Geoderma Regional 1 (2014) 48–58

Contents lists available at ScienceDirect

Geoderma Regional

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

Thyme invasion and soil properties in the Central Otago region of New Zealand

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ARTICLE INFO

Article history:
Received 26 March 2014
Received in revised form 28 July 2014
Accepted 4 August 2014
Available online 6 August 2014

Keywords:
Exotic plant invasion
Soil physicochemical properties
Soil bacterial diversity
Thymus vulgaris
PCR–DGGE
Semi-arid Central Otago
Luvisols

ABSTRACT

The aim of this research was to increase the understanding of how exotic plant invasion can alter abiotic and biotic soil properties across multiple sites encompassing the geographic distribution of the study species, between aspects at each site, and across the edge of invasion. Our research questions were: do soil physicochemical properties and soil bacterial community structure inside thyme-dominated communities differ from those at the edge and outside of thyme-invaded plant communities?

We compared pH, soil moisture, C, N, P, NO_3^-, NH_4^+, soil particle size and soil bacterial ribotype DGGE profiles directly inside, at the edge and outside of north- and south-facing thyme stands across semi-arid areas of Central Otago. Among the soil physicochemical factors investigated organic P was significantly lower inside thyme-invaded plant communities. Thyme's invasion had a significant correlation with increased sand content and decreased soil moisture. We did not detect any variation in soil bacterial diversity from inside to outside thyme-invaded communities. While it appears that there are significant associations between thyme invasion and soil texture, site differences appear to be the major drivers of variation in soil physicochemical properties and soil bacterial diversity.

1. Introduction

Introduced invasive plant species can have adverse ecological and economic impacts such as reducing indigenous biodiversity, threatening native communities, altering ecosystem nutrient cycling, decreasing crop yields or reducing the quality of grazing land (Callaway and Maron, 2006; Ehrenfeld, 2010; Inderjit, 2005). Studying the role that plant–soil interactions play in the invasion process aids our understanding of the mechanisms which underlie successful invasion (Van der Putten et al., 2009) and may help in the management and prevention of invasion episodes. Plants physically and chemically modify the soil environment through their root architecture and exudates and their litter deposition. Exotic plant invasions have been shown to modify physical and chemical properties of soil, including nutrient inputs and biogeochemical cycling (Ehrenfeld, 2003; Hawkes et al., 2005; Perkins et al., 2011; Sperry et al., 2006), pH (Kourtev et al., 2003), soil organic matter and particle aggregation (Saggar et al., 1999), and soil moisture (Heneghan et al., 2006). The vast majority of nutrient cycling and decomposition processes in the soil are carried out by microorganisms; thus it is not surprising that exotic plant invasions are also associated with changes to biotic components of soil such as soil food-web structures (Duda et al., 2003) and the structure and function of soil microbial communities (Belnap et al., 2005; Ehrenfeld, 2003; Hawkes et al., 2005; Peltzer et al., 2009) and of mutualistic fungi (Allen et al., 2003; Mummey and Rillig, 2006).

It is generally accepted that invasive species that release secondary metabolites both directly and indirectly impact soil chemistry and ecosystem function (reviewed in Weidenhamer and Callaway, 2010). Although there have been many studies on the effects of volatiles, leaf litter, leachates and root exudates from exotic plant species on the germination and growth of co-occurring native species (Callaway and Aschehoug, 2000; Callaway and Ridenour, 2004; Cappuccino and Arnason, 2006; Callaway et al., 2008; but see Shi et al., 2011) there have been comparatively few studies on the effects of volatile-producing invasive species on soil physicochemical and microbiological properties.

It is difficult to directly investigate soil microbial diversity due to insufficient morphological characters for taxonomy studies and species characterization, and because the vast majority of soil microbes (>95%) are not culturable using currently available techniques (Kowalchuk et al., 2002). Although molecular methodologies such as pyrosequencing, t-rflp and metagenomics are rapidly advancing, polymerase chain reaction–denaturing gradient gel electrophoresis (PCR–DGGE) is one of the easiest and least costly genetic ways to characterize bacterial communities and to compare differences in the bacterial

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http://dx.doi.org/10.1016/j.geodrs.2014.08.002

communities of samples. Soil bacterial composition can be studied by comparing DGGE profiles of 16S rRNA gene fragments amplified from soil bacterial DNA (Rösch et al., 2002).

Patterns, direction and magnitude of plant invasion impacts are influenced by interacting biotic and abiotic processes across a wide range of spatial scales (Bolton et al., 1990; Evans et al., 2001; Meyerson and Mooney, 2007). Recent meta-analyses have shown that invasive plant species impacts are site-specific (Ehrenfeld, 2010; Liao et al., 2008; Pyšek et al., 2012; Vilà et al., 2011) and may be influenced by local aspect (Scott et al., 2001) and that invasive edge studies can provide valuable information regarding the direction of ecological impacts (Fan et al., 2010; Wolf et al., 2003). However, many approaches to examining the impacts of invasive plant species on soil chemical, physical and bacterial properties are limited to either a single field location or greenhouse experiment (e.g. Hawkes et al., 2005; Kao-Kniffin and Balser, 2008; Kourtev et al., 2003; Sanon et al., 2009). While experimental approaches can reveal valuable information about the underlying mechanisms of invasion, there are limits to the inferences that can be made from studies carried out in artificially created environments such as the greenhouse or laboratory. By incorporating multiple study sites that span the entire invaded landscape, both local and regional scale soil property impacts can be observed and aid in assessing the generality of the observed impact of a given invasive species across a variety of environments (Brown et al., 2008; Egli et al., 2009; Ehrenfeld, 2003; Knapp and Smith, 2001; Lyford et al., 2003; Vanderhoeven et al., 2006).

The invasion of the aromatic Mediterranean herb *Thymus vulgaris* L. (common thyme) across the landscapes of Central Otago, New Zealand provides an excellent model system to study the effects of a volatile-producing invasive plant species on abiotic and biotic soil properties at both the regional and local scales. Thyme produces essential oil secondary metabolites (terpenes) which are released from thyme leaf litter as it decomposes (Linhart et al., 2005), and leach into the soil out of leaf litter (Tarayre et al., 1995). These terpenes may alter nitrogen availability in ecosystems by inhibiting or stimulating soil bacteria involved in nitrogen cycling (Ehrenfeld, 2003; Paavolainen et al., 1998; White, 1994). Here we examined the impact of *T. vulgaris* invasion on soil chemical and physical properties and bacterial diversity, and whether these impacts varied at different spatial scales. These scales included differences among sites, differences between aspects at the same site, and differences that occur between the inside, edge and outside of thyme stands at the same site. Specifically we tested:

1. a) Whether there were discernible changes in soil chemical and physical properties transitioning across the edge of the thyme-infested communities to the uninvaded communities, and b) if so, whether these differences will be greater on relatively warm north-facing slopes where thyme stands appear monospecific compared to cooler south-facing slopes where there is greater plant community diversity.
2. We predicted that soil bacterial ribotype DGGE profiles will be different under thyme-invaded communities compared to uninvaded communities due to the effects of thyme leachates on soil bacterial community composition.

2. Materials and methods

2.1. Study area

This study was conducted in Central Otago, south-central South Island, New Zealand (168°47′–169°32′E and 44°59′–45°37′S) at 10 sites which encompassed the extent and geographic variability of thyme's invasive range (Fig. 1). For any particular site, thyme forms dense stands that appear monospecific on dry, sunny, mainly north-facing slopes, in stark contrast to thyme stands on south-facing slopes which are patchy and appear to contain greater species diversity (Morgan, 1989). At the base of the slopes, thyme stands are clearly delineated by an invasion front forming a distinct edge where plant community composition transitions from being dominated by thyme to becoming a mix of mainly exotic grasses, shrubs and herbs.

Central Otago is a region of 'basin and range' topography, with an area of flat-bottomed basins separated by block-faulted chlorite schist mountains (Molloy, 1988). Soils across the region, especially in the basins, are mainly brown–gray earths derived from schist bedrock, alluvium and colluvium. These semi-arid soils are predominantly sandy or silty loams that tentatively equate with Luvisols of the World Soil Map, and either Ustalfs or Agrids in the U.S. Soil Taxonomy. Clay content is low and soil moisture is generally at or below wilting point for long periods of the year (Gibbs, 1980). Due to the depletion of vegetation cover by pastoral exploitation since European settlement in the 1850s (McCraw, 1965), these soils are vulnerable to wind and water erosion (Gibbs, 1980; McCraw, 1965) resulting in shallow soil profiles. In general, soil nutrient status is considered of medium quality according to Hill Laboratory guidelines for agricultural soils (N, 0.2–0.5%; P, 20–30 mg/L; Hill Laboratories, 2012). However sulfur is deficient and available nitrogen and organic carbon contents are low with highly variable rates of decomposition depending on the soil moisture content and activity of microorganisms and mesofauna such as earthworms and mites. Soil pH varies from weakly acidic to slightly alkaline (6.0–7.8) (Gibbs, 1980). Study sites ranged in elevation (164–512 m a.s.l.). Each site included both north- and south-facing slopes supporting dense, relatively monocultural thyme stands with clearly delineated invasion fronts forming a distinct edge where plant community composition transitioned to mixtures of mainly exotic grasses, shrubs and herbs. Management history is not known in detail but the region has been burnt and heavily grazed in the past although current levels of both are much more lenient. The Central Otago region has also experienced several phases of rabbit plagues and while populations at the time of this study were not at these levels, rabbits were certainly evident.

2.2. Experimental design and sample collection

To test for differences in soil physicochemical and bacterial diversity properties inside, at the edge and outside (in the invasion trajectory) of north- and south-facing thyme stands, five soil replicates were taken at each site for each combination of factors (site × 10, aspect × 2, position relative to thyme stand × 3) making a total of 300 samples (5 × 10 × 2 × 3). Soil samples were collected using an 80 mm diameter soil corer to a depth of 25 cm after the surface litter was cleared, from inside, at the edge and outside of (at least 2 m away from) thyme stands in December 2009. Soil samples were stored at −20 °C (for soil chemical and physical property analysis) and −80 °C (for soil bacterial community diversity analysis) until analysis was undertaken respectively two and 12 months later.

2.3. Analysis of soil chemical and physical properties

In total 17 soil chemical and physical properties were analyzed: moisture content as a percentage of oven-dried sieved (<2 mm fractions) soil weight, pH (in water), ammonium (NH_4^+) content, nitrate (NO_3^-) content, NH_4^+:NO_3^- ratio, total, inorganic and organic phosphorus (P), soil C, soil N, C:N ratio and soil particle size composition (% pebble, sand, silt, clay (<0.002 mm) and colloid (<0.001 mm)). Within-site variation was assessed for soil chemical properties to see if the assumption of low within-site variation enabled the five replicate field samples to be pooled. This assumption is based on a previous New Zealand study by Giltrap and Hewitt (2004) that showed that in order to obtain independent soil samples in modified grasslands, with respect to potassium, pH, nitrogen and nitrate concentrations, soil samples had to be taken at distances of greater than 30 m apart. For samples from both the north- and south-facing slopes at the Alexandra site, all five individual samples for each combination of experimental factors (site × invasion × aspect)