Temperature sensitivity of bacterial growth in a hot desert soil with large temperature fluctuations

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ABSTRACT

Hot desert ecosystems are characterized by high soil temperatures with large fluctuations annually and diurnally. Thus, one could hypothesize that not only the microbial community would be adapted to high temperatures, but also have a large temperature range conducive for growth. We determined the temperature sensitivity of the soil bacterial community from the Chihuahuan Desert, Big Bend National Park, Texas, USA, using leucine incorporation as a proxy for bacterial growth. Soil samples were taken during early spring and mid-summer from the surface (0–5 cm) and deeper (15–20 cm) soil layers. Mean winter soil temperature preceding the spring samples was 15 °C and in summer 36 °C at both depths, but with larger amplitude in the top soil than deeper down. T_{min} was significantly lower in the top 0–5 cm than at 15–20 cm, −1.2 and 0.0 °C, respectively. T_{opt} also was higher in the top soil than deeper down, 42.9 and 41.4 °C, respectively, resulting in a larger temperature range for growth ($T_{opt} - T_{min}$) in the top soil reflecting the larger temperature fluctuations in this layer. There were no significant differences in cardinal temperatures for bacterial growth in soils sampled in early spring and mid-summer despite large seasonal differences in temperatures, showing that long periods of colder temperatures was less important than periods of high temperatures as selection pressure for temperature sensitivity. Comparing with earlier results from Antarctic soils (Rinnan et al., 2009), which in contrast represent an extremely low temperature environment, we suggest that the range of temperature cardinal temperatures for soil bacterial communities globally varies from around −15 to 0 °C for T_{min} and 25 to 45 °C for T_{opt}.

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1. Introduction

Soil temperature directly influences microbial activity, like growth, with usually more rapid bacterial growth at higher temperatures. Soil temperature will also determine the temperature sensitivity of the microbial community by selecting for a community adapted to the prevailing temperature regime. This has repeatedly been shown for bacterial growth in soil, both in natural temperature gradients (Tibbles and Harris, 1996; Rinnan et al., 2009), laboratory experiments (Ranneklev and Bååth, 2001; Bárcenas-Moreno et al., 2009; Birgander et al., 2013), and using experimental warming in field experiments (Rousk et al., 2012). Similar results have also been found due to temperature shifts in composts (McKinley and Vestal, 1984).

The effect of temperature on growth of bacteria is characterized by three cardinal temperatures; a minimum temperature for growth (T_{min}), an optimum temperature (T_{opt}) and a maximum temperature (T_{max}). The cardinal temperatures are determined by measuring growth at different temperatures and modeling the extreme temperatures, T_{min} and T_{max}, where growth is zero. One model, originally described by Ratkowsky et al. (1982, 1983) for pure culture of bacteria, has since been commonly used for predictive purposes in food microbiology (McMeekin et al., 2013). Growth below T_{opt} is in this model described by a quadratic relationship, resulting in the square root of bacterial growth decreasing linearly with decreases in temperature and where T_{min} can be determined by extrapolation to where growth is zero (Ross et al., 2010). T_{min} determined in this way is a theoretical concept, sometimes coined apparent T_{min}, but it is a useful characteristic supposed to be little affected by other environmental conditions (McMeekin et al., 1987, 2013). Above T_{opt} growth decreases rapidly to T_{max}, and is modeled by a negative exponential function (Ratkowsky et al., 1983). Although initially used for pure culture of microorganisms, the Ratkowsky model, especially the part below T_{opt}, has repeatedly been found also to apply to growth of bacterial

communities both in soil and water (Bell and Ahlgren, 1987; Li and Dickie, 1987; Díaz-Raviña et al., 1994; Pietikäinen et al., 2005; Rinnan et al., 2009; Rousk et al., 2012), often stated that below T_{opt} bacterial growth can be modeled by a square root equation.

The temperature relationship of bacterial growth is not symmetrical around T_{opt}. Below optimum bacterial growth exhibits a more gradual decrease with decreasing temperature compared to the drastic decrease with increasing temperature above optimum. Thus, mean T_{min} was around 30 °C lower than T_{opt}, when data from 47 different bacterial strains were compared, while mean T_{max} was only around 3 °C higher than T_{opt} (Rosso et al., 1993). A similar asymmetry is also found when bacterial communities in soil and water are studied (Li and Dickie, 1987; Pietikäinen et al., 2005; Rinnan et al., 2009; Rousk et al., 2012), which indicates a universal physiological response to changes in temperature. More important, the decreased growth rate at low temperatures is mainly due to decreased rates of enzymatic processes and not due to protein denaturation and cell death, leading to the more gradual change in growth rate with changes in temperature at lower temperatures compared to higher temperatures. Thus, even if the temperature decreases to a value resulting in only 20% of the growth at T_{opt}, this will only result in a small difference in growth rate between two communities adapted to different temperature regimes (Fig. 1). However, above T_{opt} the situation is different. Increasing temperature will decrease growth rates mainly due to cell death, where the increased growth rate cannot balance the death rate. This will result in a large difference in growth rate between communities adapted to different temperature regimes when the growth of the low temperature adapted community is reduced to 20% (Fig. 1). Furthermore, since the reason for the decreased growth is mainly death of the less adapted community, this will allow for a faster replacement by a better adapted community above T_{opt} than the similar situation at temperatures below T_{opt}. The slower turn-over rate at low temperatures compared to higher temperatures will also reinforce that high temperatures near or above optimum will rapidly result in an altered community adapted to high temperatures, while at temperatures below T_{opt}, the resulting community response will be small or non-existent. This was also found in a laboratory study, where soil was incubated for one month at temperatures from 5 to 50 °C (Bárcenas-Moreno et al., 2009). The initial bacterial community had a T_{opt} for growth around 30 °C. Only at temperatures $\geq$30 °C could a community adaptation to higher

temperatures be found. This was recently repeated with another soil (Birgander et al., 2013).

Desert soil with little vegetation cover is submitted to large fluctuations in daily and annual temperatures. Thus, although the mean annual temperature does not indicate extreme temperatures, summer temperatures during daytime can become very high, while night temperatures can be very low. In the Chihuahuan Desert in Texas, USA, the mean annual air temperature is 19 °C (Cable et al., 2011). However, soil temperatures are higher than air temperatures for most of the year (van Gestel et al., 2011) with daily temperature fluctuations up to 45 °C at the soil surface and up to 15 °C at 15 cm depth (van Gestel et al., 2011, 2013). Seasonally, soil temperature at 15 cm depth varies over the year from <10 °C in February to >40 °C in summer (van Gestel et al., 2011).

In the present study we have determined the temperature sensitivity of the soil bacterial community from the Chihuahuan Desert at Big Bend National Park, Texas, USA, using leucine incorporation as a proxy for bacterial growth. The following hypothesis were tested: 1) The cardinal points for bacterial growth will be shifted to higher temperatures in the desert soil compared to soils from a temperate climate; 2) The extent of this shift will be determined to a greater extent by high daily temperatures than by mean annual temperature; 3) The bacterial community in soils taken in the hot summer should have higher cardinal points than communities from cooler soil sampled in early spring, although the temperature relationships should be mainly determined by summer temperatures; 4) Bacterial communities from surface soils, with drastic variations in daily and yearly temperatures, should have higher T_{opt} and lower T_{min} than communities from deeper soil layers with less temperature variations. This should result in a larger temperature span of growth, expressed as $T_{opt} - T_{min}$, in the former soils. Lastly, this desert ecosystem would be representative of a habitat with some of the highest temperatures found in soil on earth. By comparing results from our study with an earlier study of temperature relationships of bacteria from a low temperature extreme, soils from the Antarctic Peninsula (Rinnan et al., 2009), we are able to suggest a lower and higher limit for temperature adaptation of the bacterial community in soils globally.

2. Materials and methods

2.1. Site description

The soils studied are from a gravelly, sandy loam (53% sand, 36% silt, 11% clay), originating from the Chihuahuan Desert at Big Bend National Park, located in West Texas, USA (N29°13′, W103°10′; elevation 962 m). They are inherently low in soil organic matter (1%). The 30-yr mean annual rainfall measured at nearby Panther Junction (ca. 10 km away) is 356 mm (1981–2010; www.ncdc.noaa.gov/oa/ncdc.html; COOP ID 416792), designating it as a semiarid site. Most of the annual rainfall (56%) occurs between June and September. Mean annual air temperature during 1981–2010 is 19.1 °C, with hot summers (June, July, August: 26.9 °C) and cool winters (December, January, February: 10.4 °C). The 10-year (2002–2012) mean of seasonal minimum and maximum soil temperatures at 15 cm depth in winter are 11 and 18.7 °C, respectively, and in summer 30.4 and 40.4 °C, respectively (Fig. 2). Soil surface temperatures (2009–2012) exhibit stronger seasonal and daily fluctuations with mean minimum and maximum temperatures of respectively 3.5 and 31.6 °C in winter and 24.9 and 60 °C in summer (Fig. 2).

2.2. Soil thermal regime

Soil temperatures were monitored at the surface by embedded loggers (HOBO® Pendant data loggers, Onset Computer Corporation,
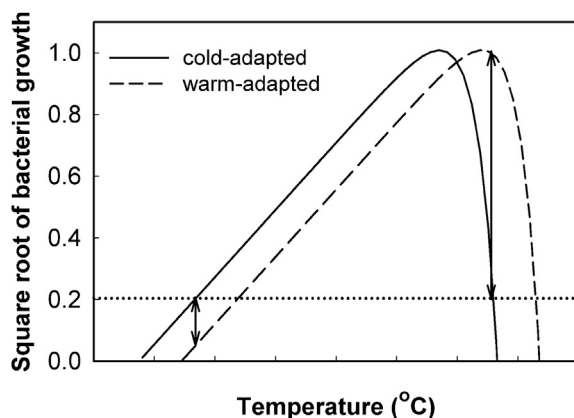
Fig. 1. Conceptual graph of the effect of temperature on the relative competitive ability of two communities differing in cardinal temperatures by 4 °C. Solid line = cold adapted community, dashed line = warm adapted community. The horizontal line indicates a growth reduction to 20% of that at optimum temperature for growth for the cold adapted community. The double arrow indicates the difference in competitive ability (using difference in growth rates as a proxy) of the two communities above and below optimum for growth of the low temperature adapted community.