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Drought manipulation and its direct and legacy effects on productivity of a monodominant and mixed-species semi-arid grassland

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ABSTRACT

Future precipitation changes in the semiarid grassland region in Central Mexico are expected to be larger for winter rainfall (−20%) than for summer rain (−10%). Winter rainfall however comprises a small proportion of annual precipitation (5–6%), therefore the potential effects on productivity are expected to be negligible. We are realizing however, that winter rain events are important controls of tiller population and consequently of grassland productivity. To attest its influence we examined rain legacy effects using rainout shelters, by reducing rainfall by 42% (2011) and 20% (2012) relative to unmanipulated rainfall on monodominant *Bouteloua gracilis* and mixed-species disturbed grasslands. In 2013 rainout shelters were removed to allow all incoming rain into the plots. Plant cover type was a significant predictor of aboveground productivity with monodominant *B. gracilis* consistently producing 50–80 g/m^2 more than mixed stands. Decreased rainfall did not have negative effects on aboveground productivity except in an extreme drought year for the mixed-species grassland. We also observed a significant legacy effect of winter precipitation on summer aboveground productivity in both grassland types, but not to previous-year total precipitation. In spite of the large annual variability of soil ψ, leaf ψ fluctuated between −0.5 and −1.5 MPa most of the year suggesting a geologic source of water.

1. Introduction

The grassland biome covers ca. 18% of the terrestrial Earth surface (Lal, 2004) and together with the deserts and semi deserts are considered the largest terrestrial biome complex on the planet (Safriel et al., 2005). Grasslands are also present on all continents (Archibold, 1995). In North America, temperate and semiarid grasslands are highly diverse in numbers of species and communities assemblages, and are distributed from Southern Canada in the Saskatchewan province to Central México in the Llanos de Ojuelos subprovince (Rzedowski, 1975; Archibold, 1995; Aguado-Santacruz and García-Moya, 1998). Evolutionarily, grassland ecosystems developed under a diverse set of natural disturbance agents that included natural fire, grazing by native ungulates and frequently recurring droughts, evolving ecophysiological traits adapted to their complex natural disturbance regime (Kotanen and Bergelson, 2000). These grasslands are now also subjected to chronic human-induced disturbances such as altered temperature regimes, increasing atmospheric CO$_2$ concentration and atmospheric nitrogen deposition (Smith et al., 2009).

Globally, the grassland biome has been underestimated with regard to its functional and regulatory role of Earth's carbon (C) cycle. To date, no global policy has been implemented to manage grassland C (IPCC, 2013). Some studies show grasslands to be neutral contributors to atmospheric CO$_2$ concentration (Archibald et al., 2009; Rajan et al., 2013). Nevertheless, the quantity of organic C stored in grassland soils is substantial, i.e., organic C stocks observed in soils range from 10 to ~100 MT C ha^{-1} (23 kg m^{-2} in 0–3 m depth; Jobbágy and Jackson, 2000), which are dependent on the grassland ecosystem type and management. However, small changes in the drivers of C cycling affecting the C source/sink sta-

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tus of grasslands, may translate into large alterations of the global C balance because of the vast geographical extent of this biome.

Still, what is not well understood is the relative and interactive effects of each of the C cycling drivers on grasslands in arid and semiarid regions. Among these drivers, climate change has been receiving much attention by decision-makers and researchers; they call for understanding of ecosystem resilience, critical tipping points, risks associated with alternative ecosystem states and regimes, in order to develop early warning capabilities, and adaptation strategies (Huber-Sannwald et al., 2012).

Net primary productivity (NPP) is a key comparative measure of the many ecosystem services and goods, directly (forage, changes in carbon pools) or indirectly (climate feedbacks, water fluxes) (Chapin et al., 2009). In arid and semi-arid grassland ecosystems, NPP is strongly controlled by precipitation (PTT; Lauenroth and Sala, 1992). Consequently, decreased annual precipitation will likely cause NPP to decline, and in turn, affect food production in the global dryland biome (IPCC, 2013). Sala et al. (2012) reported that PTT control on aboveground net primary production (ANPP) is dependent on whether this relationship is examined either spatially or temporally, with stronger correlations when considering the spatial context. They attributed the lower temporal correlations to our inability to account for lag effects in current year ANPP, derived from legacy effects from previous dry or wet years. The strength of these legacy effects is also dependent on vegetation and species characteristics (i.e., morphological, physiological, chemical, etc.). For instance, Knapp and Smith (2001) reported that the largest interannual variability in ANPP was observed in grasslands that have high potential growth rates in herbaceous species combined with moderate variability in precipitation. Similarly, Weltzin et al. (2003) found that changes in species composition were likely as important as the direct effect of climate change in altering annual ANPP.

The southernmost extent of the North American grassland biome in Central Mexico (Aguado-Santacruz and García-Moya, 1998) is the only grassland representative of the semiarid tropical grassland in North America. For this region, scenarios of future climate project a 20–30% decrease in annual precipitation for 2050 (Karmalkar et al., 2011) as well as an increase in frequency and intensity of droughts (Seager et al., 2007; IPCC, 2007; Seager and Vecchi 2010). In addition, land cover and land use change favor a conversion from predominantly *Bouteloua gracilis* grasslands to highly diverse mixed grassland communities with perennial and annual grass species (Arredondo-Moreno et al., 2005; Delgado-Balbuena et al., 2013).

The unique, monospecific *B. gracilis* grassland consists of perennial grasses with C_4 photosynthetic pathway (C_3 perennial grasses are absent) that harbor an exceptionally high genotypic diversity (Aguado-Santacruz et al., 2002; Arredondo-Moreno et al., 2005; Medina-Roldán et al., 2013). In sites that experience a high degree of disturbance (i.e., overgrazing), the dominant species is replaced by several commonly subordinate C_4 perennial grasses, annual C_3 grasses and several C_3 forbs that form diverse mixed (C_3 and C_4) grassland communities with different functional characteristics (Medina-Roldán et al., 2007; Delgado-Balbuena et al., 2013). For example, Medina-Roldán et al. (2007) reported that a reduction of *B. gracilis* to under 75% of total abundance reduced soil water uptake capacity by the community and belowground biomass production. C_4 grasses show also higher water use efficiency (WUE = g CO_2 uptake via net photosynthetic assimilation/g water loss by transpiration), and are generally more drought tolerant than native C_3 species (Pearcy and Ehleringer 1984; Pearcy et al., 1987). The C_3 photosynthetic pathway, however, benefits from atmospheric CO_2 fertilization more than the C_4 pathway (Ainsworth and Young, 2005).

Given the projections of decreased rain, future trajectories of these grassland communities, will likely experience more frequent droughts, higher temperatures and a background increase of atmospheric CO_2 the overall effect of which is unknown. On one hand, C_4 communities can be favored with their inherently higher WUE, and on the other, C_3 species may have a temporal competitive advantage given their response to chronic increases in atmospheric CO_2. In both cases, biomass may be reduced despite the higher WUE. We still do not know whether these functional differences equate to increase the effect of climate and/or legacy on productivity, and the probability of new ecosystem states characterized by either monospecific C_4 dominated or by mixed-species grassland including a large proportion of C_3 species.

We established a rainout shelter experiment to manipulate drought on tropical semiarid grasslands of central Mexico, and examined productivity measures of both monospecific and mixed grasslands as well as legacy effects of drought on above- and belowground productivity. Based on studies that show *B. gracilis* stands exhibit higher efficiency (faster rate of soil water depletion) than mixed grasslands for soil water acquisition, higher WUE and drought tolerance (Medina-Roldán et al., 2007), we hypothesized that under reduced annual precipitation, mixed grasslands should have lower productivity rates (above- and belowground biomass) compared to natural monospecific grasslands (H_1). On the other hand, given the differences in growth rates between monospecific and mixed grassland stands, and the greater nutrient demand by *B. gracilis* (data unpublished), drought legacy effects will reduce above- and belowground biomass productivity to a greater extent in monospecific than mixed grasslands (H_2).

2. Methods

2.1. Site

The study was carried out at the *Vaquerias* grassland research station of the National Institute for Agriculture, Animal Production and Forestry Research located in the geographic subprovince Llanos de Ojuelos, Jalisco, Mexico (21°46′52.25″N, 101°36′29.56″W). Vegetation corresponds to the southernmost extension of the shortgrass steppe biome in North America (Aguado-Santacruz and García-Moya, 1998). Topography consists of plain terrain with gentle rolling hills (COTECOCA, 1979). Soils are Xerosols with pH values ranging between 5.5 and 6.5 and low content of organic matter and cation exchange capacity (Aguado-Santacruz and García-Moya, 1998). Climate is semiarid with an average of 380 mm annual rainfall for the last 30-year, with most rain falling between July and September, and an average annual temperature of 18 °C (COTECOCA, 1979). Other details on topography, climate and plant species composition can be found in Aguado-Santacruz and García-Moya (1998) and Medina-Roldán et al. (2007).

An experimental approach was used to test our hypotheses, by using rainout shelters to reduce the natural annual precipitation (rf. Yadhjian and Sala, 2002) on both transplanted 8-year old monospecific *B. gracilis* plots (2.0 × 2.0 m) and 70-year mixed grassland plots (2.0 × 2.0 m) recovered from abandoned agriculture land. This study was carried out in 2011–2013.

2.2. Rainout shelters and plot structure

For each plot, V-shaped acrylic strips without UV-filters (ACRYLITE® GP-OP4, Evonik Cyro LLC, Parsippany, NJ) of 0.11 m width and 2.2 m length, were installed atop of two pairs of metallic supports at different height (1.10 m in the back and 0.90 m in the front of plots). Paired metal legs supported (2.00 m apart) each structure (Fig. 1). During the first rain season (2011), we installed