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Responses of the soil microbial catabolic profile and diversity to vegetation rehabilitation in degraded semiarid grassland

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ABSTRACT

Changes in the soil labile C pools induced by vegetation rehabilitation on semiarid lands are assumed to correlate with changes in the microbial catabolic profiles. To verify this, soil was sampled under the canopies of 12-year-old (R12Y) and 30-year-old (R30Y) planted *Caragana microphylla* shrubs, as well as native *C. microphylla* shrubs, all located in the Horqin Sandy Land, China. Community Level Physiological Profiles (CLPPs) of soils were determined to reveal any qualitative and quantitative shifts in soil microbial catabolism linked with the revegetation process. water-soluble C (WSC) and hot-water extractable C (HWEC) were measured to indicate the availability of labile C pools. As the restoration proceeds, soil organic C (C_{org}) increased 2–3 times at the R30Y habitat compared to the R12Y habitat. The total utilization rate of the 15 C substrates also increased from 0.68 μg CO_2-C g^{-1} soil h^{-1} at the R12Y habitat to 4.90 μg CO_2-C g^{-1} soil h^{-1} at the R30Y habitat, but a slight decline in catabolic diversity, from 2.53 to 2.29, was recorded. Principal component analysis and redundancy analysis revealed that soil microbial communities colonizing the R12Y habitat exhibited an affinity to carbohydrates, which positively correlated to the relative concentration of WSC. Those colonizing the R30Y and native habitats mainly preferred carboxylic acids and 3,4-dihydroxybenzoic acid due to higher C_{org} content and relative concentration of HWEC.

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1. Introduction

Microorganisms play crucial roles in soil structure formation, mineralization, humification, nutrient cycles, and contaminant decomposition and detoxification in terrestrial ecosystems (García-Palacios et al., 2011). They are sensitive to disturbance and environmental changes, and are considered accurate bio-indicators of soil quality (Anderson, 2003; Avidano et al., 2005; Bastida et al., 2008; Nielsen et al., 2002). Microbial parameters, such as metabolic quotient (qCO_2), microbial coefficient (the proportion of organic C present as microbial biomass C, C_{mic}/C_{org}), and species and functional diversity have been widely used as indicators for soil quality in agricultural and natural ecosystems since the late 1990s (Harris, 2003; Lewis et al., 2010).

Compared with species diversity estimates that requires highly specialized skills or equipment, measurements of soil microbial functional diversity such as catabolic diversity is more easily carried out, and can be directly linked to soil functions (Avidano et al., 2005; Chapman et al., 2007; Graham and Haynes, 2004). Therefore soil microbial catabolic diversity has been widely used to monitor and evaluate restoration of disturbed or contaminated sites, predict soil quality shifts and thus the success of restoration (Andersen et al., 2013; Waterhouse et al., 2014).

In previous studies, the Community Level Physiological Profile (CLPP) of soil revealed significant distinctions in soil microbial catabolic characteristics between disturbed, restored and native habitats, or along a chronosequence of restored habitats (Banning et al., 2012; Graham and Haynes, 2004). Variations in the quality rather than quantity of soil organic C between the studied habitats or succession stages were assumed to primarily govern such differences (Gömöryová et al., 2009). Over the course of revegetation, both plant biomass and species diversity increase at the remediated sites. Given that the chemical composition of

Abbreviations: R12Y, 12-year-old planted *Caragana microphylla* shrubs; R30Y, 30-year-old planted *Caragana microphylla* shrubs; WSC, water-soluble carbon; HWEC, hot-water extractable carbon.

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litter and root exudates vary greatly among plant species and that these plant inputs are principal sources for soil organic C pools, it is reasonable to expect a positive response of soil microbial catabolic diversity to restored vegetation stand age (Artz et al., 2008; Banning et al., 2012; Eskelinen et al., 2009; Gömöryová et al., 2009).

The composition of soil labile C is complex, and only low molecular compounds such as amino acids, carbohydrates, carboxylic acids, can be identified chemically (Herbert and Bertsch, 1995; Kalbitz et al., 2000). Consequently the water-soluble C (WSC) and/or hot-water extractable C (HWEC) are commonly used to investigate the relationship between soil labile C pools and soil microbial communities. WSC is part of the highly labile pool of soil organic matter and can be utilized directly by soil microbial communities. Marschner et al. (2011) reported that WSC was the main C source for soil microorganisms during the first 5 days of crop residue decomposition. A subsequent increase in fungal abundance, which coincided with a decrease in bacterial abundance, was attributed to the depletion of WSC after the first decomposition stage. The HWEC fraction also belongs to soil labile C pools, and it is mainly associated with microbial biomass C, amines, soluble carbohydrates and amorphous polysaccharides, phenols and lignin monomers (Ghani et al., 2003; Huang et al., 2008). Moreover, HWEC pools are much larger than the WSC pools and better correlated to soil aggregate stability, microbial biomass C, soil organic C and soil microbial functional diversity (Ghani et al., 2003; Huang et al., 2008).

To gain a better understanding of the alterations in soil labile C pools during the vegetation rehabilitation of degraded semiarid grasslands, and the relationship with soil microbial catabolic profiles, we conducted a study in the semiarid Horqin Sandy Land in Inner Mongolia, China. Seasonal sampling of topsoil was carried out for two habitats representing the early- and late-succession stages of vegetation rehabilitation. WSE and HWEC were measured to indicate the labile C variations, and the MicroResp™ (Campbell et al., 2003) was employed to determine shifts in the soil microbial catabolic profile and diversity. The MicroResp™ is used for the determination of the capability of "whole soil" to utilize carbon sources representative of plant root exudates, as previously described (Campbell et al., 2003). Unlike BIOLOG assay (Garland and Mills, 1991), which is biased by the selection toward culturable and fast-growing bacteria and is sensitive to dilution rate and incubation length (Bending et al., 2002; Nannipieri et al., 2003), MicroResp™ reflects the true function of the in situ soil microbial communities. Moreover, since the concomitant CO_2 production and quantification can be multiplexed in a sealed 96-well microtitre system MicroResp™ is more time and labor effective than the standard substrate induced respiration method developed by Degens and Harris (1997) (Campbell et al., 2003; Chapman et al., 2007). Our working hypotheses were that (i) catabolic diversity of soil microbial community increases during vegetation rehabilitation as plant cover increases; and (ii) changes in availability of WSC and HWEC during revegetation aging alters the ability of soil microbial community to utilize different C sources.

2. Materials and methods

2.1. Study site

This study was conducted in the Wulanaodu village (43°02′N, 119°39′E, 479 m above sea level) located in the Horqin Sandy Land, Inner Mongolia, China. It has a temperate, semi-arid continental and monsoonal climate, receiving multi-annual (21 years) mean precipitation of 310 mm, with 70% of this occurring during June and August. The multi-annual mean temperature and pan-evaporation in this area is 6.3 °C and around 2500 mm, respectively. The landscape is characterized by undulating shifting and semi-fixed sand dunes. The soils are classified as cambic arenosols (FAO, 2006). The original landscape in this area was grassland with sparsely scattered woods (mainly *Ulmus pumila*). Due to the severe disturbance of fixed sandy land by extensive firewood gathering and overgrazing, sandification in this area reached a climax in the mid 1970s. To prevent desertification, arbors (e.g., *Pinus sylvestris*) and indigenous perennial shrubs (e.g., *Caragana microphylla*,*Salix gordejevii*, and *Artemisia halodendron*) have been widely planted since the early 1980s in straw checkerboards on the windward slope of shifting sand dunes (Cao et al., 2008).

2.2. Soil sampling

Soil was sampled from three habitats, i.e., a 12-year-old (representing the early-succession stage, R12Y), a 30-year-old (representing the late-succession stage, R30Y) planted *C. microphylla* stand, and a reference habitat with native *C. microphylla* vegetation (Native). Habitats were selected from the same region, relatively close to each other, with the distances between any two habitats varying from 1 to maximum 3 km. At each habitat, four 8×8 m^2 plots, i.e., replicates, were established at 10-m intervals on the windward slope of a sand dune. For each plot, soil samples (0–10 cm) were collected at two sites, (i) under the canopies of five *C. microphylla* shrubs, randomly chosen (Und sites), and (ii) at the interspaces between them (Int sites) on August 24th 2013 (S1), June 4th (S2) and September 4th (S3), 2014. Among the three sampling season, S1 and S3 represent the end of rainy season, while S2 represents the beginning of the rainy season at the study site. All five soil samples collected under *C. microphylla* canopies in the same plot were composited and placed in a plastic bag in the field, as one replicate. Interspace samples were similarly handled. Insulated containers with ice bags were used to store soil samples as they were transported to the laboratory. Prior to chemical analyses soils were sieved (2 mm) to remove stones, roots, and other organic debris, and then stored at 4 °C for no more than 2 weeks until CLPP determination. Background information on bulk density (BD), content of sand/silt/clay particles, pH, electric

Table 1
Values (mean ± standard error) of bulk density (BD), content of sand/silt/clay particles, pH, electric conductivity (EC), and total nitrogen (TN) content in 0–10 cm soils under the canopy of *Caragana microphylla* shrubs (Und) with different stand ages and at the interspaces between the shrubs (Int).

	Und R12Y	Int R12Y	Und R30Y	Int R30Y	Und Native	Int Native
BD (g cm^{-3})	1.64 ± 0.00 ab	1.69 ± 0.02 a	1.56 ± 0.03 c	1.55 ± 0.01 c	1.60 ± 0.02 bc	1.63 ± 0.02 abc
Sand (%)	98.25 ± 0.20	98.40 ± 0.45	95.30 ± 0.15	97.45 ± 0.40	96.95 ± 1.00	96.85 ± 0.30
Silt (%)	1.60 ± 0.20	0.60 ± 0.30	1.85 ± 0.05	1.35 ± 0.05	2.40 ± 1.50	1.30 ± 0.20
Clay (%)	0.15 ± 0.00	1.00 ± 0.15	2.85 ± 0.20	1.20 ± 0.35	0.65 ± 0.50	0.50 ± 0.10
pH	7.30 ± 0.05	7.38 ± 0.06	6.94 ± 0.09	7.31 ± 0.11	7.24 ± 0.01	7.19 ± 0.00
EC (μS cm^{-1})	34.8 ± 1.7 bb	30.3 ± 1.3 bb	48.4 ± 4.7 a	37.8 ± 1.0 ab	40.2 ± 3.4 ab	37.3 ± 2.7 ab
TN (mg g^{-1})	0.10 ± 0.01 b01 b	0.10 ± 0.03 b	0.30 ± 0.03 a	0.20 ± 0.01 b	0.17 ± 0.02 b	0.17 ± 0.03 b

R12Y: 12-year-old C. microphylla shrubs. R30Y: 30-year-old C. microphylla shrubs. Native: Native C. microphylla shrubs. Lower-case letters in each row signify the differences between the six sampling sites.

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