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Environmental effects on distributions of culturable soil oligotrophic bacteria along an elevational gradient in the Chihuahuan Desert

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ABSTRACT

Oligotrophic bacteria have been isolated from many habitats, yet environmental regulation of their distributions in soil has not been elucidated. To address the issue of environmental influence upon oligotrophic distributions, Chihuahuan Desert soils were sampled from five sites along an elevational and vegetational gradient within Big Bend National Park during January and August of 2002 and 2003. Soils were diluted and plated on oligotrophic media, and plates were incubated at 15, 25, 35, 45 and 60 °C. Additionally, measurements of soil organic matter, pH, moisture, extractable nitrate, extractable ammonium and microbial biomass carbon were collected for each sample to relate oligotrophic bacterial distributions to soil nutrient and edaphic characteristics. Analysis of variance indicated significant site, season, incubation-temperature and interaction effects on total oligotroph numbers. Canonical correspondence analysis and multiple regressions indicated that all soil-chemistry variables significantly influenced discrete morphologies of oligotrophs. Oligotroph distributions were most congruent with soil-chemistry variation in three sites, whereas oligotrophic diversity in two sites did not adhere closely to measured environmental variables. While vegetation type may structure oligotroph communities at the two mid-elevational sites, abiotic constraints are drivers in low-desert sites.

1. Introduction

Microbial growth in stressful environments has been of interest for decades. Because many natural environments are nutrient limited (Morita, 1988), this was among the first stressors to be investigated. Microbes capable of metabolism at low concentrations of carbon are known as oligotrophs, oligophiles or oligocarbophiles. The literature is replete with studies of oligotrophs and descriptions of oligotrophic environments, but many questions concerning the ecological significance of oligotrophy remain unresolved. Of particular importance and confusion is the actual definition of oligotrophy (Schut et al., 1997). Some researchers clearly demarcate the maximum carbon content that will allow growth of oligotrophs on synthetic media, whereas others contend oligotrophs are able to divide in “weak” or “poor” media but not in “rich” media and gradients of microbial responses to environmental carbon levels have been proposed. Obligately oligotrophic bacteria (Ishida and Kadota, 1981; Ohta and Hattori, 1983) should be unable to divide (or grow poorly) once an upper threshold of carbon is encountered, whereas copiotrophs (Poindexter, 1981) divide only at relatively high nutrient concentrations. Facultative oligotrophs (Akagi et al., 1980) have been reported to grow across a wide gradient of available carbon. However, studies have not attempted to link oligotroph distributions to soil nutrients and edaphic patterns.

Oligotrophic bacteria have been isolated from marine environments (Emiliani, 1984), freshwater (Cho and Giovannoni, 2004), soils (Whang and Hattori, 1988), clinical materials (Tada et al., 1995) and ultrapure water (Kulakov et al., 2002). Studies of oligotrophs in the environment have expanded our knowledge of environmental microbiology directly, and use of dilute media has resulted in the cultivation of novel species (Davis et al., 2005). However, our understanding of oligotroph biology is limited. Very few studies have described distributions of oligotrophs relative to abiotic factors other than carbon availability. Moreover, most distributional studies of oligotrophic bacteria have been conducted in aquatic environments. Akagi et al. (1977) reported a high correlation between abundance of oligotrophs and sample depth in the Pacific Ocean. In addition, numbers of oligotrophs greatly exceeded numbers of copiotrophs and increased as carbohydrate levels decreased (Akagi et al., 1977). Yanagita et al. (1978) surveyed both freshwater and marine environments in Japan and determined that

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nitrate and dissolved organic nitrogen limited numbers of freshwater oligotrophs, whereas nitrate levels limited marine bacteria. Emiliani (1984) collected extensive abiotic data from a river system and found oligotroph distributions to be positively correlated with individual environmental factors, such as water flow rate, hydrometric level, amount of suspended solids, turbidity, temperature, conductivity, phosphate levels, primary production, water transparency and pH. However, studies of soil oligotrophs have not attempted to link distributions to environmental gradients.

Bacterial cells contain a significant portion of global carbon, nitrogen and phosphorus (Whitman et al., 1998). Moreover, it is increasingly clear that oligotrophs are common among environmental bacteria (Watve et al., 2000), and a better understanding of their distributions in nutrient-limited environments is needed. Elucidation of linkages between oligotrophic bacteria and global nutrient cycling will become more important in the face of global climate change (Zak, 2005). Therefore, the goal of this study was to determine correspondence of culturable oligotrophic bacteria to a suite of environmental parameters in an arid landscape where carbon input is limiting and low soil moisture reduces carbon availability. To quantify these linkages, plate counts of oligotrophic bacterial morphotypes on dilute media were compared to measurements of soil organic matter, pH, extractable ammonium, extractable nitrate and soil moisture along an elevational gradient in the Chihuahuan Desert. Although bacterial morphotypes cannot directly resolve responses of taxonomic groups to environmental gradients, use of morphotypes (Palumbo et al., 1994) can provide suitable spatial and temporal metrics of the culturable bacterial community.

2. Materials and methods

2.1. Study site

Big Bend National Park (BBNP), located along the United States-Mexico Border in southwest Texas, is the best expression of the Chihuahuan Desert in the United States and was the site for this study. Five sites (Fig. 1) along the Pine Canyon Watershed are being studied (Dobranic and Zak, 1999) in BBNP as part of a network of watershed sites established in five national parks and equivalent reserves (Herrmann et al., 2000). Each site is unique with respect to vegetation and elevation. The lowest elevational site sampled is within the Chihuahuan Desert scrub association near the abandoned town site of Glenn Springs (GS; 793 m) and is dominated by *Leucophyllum*, *Agave*, *Opuntia*, a number of shrub species and several species of grasses. The second site along the watershed is a creosote bajada (CR; 1010 m) dominated by *Larrea*, *Agave* and *Opuntia*. The mid-elevational site is a sotol grassland (SG; 1526 m) dominated by *Dasylirion*, *Nolina* and *Bouteloua*. The fourth site is a closed-canopy forest (OF; 1824 m) consisting of *Quercus*, *Pinus*, *Juniperus* and understory shrubs that contribute a dense layer of leaf litter throughout the year. The highest elevational site sampled is near Lost Mine Peak (LM; 2098 m) and is a high-elevation forest dominated by *Quercus*, *Juniperus* and *Pinus* with an understory of grasses.

2.2. Sample collection

Each of the five sites contains two permanently marked belt transects (100 m × 30 m) along which soils were collected. At each sampling period, five soil samples were collected along each transect at each site for bacterial cultivation. Sites were sampled during January and August of 2002 and 2003, reflecting temperature extremes encountered in BBNP. Therefore, at the scale of bacterial communities, 200 independent soil samples were collected during this study.

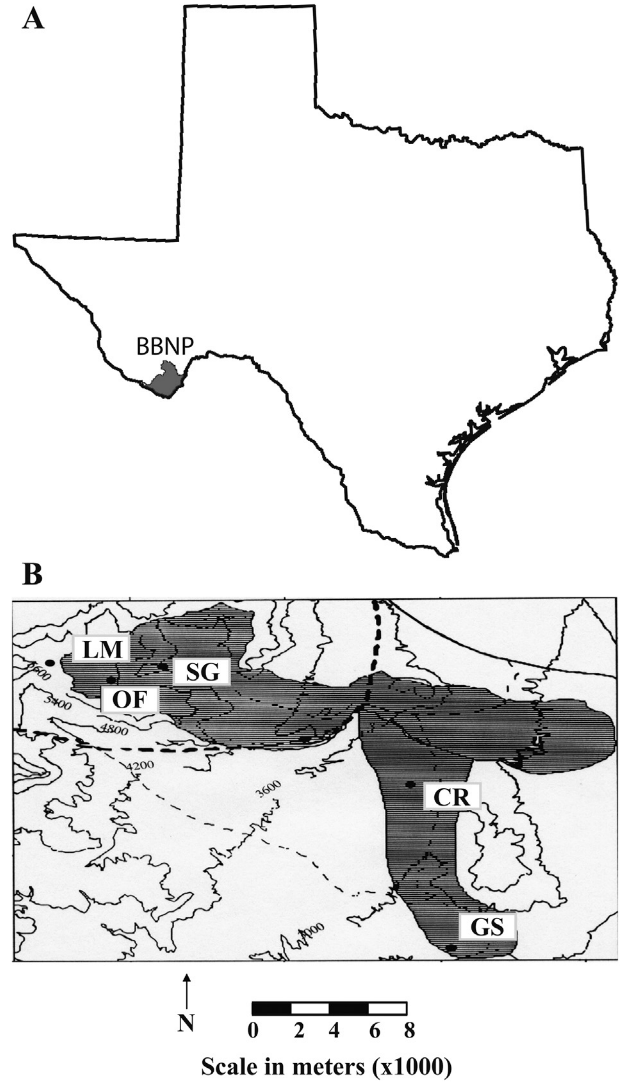

Fig. 1. Map of study site. (A) The area of Texas in which Big Bend National Park (BBNP) is located is shaded. (B) Areas of the Pine Canyon Watershed at BBNP sampled included a lowland desert scrub near the abandoned town of Glenn Springs (GS; 793 m), a creosote bajada (CR; 1010 m), a sotol grassland (SG; 1526 m), a closed-canopy oak forest (OF; 1824 m) and a high elevation oak-pine forest near Lost Mine Peak (LM; 2098 m).

Each soil sample (approximately 300 g each) was collected to a depth of 10 cm and passed through a 2.0-mm sieve in the field to remove large pieces of rock and plant material. Sieved soils were stored in plastic freezer bags at 4 °C until they could be processed (2–3 days). All nutrient and edaphic characteristics were collected for each sample.

2.3. Medium and growth conditions

An isolation medium was formulated from tryptone (0.02 g l^{-1}) and yeast extract (0.002 g l^{-1}) to provide a total carbon content of approximately 12 mg l^{-1}, adhering to Kuznetsov's definition of oligotrophy (Kuznetsov et al., 1979). Noble agar (1.5%) was used as a solidifying agent to reduce carbonaceous contaminants (Martin and MacLeod, 1984; Palumbo et al., 1994; Smith et al., 1991). All medium components were manufactured by BD Diagnostics (Sparks, MD). Soil samples (10 g) were diluted in sterile distilled