Journal of Arid Environments 111 (2014) 91–97

Contents lists available at ScienceDirect

Journal of Arid Environments

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

Soil sterilization alters interactions between the native grass *Bouteloua gracilis* and invasive *Bromus tectorum*

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ARTICLE INFO

Article history:
Received 24 February 2014
Received in revised form
7 August 2014
Accepted 25 August 2014
Available online 16 September 2014

Keywords:
Competition
Great Plains
Plant–soil feedback
Soil microbes

ABSTRACT

The invasive grass *Bromus tectorum* negatively impacts grass and shrublands throughout the western U.S., particularly in arid and semiarid regions. We asked whether soil microbes associated with a native grass (*Bouteloua gracilis*) affect growth of *Bromus* and competition between *Bromus* and *Bouteloua*. We also examined whether plant responses varied between soils from 15 sites in the Northern Great Plains. *Bromus* and *Bouteloua* were grown in media with sterilized or unsterilized soil, alone and together. Soil sterilization reduced biomass of *Bouteloua* and *Bromus* grown alone by an estimated 50% and 48%, respectively. Additionally, results provided evidence that sterilization increased the effect of competition on *Bromus*, and may have reduced the effect of competition on *Bouteloua*. *Bouteloua* likely had a stronger negative effect on *Bromus* in sterilized soils because sterilization reduced *Bromus* biomass by a greater absolute amount. Response to sterilization varied appreciably by site for *Bromus,* but not *Bouteloua.* Our results support the hypothesis that invasive species such as *Bromus* often have positive responses to soil biota in the invaded range. Soil microbes are one factor that may be important in determining dynamics of plant invasions, and plant responses to new sites and competition with natives.

1. Introduction

The non-native grass *Bromus tectorum* L. (hereafter referred to as *Bromus*) currently occupies over 22 million hectares in the western United States (Duncan et al., 2009), and during the first decades of invasion from 1889 to 1929, it spread at one of the fastest documented rates of invasion for plants (Pyšek and Hulme, 2005). *Bromus* has greatly altered ecosystem processes in the arid western U.S. by increasing fire frequency (Balch et al., 2013) and outcompeting native plants (Mack, 1981). Much research effort has been expended to determine the traits of *Bromus* that lead to its dominance in arid and semiarid lands. Explanations include prolific seed production, a phenology which enables early access to spring moisture, and being adapted to large grazers (Harris, 1967; Hulbert, 1955; Mack, 1989). Relationships with soil biota may be another determinant of *Bromus* invasion dynamics. Past research has demonstrated effects of *Bromus* invasion on resident soil biota and nutrient cycling (e.g., Hawkes et al., 2006; Schaeffer et al., 2012). However, the effects of resident soil biota on *Bromus* remain unclear, as past studies have shown positive, negative, or no detected effects of soil biota on *Bromus* growth (Al-Qarawi, 2002; Rowe et al., 2009; Wilson and Hartnett, 1998). Factors such as variation in abiotic conditions across sites may influence the net effect of soil biota on *Bromus*, and interspecific competition may alter responses to soil biota (e.g., Callaway et al., 2004). Examining the role of soil biota in *Bromus* invasion may assist in identifying new methods for preventing or controlling *Bromus* (e.g., Meyer and Nelson, 2006; Rowe et al., 2009). In addition, interactions between plants and soil biota influence multiple processes including succession, plant community diversity, and productivity (Bever et al., 2010; Inderjit and van der Putten, 2010), but further study is needed to understand how plant–plant interactions and geographic variation shape these interactions.

1.1. Plant–soil feedbacks influence invasion

Plant–soil feedbacks – plant effects on soil biotic and/or abiotic factors which affect subsequent plant growth – can influence invasion processes (Inderjit and van der Putten, 2010; Klironomos, 2002). Most native species exhibit a negative conspecific feedback: a species' fitness is often lower in soil previously occupied by conspecifics than in sterilized soil or soil previously occupied by

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http://dx.doi.org/10.1016/j.jaridenv.2014.08.006
0140-1963/

heterospecifics (Brinkman et al., 2010; Kulmatiski et al., 2008). These negative plant–soil feedbacks are thought to be due to the accumulation of specialist pathogens, parasites, and herbivores (Reynolds et al., 2003). Negative feedbacks are particularly prevalent among grasses: Kulmatiski et al. (2008) suggest that characteristics of grasses adapted to competing for water in semiarid lands may lead to greater exposure to soil enemies.

The prevalence of negative conspecific feedbacks may promote coexistence of competing plant species and thereby contribute to maintenance of biodiversity (Bever, 2003). However, among invasive plant species, many studies have found positive (or failed to detect negative) conspecific feedbacks in the invaded range (Inderjit and van der Putten, 2010). Positive feedbacks with soil biota occur when the benefits of soil mutualists outweigh the negative effects of natural enemies, which are thought to lead to increased interspecific competition and competitive exclusion of native plant species by invasive species (Bever, 2003). Several studies have found that while native plant species tend to generate feedbacks that benefit community diversity and coexistence of multiple species (i.e., negative conspecific effects but positive effects on others), invasive species tend to generate feedbacks that promote their own growth; this phenomenon has been documented in arid lands as well as through meta-analysis of many systems (Kulmatiski et al., 2008; Perkins and Nowak, 2013). Using the context of feedbacks between plants and soil biota, we attempted to examine how interactions between an invasive species (*Bromus*) and a native species (*Bouteloua gracilis*) responded to the soil community across a range of sites.

1.2. Study aims

We conducted a greenhouse study comparing the responses of *Bromus* and a native grass (*Bouteloua gracilis* H.B.K. Lag. ex Steud, hereafter referred to as *Bouteloua*) to growth media inoculated with soil gathered beneath *Bouteloua* in the field. We chose *Bouteloua gracilis* as a study species because it is a key late-seral species of Great Plains mixed and shortgrass prairie, and was historically the dominant species in terms of frequency and biomass (Costello, 1944). Moreover, *Bouteloua* is common throughout western North America and occurs throughout much of the invasive range of *Bromus*. *Bromus* interacting with *Bouteloua*-associated soil microbes therefore represents a realistic invasion scenario in the Great Plains. We expected *Bouteloua* and *Bromus* to differ appreciably in their response to soil microbes. *Bromus* is a non-native cool-season annual grass, while *Bouteloua* is a native, warm-season perennial C_4 grass. C_4 grasses are known to respond more positively to mycorrhizal fungi (Hoeksema et al., 2010), and differences in photosynthetic pathways between these two species may affect species compositions of associated soil bacteria (Porazinska and Bardgett, 2003).

We collected soil samples from beneath patches of *Bouteloua* at 15 sites in the semiarid Northern Great Plains to serve as a source of microbial inoculum. *Bromus* and *Bouteloua* were grown alone and together, with soil sterilized by autoclaving and unsterilized, in a factorial experiment to examine whether soil sterilization affected plant–plant interactions, and whether there was substantial variation in the responses of *Bromus* and *Bouteloua* among sites of soil collection.

We tested the following hypotheses:

(1) Unsterilized soil from beneath *Bouteloua* plants will have a negative effect on *Bouteloua* biomass and a positive effect on *Bromus* biomass, because native species tend to generate negative conspecific feedbacks and positive heterospecific feedbacks (Perkins and Nowak, 2013).

(2) If *Bouteloua* biomass is reduced in the unsterilized soil, *Bromus* presence will have a greater negative effect on *Bouteloua* when the two species are grown together in unsterilized soil as opposed to sterilized soil.

Testing these two hypotheses provides information regarding how *Bromus* might invade established communities of the Great Plains or those undergoing restoration: if *Bromus* has an advantage in unsterilized soils, this would suggest that soil microbes may contribute to competitive exclusion of *Bouteloua* by *Bromus*. Because we studied multiple sites, we were also able to examine variation in response to soil sterilization.

2. Materials and methods

2.1. Collection of soil samples and seeds

In summer 2012, soil samples were collected from 15 sites in eastern Montana or northeastern Wyoming, U.S. (Appendix Fig. A.1). Sites were located within 6 sampling areas: 1) Caballo, 2) Eagle Butte, and 3) Spring Creek mines, 4) North and 5) South regions of the Thunder Basin National Grassland, and 6) Fort Keogh Livestock and Range Research Laboratory. Climate, landscape, soil, and site history are described in Table 1. Landscape and soil data for mined sites were collected by the U.S. Department of Agriculture as part of a study of these sites. At Thunder Basin and Fort Keogh, soil pH and texture were analyzed by A&L Western Laboratories, Inc. (Modesto, CA), and site slope and aspect were assessed in November 2013. Sites with a mining history had been strip-mined for coal. Reclamation activities at mines included soil replacement, mulching and fertilizing at some sites, and seeding with *Bouteloua* and a variety of other species. Vegetative cover at sites was predominantly made up of native perennial grasses, *Agropyron cristatum* (L.) Gaertn. and annual *Bromus* species. Total cover was relatively low across sites, averaging between approximately 5% and 30%. Though cover was low and soil was sampled from directly beneath *Bouteloua*, it is possible that any neighboring plant species present may have influenced the soil community as well.

Table 1
Characteristics of the 15 sites used in this study. Sampling area names are followed by total annual precipitation (Precip) in mm and mean annual temperature (MAT) in °C averaged from 1983 to 2012. Aspect of "Und" indicates undulating terrain where aspect could not be determined. Soil texture: C = clay, F = fine, L = loam, S = sand. Sites with no mining history have a reclamation year of "N/A". Missing data are indicated by "–". Climate data were obtained from PRISM Climate Group (available online at www.prismclimate.org).

Sampling area	Site#	Slope (%)	Aspect	Soil texture	Soil pH	Reclamation year
Caballo Mine	1	1	Und	SCL	7.4	1990
Precip: 384	2	1	Und	SCL	7.4	1990
MAT: 7.4	3	2	S	C	7.6	1998
	4	2	S	SCL	7.4	1998
Eagle Butte Mine	1	3	SE	FSCL	7.2	1992
Precip: 378	2	2	NW	FSCL	8.0	1999
MAT: 7.5	3	2	N	SCL	7.4	1999
	4	3	NW	SL	7.6	1992
Fort Keogh	1	4	NNW	SCL	7.4	N/A
Precip: 348	2	7	SSE	SL	7.3	N/A
MAT: 7.7						
Spring Creek Mine	1	1	Und	L	7.8	2001
Precip: 378						
MAT: 7.0						
Thunder Basin North	1	0	Neutral	C	6.1	N/A
Precip: 384	2	3	NNE	SL	6.0	N/A
MAT: 7.4						
Thunder Basin South	1	–	–	–	–	N/A
Precip: 325	2	–	–	–	–	N/A
MAT: 8.1						