Soil Biology & Biochemistry 43 (2011) 1245–1253

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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

Early-successional vegetation changes after roadside prairie restoration modify processes related with soil functioning by changing microbial functional diversity

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ARTICLE INFO

Article history:
Received 12 April 2010
Received in revised form
15 February 2011
Accepted 18 February 2011
Available online 4 March 2011

Keywords:
Roadside slopes
Restoration
Soil functioning
Plant–soil interactions
Dominant species
Community level physiological profiles
Secondary succession

ABSTRACT

Because of their rapidly changing vegetation dynamics and harsh environmental conditions, roadside prairies in semi-arid regions represent an exceptional study system in which to investigate the effects of plant-soil interactions on ecosystem functioning. We conducted a two-year field experiment on two roadside embankments in semi-arid central Spain differing in construction age to answer the following questions: (i) do commonly used restoration treatments (hydroseeding, fertilization and irrigation) affect soil microbial functional diversity and processes related to soil functioning (basal respiration, total N and P and *in situ* N availability rate)? (ii) what portion of plant effects on processes related to soil functioning is mediated indirectly by microbial functional diversity? Except for a small and negative irrigation effect on the microbial functional diversity in the three-year old site, the restoration treatments employed did not affect this variable. Fertilization increased plant diversity, an effect likely mediated by the enhanced soil nutrient availability with this treatment at early stages of secondary succession. In contrast, hydroseeding did not affect processes related to soil functioning. The total effect of the plant community on these processes was higher than that of the microbial functional diversity alone, suggesting that the studied slopes are to the greater extent regulated by plants. However, soil microbes are a key proximate influence in the system, as the indirect effects of plant community on soil functioning processes mediated by soil microbes represented 37–41% of the total plant effects observed. Our results indicate that the restoration of recently built slopes can potentially be improved with treatments that promote plant compositional shifts, such as fertilization, or alter soil function, such as the enhancement of soil microbial functional diversity. They also highlight that plant-soil interactions are an important process that can be manipulated for restoration purposes in early-successional stages, especially in nutrient-poor semi-arid ecosystems.

1. Introduction

Most of the world's ecosystems are now impacted by humans to a greater or lesser extent (Vitousek et al., 1997), and therefore ecological restoration of degraded systems play a major role in re-establishing ecosystem structure and functioning (Hobbs et al., 2006). Ecosystem succession is a suitable framework for guiding restoration efforts aiming to recover plant communities and soil processes because it incorporates the temporal dynamics of the ecosystems and the barriers to their development (Walker et al., 2007). Knowledge of classical successional dynamics (Connell and Slatyer, 1977) has guided the development of restoration techniques in several systems (Walker et al., 2007). Nevertheless, ongoing environmental changes and the increasing prevalent anthropogenic disturbance may result in novel ecosystems whose composition and/or function differ from any historical system (see Cramer et al., 2008 for a review). Degraded landscapes such as opencast mines, quarries or roadside slopes represent good examples of novel communities which may or may not function as

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doi:10.1016/j.soilbio.2011.02.014

natural assemblages (Hobbs et al., 2006). Thus, ecosystem functioning in this potentially new succession context remains unknown, as well as the suitability of widely used restoration treatments for recovering vegetation and soil processes (Matesanz et al., 2006).

With more than 50% of net primary production being returned to the soil (Wardle et al., 2004), plant-soil interactions are of major importance in understanding the role of biodiversity in controlling ecosystem processes and properties (Van der Putten et al., 2001). However, little is known about these links in the context of ecosystem restoration and succession (Kardol et al., 2006). In order to study the responses of ecosystem functioning to restoration actions, special attention should be paid to the relationships between plants, microorganisms and soil processes (Harris, 2009). Plant community succession can drive the development of ecosystem functioning (Chapin et al., 1994). Since the responses of single plant species fail to match patterns observed in the field where multiple species interact with each other (Blomqvist et al., 2000), a community perspective would be very useful (Ehrenfeld et al., 2005). Given the relevance of temporal variations in plant-soil interactions to control ecosystem development (Kardol et al., 2006), it is worth including soil communities in the study of newly developing soils (Bardgett et al., 2007). In the same way, the effectiveness of restoration treatments must be partially assessed belowground, where the manipulation of the communities enhances the rate of recovery of degraded soils (Harris, 2009). Therefore, in order to provide a more inclusive community viewpoint that improves management practices, it is necessary to perform community level studies that test plant-soil interactions (Ehrenfeld et al., 2005). This implies to achieve a better knowledge of how changes in plant composition, and therefore in resource input quality, affect soil communities (Bardgett et al., 2005). To adequately interpret this interaction, it is particularly useful to assess the ability of soil microbial communities to metabolize a range of substrates that vary in structural complexity (Schipper et al., 2001; Oren and Steinberger, 2008). Relatively few studies have simultaneously considered plant effects on both soil biota and soil processes (Wardle et al., 1999; Porazinska et al., 2003), and many of them have focused on individually grown plants in pot experiments (Besmear et al., 2006) and only a few have attempted to determine these effects in natural ecosystems (e.g. Wardle, 2005; Maestre et al., 2009).

Prairie communities of roadside slopes in semi-arid regions represent an exceptional study system in which to investigate plant-soil diversity effects on ecosystem functioning with a succession perspective. First of all, similarly to opencast sites or strip mines, both plant and soil communities are nearly completely reset due to the use of subsoil and foreign construction materials re-instated after storage (Harris et al., 2005). Therefore, changes in the microbial community follow a similar trajectory to those recorded during primary succession (Harris, 2009). Second, these prairies, dominated by annual plant species, are extraordinarily dynamic, with rapid structural and compositional changes (Wali, 1999). These novel communities are also characterized by a high proportion by exotic species artificially introduced in revegetation practices because they are cheap, readily available and easy to establish on disturbed sites (Matesanz et al., 2006). Thus, since legacy effects of past biota on ecosystem functioning have largely been erased, and because succession occurs more quickly than in most other ecosystems, investigators can easily track its effects on ecosystem functioning. In addition, the soil is nutrient-poor and limited by the short duration of available water (Bochet et al., 2007). Temporal patterns of soil biodiversity are context-dependent, being more evident in managed systems with nutrient-limited soils (Bardgett et al., 1996). Restoration treatments inducing shifts in the composition of soil communities thereby give a sign of improvement in the efficiency of nutrient cycling and decomposition processes.

Community-level studies focusing on plant-soil interactions in a restoration context have looked at grassland types in different biogeographic areas (Donnison et al., 2000; Grayston et al., 2004). However, not many studies to date have evaluated whether soil microbial communities and soil functioning are driven by changes in plant community composition along a continuum of plant diversity plots with similar climatic conditions and grazing pressures, and whether these interactions change along succession. To overcome this gap in our knowledge, we conducted a field experiment on two different roadside prairie slopes in semi-arid central Spain differing in construction age. A previous study carried out on the same sites indicated that plant community responses to the restoration treatments evaluated (irrigation, fertilization and hydroseeding) were site-specific and responded to the dominance of several fast-growing plant species (García-Palacios et al., 2010). In the present study, we aim to evaluate the effect of these treatments on belowground microbial communities and soil functioning. Microbial functional diversity and surrogates of soil functioning were sampled in parallel with the vegetation to answer the following questions: i) do commonly used restoration treatments (hydroseeding, fertilization and irrigation) affect soil microbial communities and processes related to soil functioning (basal respiration, total N and P and *in situ* N availability rate)? (ii) what portion of plant effects on processes related to soil functioning is mediated indirectly by microbial communities?

2. Materials and methods

2.1. Study area and experimental design

The experiment was developed at two roadside embankments with similar slope and aspect located in the center of the Iberian Peninsula. The climate is semi-arid, with cold winters and a severe summer drought; annual mean temperature and precipitation are 15 °C and 450 mm, respectively (Getafe Air Base climatic station 40°18′N, 3°44′W, 710 m a.s.l., 1971–2000). One of the sites was a recently built embankment, where construction was finished three months prior to the field surveys. Therefore, vegetation succession and soil dynamics were just recovering after perturbation of land movements. The other site was a three-year old embankment. Both sites are nutrient poor, with low levels of soil organic carbon (hereafter SOC), total N and P, scarce soil biological activity and alkaline pH (Table 1). Three restoration treatments (hydroseeding, fertilization and irrigation) were evaluated in this study. Six blocks containing 12 1 m × 1 m plots per block, with at least 1 m buffer between plots, were randomly established at each site. Each block contained a full factorial design with the three treatments employed, which were randomly assigned to the plots

Table 1
Main characteristics and soil properties of the two roadside slopes studied at the beginning of the experiment (December 2006). Numerical values are means ± SE ($n = 30$).

	Recently built site	Three-year old site
Initial plant cover (%)	12	58
Water holding capacity (ml water g^{-1} soil)	0.36 ± 0.03	0.43 ± 0.03
Total N (mg N g^{-1} soil)	0.14 ± 0.01	0.34 ± 0.04
Total P (mg P g^{-1} soil)	0.16 ± 0.01	0.35 ± 0.01
Basal respiration (mg CO_2–C g^{-1} soil day^{-1})	0.01 ± 0.01	0.04 ± 0.01
SOC (g C kg^{-1} soil)	5.30 ± 0.06	9.90 ± 0.09
pH	8.35 ± 0.14	8.06 ± 0.15