Soil Biology & Biochemistry 41 (2009) 102–109

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Abiotic conditions and plant cover differentially affect microbial biomass and community composition on dune gradients

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ARTICLE INFO

Article history:
Received 31 January 2008
Received in revised form
29 September 2008
Accepted 4 October 2008
Available online 31 October 2008

Keywords:
Coastal dunes
Soil microbial community
Microbial biomass
Community composition
Stress gradients
Facilitation

ABSTRACT

Dune systems are characterized by strong gradients of physical stress, with blowing sand and salt spray decreasing with distance from the ocean, and soil nutrients increasing. In this study we ask how soil microbial community composition and biomass change along transects away from the ocean, and whether these changes are regulated by abiotic stress or by resource availability. We collected bulk soil from under three plant species representative of the dune front, back, and flat: *Ammophila breviligulata*, *Rosa rugosa*, and *Myrica pensylvanica*. The biomass and composition of microbial communities were examined using phospholipid fatty acid (PLFA) analysis under patches of dominant vegetation, and in paired bare plots. We found that microbial biomass was strongly correlated with soil C, and thus the presence of vegetation. Community composition, on the other hand, varied with abiotic stresses, especially soil salinity. These variables in turn depended on distance from the shore, and were ameliorated in some cases by vegetation. These findings demonstrate that biomass and community composition are influenced by different environmental variables. Thus, relationships between biomass and composition are unlikely to be readily predicted on the basis of a single resource.

1. Introduction

Dunes represent an environment with strong gradients of physical stress: at the extreme of these gradients, resource limitation or physical conditions severely limit biomass accumulation. These strong abiotic gradients have been demonstrated to influence plant community composition. For example, strong winds and salt spray from the ocean reduce germination and survival of dune forbs (van der Valk, 1974). Species differ in salt spray tolerance, resulting in different species occurring on different parts of the dune (Wilson and Sykes, 1999). Low nutrient content of the substrate results in nutrient limitation on plant growth, particularly by nitrogen (Kachi and Hirose, 1983), and abundance of plant species may be associated with soil nutrient content (Houle, 1997). Further, tolerance to burial by blowing sand may also affect which species are found in different areas of the dune (Wilson and Sykes, 1999).

Although not well studied, these same abiotic gradients have the potential to influence microbial community composition and biomass. In general, total microbial biomass appears to be most strongly controlled by soil carbon availability (Wardle, 1992; Yao et al., 2000; Allison et al., 2007). In dune systems, this in turn appears to be regulated by vegetation cover, with vegetation islands promoting the accumulation of soil carbon and hence microbial biomass (Sarig et al., 1999; Su et al., 2004). While carbon appears to be an effective surrogate measure of energy and thus the total biomass a system can support, composition is likely to be dependent on a multitude of environmental factors that different organisms differ in their ability to tolerate or take advantage of. In general, lower fertility sites have higher abundances of fungi relative to bacteria than do high fertility sites, possibly due to the greater ability of fungi to degrade recalcitrant materials such as lignin (Beare, 1997; Zeller et al., 2001). In addition, disturbance reduces fungal biomass, presumably by disrupting hyphal networks (Hedlund, 2002; Allison et al., 2005). Further, Allison et al. (2007) found that microbial community composition in a prairie system was dependent on phosphorus, calcium and water, and only indirectly on soil carbon.

These results suggest that while the presence of plants is likely to have strong effects on microbial biomass, microbial community composition may be more strongly regulated by abiotic gradients such as disturbance and nutrient availability. These abiotic factors may, in turn, be influenced by the establishment of dune plants. For example, soil temperatures (Martinez, 2003), wind speed (Cowles,

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0038-0717/$ – see front matter © 2008 Elsevier Ltd. All rights reserved.
doi:10.1016/j.soilbio.2008.10.001

1899), and sand accretion (Martinez, 2003) are lower under shrub canopies. Soil nitrogen, while highly variable, is higher beneath nitrogen-fixing shrubs (Alpert and Mooney, 1996; Shumway, 2000), while vegetation cover promotes accumulation of carbon irrespective of plant species (Lichter, 1998; Su et al., 2004).

In this paper, we examine shifts in microbial community composition and biomass along a foredune gradient. Our study area consisted of a barrier dune system with a single, low dune crest. Soil was collected from three zones: the dune front (nearest the ocean); the dune back (just behind the crest); and the flat area behind the dune itself. The biomass and composition of microbial communities were examined both in patches of dominant vegetation and in paired bare plots. These paired comparisons enable us to tease apart the effects of plant islands versus abiotic stressors on microbial community composition and biomass.

We hypothesized that microbial biomass would be dependent on plant biomass rather than position on the dune, as soil C is an excellent predictor of microbial biomass. In contrast, we hypothesized that microbial community composition would depend on the abiotic environment, with any plant effects due to plant-mediated amelioration of abiotic stress.

2. Materials and methods

2.1. Study area

This research was conducted at Waquoit Bay National Estuarine Research Reserve in Falmouth, Massachusetts (N41°33 5″, W70°30′22″). The mean air temperature and precipitation are 9.8 °C and 1039.5 mm, respectively (averages from 1949 to 1970 and 1976 to 1982, respectively;WorldClimate.com). The study site is a barrier dune system, separating the Atlantic Ocean from Waquoit Bay. The dune system consists of a single, low dune crest, 2 m or less in height and 5–20 m from the high tide line. A largely flat area behind the crest extends 100–200 m to wetlands or the bay. In some areas, there is a second dune crest on the bay-side shore, but these were not included in sampling. The soil throughout the dune system is a coarse sand with low organic matter content (mean total carbon 0.14%, maximum observed 0.93%). All sampling sites were located on Hooksan series soil, a very deep, excessively drained soil typical of vegetated sand dunes on the coast.

The area shows a typical loose zonation of plant species. *Ammophila breviligulata* Fern., American beachgrass, is a dune-stabilizing grass dominating the dune front. On the dune back, beachgrass is interspersed with patchy shrubs, primarily the rose *Rosa rugosa* Thunb. In the flat area behind the dune, grass abundance declines, and the dominant shrub switches to the nitrogen-fixing bayberry (*Myrica pensylvanica* Mirbel) (species referred to hereafter by genus names). Forbs, including beach pea (*Lathyrus japonicus* Willd.) and seaside goldenrod (*Solidago sempervirens* L.), occur at low density throughout the dune system. Wormwood (*Artemisia caudata* Michx., a forb) and beach plum (*Prunus maritima* Marsh., a shrub) are also common in the dune flat.

2.2. Sampling and laboratory analyses

Samples were collected in a series of paired plots in July and August 2006. On ten transects, each 120 m apart, densely vegetated plots (1 m^2) were paired with sparsely vegetated or bare plots, for each of the three zones. Along each transect, a dune front plot with dense *Ammophila* was paired with a plot with sparse *Ammophila* (entirely bare areas were rare in this zone); a dune back plot beneath a large *Rosa* shrub was paired with a nearby plot empty or nearly empty of vegetation, and a dune flat plot beneath a large *Myrica* shrub was paired with a nearby bare area. Bare areas were located at least 1 m from the dense grass or the shrubs, and the plot pairs were located at the same distance from the dune crest whenever possible. Distance from the dune crest was recorded for each plot (as a negative value for plots in front of the dune crest).

In each plot, percent cover of each plant species was determined visually, soil cores were collected, and a series of environmental variables were measured.

The temperature was recorded on a sunny day within 2 h of solar noon at the soil surface and at a depth of 30 cm. Soil moisture was measured by time domain reflectometry with a MiniTrase system (SoilMoisture Equipment Corp., Santa Barbara, CA). Soil moisture was measured two days after a rainfall, when moisture in these typically dry, sandy soils was expected to vary the most. Finally, salt spray was measured with salt spray traps (following Cartica and Quinn, 1980). A piece of cheesecloth was suspended in a wooden frame 20 cm above the soil surface for 24 h, and a 10 cm × 10 cm section from the center of the cheesecloth was removed for analysis. The cheesecloths from each salt spray trap were immersed and swirled in 100 ml of deionized water. Salinity of the water was then measured with a conductivity meter (SevenEasy, Mettler Toledo, Columbus, OH).

Three soil cores (1.7 cm in diameter and 30 cm deep) were collected from random positions within each plot and composited. Soil samples were kept on ice for several hours until returned to the lab, then refrigerated (4 °C). The soil samples were analyzed for available N, total C and N, and salinity. Plant-available nitrogen (NH_4^+ and NO_3^-) was extracted from a 5-g subsample of field-moist soil in 50 ml of 2 M KCl; extracts were analyzed for ammonium and nitrate at the Soil and Plant Nutrient Laboratory at Michigan State University. Nitrate in extracts was analysed on a Lachat Flow-injection-analyser (FIA; Lachat Instruments, Loveland, CO) using the cadmium reduction method, while ammonium was analysed on an FIA using the salicylate method. A portion of each soil sample was ground in a Spex 8000M mixer mill (SPEX CertiPrep, Metuchen, NJ) and analyzed for total C and total N by dry combustion by the Stable Isotope/Soil Biology Laboratory of the University of Georgia Institute of Ecology. Finally, soil salinity was determined by combining 20 g of field-moist soil with 100 ml of distilled water, shaking for 30 min, and measuring conductivity of the solution after settling (Rowell, 1994).

Microbial biomass and community composition in soil samples were assessed using phospholipid fatty acids (PLFAs). Phospholipids are integral components of cell membranes, and are metabolized rapidly upon cell death: as a result, PLFAs reflect viable biomass (Frostegård and Bååth, 1996). Further, specific signature PLFAs are associated with subsets of the microbial community, and thus reveal shifts in microbial community composition (Vestal and White, 1989; Tunlid and White, 1992). Lipids were extracted from refrigerated soil, immediately upon receipt at the PLFA laboratory.

Lipids were extracted from 10 g of field-moist soil, in a single-phase mixture of chloroform, methanol, and phosphate buffer (0.05 mol L^{-1}, pH 7.4) in a ratio of 1:2:0.8, by an adaptation of the method described by Bligh and Dyer (1959). After 2 h, water and chloroform were added to separate the mixture into polar and nonpolar fractions, and total lipids were extracted from the nonpolar chloroform phase. The PLFAs were separated from other lipid classes by using silicic acid column chromatography (Vestal and White, 1989; Zak et al., 1996). FAME 19:0 was added as an internal standard at a concentration of 70 ng/μl, and the PLFAs subsequently methylated by using a mild-alkaline methanol–toluene solution. We assume that any loss of the internal standard during the methylation step occurs at the same rate as loss of extracted PLFAs.

Methylated PLFAs were dissolved in ethyl acetate, then separated and identified on an Agilent 6890 GC (Agilent Technologies, Santa Clara, CA), equipped with a 25-m BP-5 column. Helium was