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Climate change effects in a semiarid grassland: Physiological responses to shifts in rain patterns

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ABSTRACT

Several studies have predicted changes in precipitation patterns affecting both rain quantity and its temporal distribution for the Mediterranean Basin. This three-year study was performed to determine the physiological response of *Macrochloa tenacissima*, a dominant species in the western Mediterranean grasslands, to these changes. A rainfall manipulation experiment was therefore conducted to test the interaction of two factors: quantity (Q) and frequency (F) of rainfall, both at three levels (100%, 75% and 50% of natural rainfall). A mobile transparent polycarbonate rain-out shelter was designed to cover experimental plots of *M. tenacissima* when it rained, and then treatments were implemented by watering. Reductions in Q and F caused seasonal down-regulation of net photosynthesis (A) and stomatal conductance (g_s), but the first variable showed greater resistance to change. At the annual scale, only the reductions of F had negative effects on A rates, but without causing significant changes to g_s. The decrease in Q and F had opposite effects on intrinsic water-use efficiency (IWUE), enhancing and diminishing it, respectively. However, the response to Q was stronger, even exceeding the range of natural interannual variability. Rainfall Q and F reduction did not decrease F_v/F_m, as compared to ambient conditions. In conclusion, although the responses to the simulated rainfall patterns did not surpass the current seasonal oscillations of *M. tenacissima*'s physiological parameters, they caused a down-regulation of its gas exchange and increased its water-use efficiency.

1. Introduction

Although the predicted changes in rainfall are subject to higher uncertainty than temperature (De Castro et al., 2005), climate change models for the Mediterranean region of Europe have found robust signs indicating a decrease in both quantity and number of annual rainfall events. Changes in their size and seasonal distribution are also expected. This will lead to a greater concentration of events in winter, longer droughts in summer and an increase in extreme events (Giorgi and Lionello, 2008). The effects of annual rainfall amount on vegetation have been studied extensively (e.g., Le Houérou and Hoste, 1977; Aronson and Shmida, 1992; Epstein et al., 1997; Knapp and Smith, 2001). However, evidence of the importance of other rainfall pattern components on ecosystem responses to climate, such as seasonal timing, frequency and intensity of precipitation, and drought length, has increased since the start of the century (e.g., Bates et al., 2006; Chou et al., 2008; Knapp et al., 2008).

Rain manipulation experiments in hyperarid, arid, semiarid and dry-subhumid ecosystems (drylands) have been rarely implemented until recent years (e.g., Yahdjian and Sala, 2006; Thomey et al., 2011; Tielbörger et al., 2014). Nonetheless, this fact is not an indication of lack of interest, as these areas occupy ~41% of the terrestrial surface, contain ~46% of global carbon (C) reserves (Safriel and Adeel, 2005) and support ~50% of livestock

Abbreviations: Q, rainfall quantity; F, rainfall frequency; A, net photosynthesis at leaf-scale; g_s, stomatal conductance at leaf-scale; IWUE, intrinsic water-use efficiency; F_v/F_m, maximum photochemical efficiency of photosystem II; PAR, photosynthetically active radiation; ITRV, inter-treatment response variability; ISRV, interseasonal response variability; IARV, interannual response variability.

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(Puigdefábregas and Pugnaire, 1999). In addition, water availability mediates the responsiveness of these ecosystems to global change (Huxman et al., 2004). Plant community responses to changes in rainfall patterns vary according to the characteristics (such as phenology, morphology and physiology) of the component species (Robertson et al., 2010). *Macrochloa tenacissima* (L.) Kunth (=*Stipa tenacissima* L., alpha grass, esparto) is a rhizomatous, C_3 perennial tussock grass that is widespread and endemic in western Mediterranean drylands (Gutiérrez, 2000). Besides, it is one of the few species that is usually dominant in its community. So exploring how this species responds to changes in rainfall can reflect the direction of the responses at the community level. This species is ecologically important not only for its spatial predominance, but also due to its morpho-physiological adaptation to this semiarid climate (Ramírez, 2006). Xerophytic communities in Mediterranean grasslands must endure different gradients of water, light and temperature stresses caused by harsh seasonal variations (Madon and Médail, 1997). The *M. tenacissima* strategy for coping with wide variability in abiotic stress, especially related to water availability, is seasonal changes in its physiological parameters (e.g., Domingo et al., 1991, 2003; Haase et al., 1999; Balaguer et al., 2002; Ramírez et al., 2008). In light of the above, the purposes of this three-year study were to i) evaluate *M. tenacissima*'s leaf-scale ecophysiological responses to changes in rainfall patterns (amount and frequency of precipitation); ii) explore the consistency of these responses on two time scales (seasonal and annual) and any change in their importance; and iii) determine whether the responses to the simulated rainfall patterns could exceed the variability of the response to the current rainfall pattern. To pursue these objectives, we designed a full-factorial rainfall exclusion experiment in which two factors were manipulated: rainfall quantity (Q) and frequency (F). Ecophysiological responses of *M. tenacissima* to the treatments were monitored by measuring its leaf-scale gas exchange (CO_2 and H_2O) and maximum photosystem II (PSII) photochemical efficiency (F_v/F_m) after each rainfall event for a continuous three-year period.

Previous studies on *M. tenacissima* suggest that a decrease in rainfall will limit its C assimilation (Haase et al., 1999), but it can tolerate prolonged drought because it is able to withstand extreme leaf dehydration (Balaguer et al., 2002). In addition, this species can respond quickly to individual water pulses to partly recover gas exchange activity after severe water stress (Pugnaire et al., 1996). These physiological features, as well as the apparent coupling of leaf water content and soil moisture, have led to its classification as a functional poikilohydric species (Balaguer et al., 2002). Hence, we hypothesized that i) the predicted changes in rainfall patterns cause down-regulation in net photosynthesis (*A*), stomatal conductance (g_s) and F_v/F_m; ii) severe water stress increases the instantaneous intrinsic water-use efficiency (IWUE), as noted in a previous study in which this variable increased sharply with decreasing g_s (Ramírez et al., 2009); and iii) response to change in rainfall could surpass the current interannual response range. However, this assumption is less likely for interseasonal response since *M. tenacissima* is a drought-resistant species with several water control mechanisms, one of them consisting in reducing gas exchange to near zero in the season with increased water stress (Haase et al., 1999; Ramírez et al., 2009).

2. Materials and methods

2.1. Study site

Rainfall manipulation was done at the Balsa Blanca experimental site, an *M. tenacissima*-dominated grassland with gentle topography located in the Cabo de Gata Natural Park, Almería, SE Spain (N36°56′26.0″, W2°01′58.8″) at 200 m a.s.l. The climate is semiarid warm Mediterranean, with prolonged summer droughts. Mean annual precipitation and temperature are ~220 mm and 18 °C, respectively, with strong intra- and interannual variability in precipitation. This rainfall is far from enough to compensate the potential evapotranspiration (~1390 mm). The soil at Balsa Blanca is classified as Calcaric Mollic Lithic Leptosols (IUSS Working Group WRB, 2006). It is shallow, of variable depth (down to a maximum of ca. 0.3 m, but on average 0.1 m), stony, alkaline (pH > 8) and with carbonate saturation that has led to the formation of a petrocalcic horizon. This horizon is highly permeable due to its porosity and the presence of fissures and fractures (Rey et al., 2012).

The vegetation is dominated by *M. tenacissima*, which represents ~80–85% of the cover of vascular plants (Oyonarte, pers. comm.). This ecosystem also includes xeric shrubs (e.g., *Phlomis purpurea* L., *Thymus hyemalis* Lange, *Thymelaea hirsuta* L., *Ulex parviflorus* Pourr.), some other grasses (*Brachypodium retusum* Beauv.) and scattered individuals of climactic shrubs (*Chamaerops humilis* L., *Olea europaea* L. var. *sylvestris* Brot., *Rhamnus lycioides* L.). Annual plants show considerable biodiversity, although their covers are usually low. There are no trees, and lichen (*Diploschistes diacapsis* Lumbsch., *Cladonia convoluta* Cout.) or moss-dominated biocrusts often occupy plant interspaces. Vascular plant cover is ~55%, and according to Mora and Lázaro (2013), this vegetation has not undergone significant alteration since at least 1955.

2.2. Experimental design, setup and effects on microclimate

A full-factorial rainfall manipulation experiment was set up at Balsa Blanca to test the Q and F factors in February of 2009. All natural rainfall was excluded with an automatic mobile shelter and manual irrigation treatments were performed after each rain event. The reduction in precipitation in the Mediterranean Basin forecasted by climate models has a seasonal range of ~15–20% annually, but up to 30–45% in the driest season (Bates et al., 2008; Giorgi and Lionello, 2008; Mariotti et al., 2008). We set three levels in each factor (100%, 75% and 50% of the natural rainfall during the experimental period) since the use of more than two factor levels along a resource gradient is recommended to test different fitness or ecophysiological response scenarios (Feng and van Kleunen, 2014). Crossing the two factors and the three levels made nine treatments, each with three replicates, so 27 *M. tenacissima* tussocks were used in plots shaped and sized to the plants. The replicates of each treatment were applied to a small (<0.12 m^2), medium (0.12–0.25 m^2) and large (>0.25 m^2) tussock to include all the size and age variability in the site's natural population (Fig. S1). Uniform distribution of these parameters during the treatments was considered important since previous studies have revealed that small and juvenile tussocks are more vulnerable to water stress and that their physiological performance is different from mature tussocks (Armas and Pugnaire, 2005; Ramírez et al., 2008). The plots were carefully selected to fulfill the following criteria: (i) minimal area including 27 variable-sized tussocks; (ii) easy access for construction of the shelter; (iii) very little slope to avoid distortion of irrigation treatments by runoff.

The mobile 40 m^2 transparent polycarbonate shelter with a rain sensor was specially designed to automatically cover the plots when it rained and uncover them the rest of the time to minimize micrometeorological disturbances (Fig. 1). The shelter was open-sided with a curved roof. It had a minimum and maximum height of 1.55 and 2.40 m, respectively, to ensure enough air circulation underneath it and thus prevent a greenhouse effect when it was over the plots. Two methacrylate plates were also added on the frontal sides to minimize the entry of rain to the rain-out zone. The shelter orientation was north–south to minimize shading on the