µmole photons/m^2/s in the biotic zone. This is increased an order of magnitude when the rock is wet, so under ideal light conditions and saturated with water (from snow melt), the microbial community is exposed to about 0.2—200 µmole photons/m^2/s. An average light intensity would therefore be about 2—20 µmole photons/m^2/s some 2—3 mm below the rock surface.

3. EFFECT OF WATER

All cells must have water in order to carry out their necessary enzymatic reactions. In the cryptoendolithic microbiota, water comes to the cells after infrequent (10—15 times/year; FRIEDMANN et al. 1987) snowfall and subsequent melting after sunny weather returns. When the water percolates into the porous rock surface, it is, of course, vectored downward by gravity, but is also retained within the interstices. If there is a small amount of water (i. e. not enough to saturate the rock), the pore spaces just under the surface will become saturated with water and it will not progress further. As the rocks heat up, there will be some evaporation and the interstices will no longer be saturated with water liquid, but the pores will become filled with water vapor thus maintaining a high relative humidity (RH). This high RH can last for 1—2 weeks (FRIEDMANN et al. 1987) depending on the evaporative losses due to heating and wind. Under these conditions, the cryptoendolithic microbiota can carry out some metabolism, but at a rate 6—10 times less than the wet rate (VESTAL 1988a).

4. EFFECT OF TEMPERATURE

Temperature has one of the greatest influences on the cryptoendolithic microbiota. Temperature changes in the rock in summer are due to solar heating, so periods of metabolism are mostly at the mercy of the sun. Wind can affect the heat retention of the rocks and is therefore also important. It has been shown (VESTAL 1988a) that metabolism really begins at about –5° C, where light-driven CO_2 incorporation into cells is greater than that found in dark controls, after 1 hour. As the emperature increases, so does photosynthesis with optima at 5 and 15° C. Above 15° C, photosynthesis collapses. Thus the community responds according to the accepted definition of psychrophily (MORITA 1975); that is, a metabolic optimum at 20° C or lower, and a minimum temperature at 0° C or less. When the temperature remains constant, microbial photosynthetic activity actually increases linearly at temperatures below 15° C. The experiments cited were carried out for 12 hours, but longer times could be expected to yield higher production rates. At temperatures above 15° C, photosynthetic metabolism shows a typical thermal denaturation response. A similar temperature range for positive net photosynthesis was shown with cryptoendolithic lichens (KAPPEN & FRIEDMANN 1983).

In an intact rock, MCKAY & FRIEDMANN (1985) have shown that temperature excursions occur above and below 0° C on a short time scale (minutes). These temperature fluctuations thus affect the rate of metabolism of the microbiota. On a longer time scale (hours) (FRIEDMANN et al. 1987) there are definite diurnal temperature fluctuations (related to sunlight) with a daily amplitude of about 20—30° C, with excursions from +10 to –20° C having been measured. Thus there is a "normal" period of metabolism during the middle of a sunny day of 4—6 hours when metabolism is at a maximum for the temperature conditions.

5. CHEMICAL EFFECTS

When the rock becomes wet, and the cryptoendolithic zone is warm, it can carry out normal metabolism. However, when the zone is wet, the cells are also subjected to their chemical environment which can also have an impact on the photometabolism. The presence and concentration of essential inorganic elements such a nitrogen, phosphorus and sulfur, as well as trace elements, can affect the metabolic rate in the microbiota. If there have been repeated snow melts, saturating the interstices of the rock, many soluble elements may "wash through" the microbial zone so as to limit the metabolism of the microbiota. Recently, MANCINELLI et al. (1987), have shown that nitrogen does not cycle detectibly in the microbiota, but that atmospheric nitrate is the sole source of exogenous nitrogen. Nitrate deposition is about 70 mg/m^2/yr on the rocks, with the concentration of nitrate in the rock being about 4µg/g and of ammonia, about 2 µg/g rock (FRIEDMANN & KIBLER 1980). If one washes 100 g of crushed biotic zone with distilled, deionized water, about 95 µg/l of nitrate can be measured. Even though the available nitrogen levels are very small, neither nitrate, nitrite or ammonia appear to limit photometabolism of the microbiota (JOHNSTON & VESTAL 1986). Phospate concentration in the rock is also low (about 14.3 µg/l of crushed rock extract) but it appears not to be limiting to the microbiota (JOHNSTON & VESTAL 1987). JOHNSTON & VESTAL (1987) have also shown that photosynthesis is inhibited by ferrous or ferric iron at near in situ concentrations. The mechanism of this inhibition is currently under study.

The pH also has an affect. The pH of the rock has been measured to be between 4.8 and 5.8 (C Johnston and P. Hirsch pers. commun.). Inhibition occurs both below and above this range, thus the cryptoendolithic microbiota is not normally affected by changes in pH. However, ammonium produced as a result of decomposition of dead organic materials could raise the pH on a mcroscale near the cells, thus affecting photosynthesis to some extent. A graphic summary of the physical and chemical factors affecting metabolism of the cryptoendolithic microbiota can be seen in Figure 1.

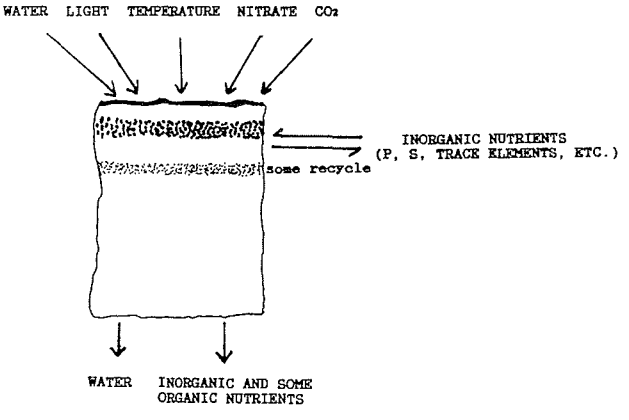

Fig. 1: Physical and chemical factors affecting the production of the cryptoendolithic microbiota from Antarctic sandstones.

6. CALCULATION OF PRODUCTION

With all of these chemical and physical factors affecting the photometabolism of the cryptoendolithic microbiota, it is a wonder that they can carry out growth and metabolism in nature. In order to try to calculate the metabolic

rate of the cryptoendolithic microbiota, temperature, light, moisture and the chemical environment must be kept in mind. So how can one come up with a reasonable primary production rate for this unique and extreme ecosystem?

The most difficult number to obtain accurately is the length of time when both physical and chemical conditions are satisfactory for metabolism in nature. If one makes a series of assumptions based on observations of the physical and chemical environment, a rough (order of magnitude) production rate can be calculated, based on $^{14}CO_2$ incorporation rates. This will now be attempted with the hope of coming up with a "best guess" for primary production in the cryptoendolithic microbiota.

FRIEDMANN et al. (1987) have shown, using annual measurements of light, temperature and moisture, that the times for northerly sloped and horizontal rocks above –5° C are about 705 and 375 hours/year, respectively (average is 540 hours/year). Time above 0° C for northerly sloped vs horizontal rocks were 520 and 110 hours/year, respectively (average is 315 hours/year). These times were also given as including a RH of above 75% and an ambient light of above 100 µmole photons/m^2/s. 75% or greater RH will allow metabolism, but at greatly reduced rates, compared to rates in liquid water. At 100% RH, VESTAL (1988a) found that metabolism was 6 times less than that of wetted cells. If light is attenutated in the rock at a rate of 1 order of magnitude/mm depth (NIENOW et al. 1988), then the highest intensity in the microbial zone would be between 10 and 180 µmoles photons/m^2/s (depending on the time of day) and much lower in regions below the upper layers of the microbial zone. At 10 µmoles photons/m^2/s (1—3 mm inside the rock), the photosynthetic rate has been measured at 0.2 mgC/m^2/hr (VESTAL et al. 1984, VESTAL 1988a) at 10° C. If one assumes this number to be appropriate for light intensity (keeping in mind that the cells below about 1 mm will be exposed to lower light intensities, due to the pigmentation of the top layer), the metabolic rate at –5° C is 10% of the 10° C rate (i. e. 0.02 mgC/m^2/hr) (VESTAL et al. 1984, VESTAL 1988a). At 0° C, the rate is 70% of the 10° C rate (i. e. 0.14 mgC/m^2/hr) (VESTAL et al. 1984, VESTAL 1988a).

Another assumption must be made at this point. When the rocks are saturated with liquid water, which occurs for a day or less after snow melts, the metabolism is at a maximum. However, the actual rate of metabolism would be on the order of 10% or less of the wet rate between 75 and 100% RH, which can last for up to two weeks (FRIEDMANN et al. 1987). For these purposes, 10% will be assumed, but 1% may be more realistic, so calculations making this assumption will also be presented.

Making the above assumptions of time, production rate and percent time that water permits metabolism, the following data can be used to calculate a production: average production rate per hour is 0.02 or 0.14 mgC/m^2/hr

TEMPERATURE	Horizontal rock	Northerly sloped rock
Time above –5° C*	375 hours	705 hours
	Average = 540 hours	
Time above 0° C*	110 hours	520 hours
	Average = 315 hours	

LIGHT
Production at 10 µmoles photons/m^2/s and 10° C = 0.2 mgC/m^2/hr**
If –5° C is 10% of 10° C rate**, then production = 0.02 mgC/m^2/hr
If 0° C is 70% 0f 10° C rate**, then production = 0.14 mgC/m^2/hr

MOISTURE
Wet rate is 6–10 times the 100% RH rate**, therefore assume 1–10% of wet rate as hours > 75% RH

CALCULATION OF PRODUCTION
ASSUPTION A: If for –5° C at 10% rate = 54 hours, then 0.02 mgC/m^2/hr X 54 hr = 1.08 mgC/m^2/yr = 0.00108 gC/m^2/yr
ASSUPTION B: If for –5° C at 1% rate = 5.4 hours, then 0.02 mgC/m^2/hr X 5.4 = 0.108 mgC = 0.000108 gC/m^2/yr
ASSUPTION C: If for 0° C at 10% rate = 31.5 hours, then 0.14 mgC/m^2/hr X 31.5 = 4.41 mgC = 0.00441 gC/m^2/yr
ASSUPTION D: If for 0° C at 1% rate = 3.15 hours,then 0.14 mgC/m^2/hr X 3.15 = 0.441 mgC = 0.000441 gC/m^2/yr

CALCULATION OF CARBON TURNOVER TIME
Biomass = 2.54 gC/m^2***
ASSUPTION A: 2.54/0.00108 = 2,352 years
ASSUPTION B: 2.54/0.000108 = 23,520 years
ASSUPTION C: 2.54/0.00441 = 576 years
ASSUPTION D: 2.54/0.000441 = 5760 years

Tab. 1: Assumptions and calculations for production of the Antarctic cryptoendolithic microbiota. * FRIEDMANN et al. 1987, **VESTAL 1988a. ***VESTAL 1988B.

ECOSYSTEM	ASSUMPTIONS*	BIOMASS (gC/m2)	PRODUCTION (gC/m2/yr)	TURNOVER (years)
Linnaeus Terrace, Antarctica	A	2.54	0.00108	2,352
	B	2.54	0.000108	23,520
	C	2.54	0.00441	576
	D	2.54	0.000441	5760
Tropical rain forest		45,000	2,200	20.5
Temperate evergreen		35,000	1,300	26.9
Temperate deciduous		30,000	1,200	25
Temperate grassland		1,600	600	2.7
Tundra and alpine		600	140	4.3
Swamp and marsh		15,000	2,000	7.5
Agriculture land		1,000	650	1.5
Open ocean		3	125	0.024
Continental shelf		10	360	0.027
Estuaries		1,000	1,500	0.7

Tab. 2: Comparison of biomass, production and carbon turnover time of the Antarctic cryptoendolithic microbial ecosystem to other ecosystems around the globe. All non-Antarctic data are from WHITTAKER (1975). * See Table 1 for explanation of the assumptions made for these calculations.

for –5 and 0° C, respectively; 1 and 10% of the time moisture is satisfactory for metabolism; 540 hours for >–5° C and 315 hours for >0° C for both northerly sloped and horizontal rocks. The calculated primary production rates and turnover times are seen (Tab. 1). The viable biomass has been measured for the cryptoendolithic microbiota and was 2.54 g C/m^2 (VESTAL 1988b).

If one compares these data with other viable biomass, primary production and carbon turnover measurements found in other ecosystems around the globe (Tab. 2), it can clearly be seen that the biomass is small, the production rate is extremely low and the carbon turnover time is very long. It should be noted that the effect of the chemical environment was not considered in the calculation, because only preliminary data are available. If it is considered that the time for metabolism could be shorter, then the production values would be smaller and the carbon turnover time would be much longer. The assumptions made, however, are probably in the right order of magnitude, so the calculations may give a fair approximation of what is occurring in nature. Obviously, much more work is needed to come up with data so that a more reliable number for primary production can be calculated. It would be important to know more precise times for metabolism due to the changes in physical conditions so that they could be integrated with the metabolic rate data under all conditions. The effects of the chemical environment on metabolism would add important information. Because the biomass measurements represent the total community biomass (i. e. algae as well as fungi and bacteria), it would be important to determine how much of the total biomass is algal. It is obvious that the Antarctic cryptoendolithic microbiota living under such extreme conditions of temperature, light, moisture and posible nutrient limitations, is the most unproductive ecosystem yet studied on planet Earth.

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