



Facilitating ecosystem assembly: Plant-soil interactions as a restoration tool

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ABSTRACT

Although plant-soil interactions are increasingly recognized as an important factor in ecosystem restoration, their effects on community assembly during de novo ecosystem establishment are largely unknown. In a heathland restoration trial after topsoil removal we introduced either only aboveground heathland species with fresh herbage or both above- and belowground heathland species with sods to facilitate community assembly. Sod inoculation increased resemblance of the microbial community to the reference system, with a higher fungal and lower bacterial proportion to the community structure. Also densities of bacteriophagous and phytophagous nematodes, Acari and Collembola increased after sod inoculation. The cover of heathland plant species increased by 49% after sod inoculation. The introduction of solely aboveground heathland species increased the cover of these species by only 13%, and did not affect soil community assembly. Additionally, the increase in cover of heathland species over time was inversely correlated to the cover of mesotrophic grassland species. Inverse correlations were also observed between changes in fungal and bacterial abundances. Simultaneous introduction of key species of both above- and below-ground communities had a critical effect on the establishment of both communities, providing a potential shortcut for successful restoration of target ecosystems on disturbed soils.

1. Introduction

Ecosystem assembly is a fundamental concept in ecology. Traditionally the focus has been on the assembly of aboveground communities (Götzenberger et al., 2011), but in recent years the importance of belowground community composition has become increasingly recognized (Reynolds et al., 2003; Wardle et al., 2004). Two major pathways are identified in plant-soil interactions: a first, direct, pathway is associated with the interaction between roots and soil organisms such as symbionts and pathogens. A second, indirect, pathway includes interactions between decomposers and plants and concerns nutrient cycling rates and soil formation (Wardle et al., 2004). The extent to which aboveground community composition affects belowground development and vice versa is still largely unclear. It is suggested that the soil community may either follow or facilitate vegetation development, dependant on the ecosystem (Harris, 2009).

Little is known about the sequence in which characteristic above- and below-ground species have to establish for a smooth ecosystem

development. While especially late-successional plants may need particular soil organisms to function properly (De Deyn et al., 2003; Frouz et al., 2008), the establishment of these soil organisms themselves may depend on the presence of characteristic plant species which promote the development of a typical organic soil layer (Frouz et al., 2009). Studies that included analysis of both above- and below-ground development during succession of semi-natural grassland or dwarf shrub vegetation reported varying results: in some studies both above- and below-ground communities develop along similar lines (Lozano et al., 2014), while others report that belowground development either lags behind aboveground changes (e.g. Frouz et al., 2009; Holtkamp et al., 2008; Jangid et al., 2011) or precedes them (Van der Bij et al., 2016).

Filters are assumed to play an important role in vegetation assembly, especially abiotic conditions, dispersal and establishment are considered critical factors (Van Diggelen and Marrs, 2003; Cramer et al., 2008). A better understanding of how plant-soil interactions affect the establishment of characteristic plant species would add significantly to this knowledge and has not only theoretical value, but

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would also provide valuable insights for practical restoration, e.g. after topsoil removal. There a bare substrate is created with suitable abiotic conditions and an opportunity for new species to establish. Previous studies have shown that vegetation assembly can be facilitated by introducing seeds of target species (Holtkamp et al., 2008; Kiehl et al., 2010; Klimkowska et al., 2010) and it sounds reasonable that similar filters also apply for belowground community assembly. For example, dispersal limitation is assumed to be strong for soil fauna as Acari (Lehmitz et al., 2012), one of the most abundant soil fauna groups in oligotrophic systems (Wardle et al., 2004; Frouz et al., 2009). Facilitation of soil community assembly would be a logical next step to further enhance ecosystem restoration (Kardol and Wardle, 2010). However, studies that explored this option by inoculation experiments showed varying results (Pywell et al., 2007; Kardol et al., 2009; Wubs et al., 2016).

Although the extent to which plant-soil interactions affect ecosystem assembly remains largely unknown, several papers emphasized their importance for restoration ecology (Harris, 2009; Kardol and Wardle, 2010; Van der Putten et al., 2013). In the present study we assessed the potential of plant-soil interactions in de novo heathland ecosystem establishment. In a field trial immediately after topsoil removal we introduced either only aboveground species by means of fresh herbage, or simultaneously both above- and below-ground species by means of sods. We monitored the parallel development of vegetation and soil community to assess the following research question: does the simultaneous introduction of above- and below-ground species in early succession have a synergistic effect on heathland community assembly? We hypothesized that introduction of the soil community in early succession would enhance vegetation assembly.

2. Materials and methods

2.1. Site description

The Dwingelderveld National Park (N 52°48'14.3, E 6°24'38.6) is a large lowland heathland (altitude 7 m) in the Netherlands. It has a maritime temperate climate (Cfb) with an average annual temperature of 8.8 °C and an annual average rainfall of 783 mm (<http://en.climate-data.org/location/105881/>). In the 1930's 200 ha in the centre of the area was converted from heathland into agricultural grasslands and restored again in 2011–2012 with topsoil removal (30–40 cm), only road sides with mesotrophic grassland were left untouched. Compared to reference values from the meta-analysis of De Graaf et al. (2009) and measurements in reference sites nearby (Table 1) pH and soil buffering were higher than in typical Dutch heathlands but after topsoil removal nutrient levels lay well within the range of typical heathlands.

2.2. Experimental setup

The experiment was installed in November 2011 immediately after topsoil removal. We manipulated both the abiotic and the biotic environment in a full-factorial set up. The soil-pH was manipulated by (1) addition of acid (150 g elemental S per m²), (2) addition of lime (200 g Dolokal per m²) or (3) left untouched. We manipulated the biotic conditions by establishing three inoculation treatments: (1) introduction of aboveground parts of heathland plant species, (2) addition of

both plant species and soil community or (3) control. We did not measure the effects of adding only the soil community, because we were not capable to remove seeds from the added soil without severely disturbing the soil community. Each combination of treatments consisted of 3 replicates. The experiment was set up in 27 random plots of 15 m × 15 m with 2 m buffers. In November 2011 we added elemental Sulfur or Dolokal and in December 2011 we spread crumbled sods from nearby well-developed dry heathlands. These sods contained the existing vegetation, the soil seed bank and the soil community. Sods were collected by cutting the upper 5 cm of a nearby dry heathland and were added immediately to the experimental plots in a ratio of 1:15 (i.e. donor material of 1 m² on 15 m² experimental plot). Aboveground plant material was added via the introduction of fresh herbage collected after seed setting of the dominant plant species *Calluna vulgaris* (L.) Hull in September 2012, the first opportunity after installing the experiment. This material was collected from a nearby well-developed dry heathland and added at the plots immediately after the mowing in a ratio of 1:2. Control plots remained unaltered after topsoil removal.

The number of germinable *C. vulgaris* seeds added per m² was expected to differ between both inoculation treatments due to the different ratios in which the donor materials were added. We assessed these figures by using data from Legg et al. (1992) on the number of viable seeds in the seed bank and the annual seed production per m² for mature dry heathlands in combination with a germination percentage of 75% of fresh heather seeds (Spindelböck et al., 2013). We calculated that we added an average of 34,125 germinable seeds per m² with fresh herbage and 15,800 per m² with sods. Since we introduced a high number of seeds in both treatments, we expected that seed availability was not a limiting factor for the establishment of *C. vulgaris*.

2.3. Microbial community

In 2009, before topsoil removal, we took three soil samples in the agricultural grassland from a layer just below the planned removal depth as starting point for microbial community development. Soil samples from the experimental plots (5 cm depth) were taken immediately after topsoil removal before the treatments were imposed and after 2 years in November 2013. Nearby dry heathlands which were used as source for the sod-treatment were sampled as a reference soil (n = 3) at the same time. In each sampling point a composite sample of 3 × 100 cm³ soil was obtained with Kopecky rings. Aliquots of the soil were refrigerated for the analysis of microbial biomass or freeze-dried for phospholipid fatty acid (PLFA) analysis.

Microbial biomass-C was determined with the fumigation-extraction procedure (Jenkinson and Powlson, 1976) using K_{ec} of 0.45 (Vance and Jenkinson, 1987). Microbial community phenotypic structure was measured with PLFA analysis using a modified method from Frostegård et al. (1993) according to the methods described by Courtney et al. (2014).

2.4. Soil fauna

Soil fauna was sampled together with the microbial samples. Samples were stored at 10 °C for nematode community analysis. Nematodes were extracted from 10 g soil with a modified Bergmann funnel (Háněl, 1995) for 48 h, after which they were fixed with

Table 1

Soil parameters in experimental site immediately after topsoil removal (Means ± S.E.; n = 27) as compared to reference sites nearby (range; n = 3).

Site	Soil pH-H ₂ O	Exchangeable base cations	Plant available phosphorus	N mineral (NO ₃ + NH ₄)	Organic matter
		µeq/kg soil	µmol/kg soil	µmol/kg soil	% dry soil
Experiment	5.61 (0.03)	10,304 ± 894	296.0 ± 48.6	40.4 ± 16.6	2.1 ± 0.2
Dry heath reference	3.8–4.9	485–7690	100–700	1–220	1.6–11.9

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