

Climatic change and rainfall patterns: Effects on semi-arid plant communities of the Iberian Southeast

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ABSTRACT

The structure and functioning of semi-arid ecosystems are strongly influenced by precipitation patterns. Water availability in such environments is highly pulsed, and discrete rainfall events interspersed with drought periods are important components of the annual water supply. Plant communities do not only respond to rainfall quantity, but also to variations in time, so that relatively small changes in rainfall frequency (i.e., pulsed inputs) may have strong effects on communities. Within the Mediterranean basin, climate change models forecast a decrease in mean annual precipitation and more extreme events (i.e., less rainy days and longer drought periods between events), along with seasonal changes. However, little is known on the consequences of these future precipitation changes on plant communities, especially in semi-arid environments. Here, we summarize the few experiments that have manipulated rainfall patterns in arid and semi-arid areas worldwide, and introduce the first results of a pioneer, long-term rainfall exclusion in the semi-arid southeast region of the Iberian Peninsula. The experiment is not only manipulating the amount of rainfall, but also its frequency and seasonal distribution in a grassland-shrubland in the Tabernas desert (Almería, Spain). This work monitored the effect of precipitation changes on different ecosystem processes for five years, at the species and community level, concluding that this plant community (as other communities studied in the same area) exhibited great resilience to changes in rainfall availability, likely caused by plant adaptation to large intra- and inter-annual precipitation variability.

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1. Introduction

Changes in climate and land-use induced by human activities affect productivity, water regime and biodiversity, and result in changes in the structure and functioning of terrestrial ecosystems (Fay et al., 2000; Rustad and Norby, 2002). These alterations would probably intensify in the near future (Sala et al., 1999). There is an extensive literature analyzing the potential effects of increased greenhouse gas concentrations in the atmosphere on ecosystem function and services. However, an almost unexplored but important characteristic of global change is the alteration of rainfall patterns, with probable increases in rainfall variability (IPCC, 2007). General Circulation Models predict higher frequencies of extreme precipitation events, fewer rainy days, and longer drought periods (IPCC, 2007; Rind et al., 1989). These alterations could have

important consequences on processes such as nutrient cycling, plant growth, or population and community dynamics (Weltzin et al., 2003).

Available evidence shows that the structure and function of terrestrial ecosystems are vulnerable to hydrological modifications even in the absence of changes in mean annual precipitation (IPCC, 2007; Knapp et al., 2002; Mearns et al., 1997). Therefore, the analysis of climate change should not rely exclusively on scenarios based on climatic averages (Katz and Brown, 1992) but incorporate seasonal changes in amount and frequency of rain events (Mearns et al., 1997) in order to accurately predict ecosystem responses to future precipitation regimes.

Mediterranean ecosystems are especially sensitive to climate change because they have large topographic complexity with disparate land uses as well as marked water availability gradients (Lavorel et al., 1998). Mediterranean shrubland ecosystems are quite vulnerable to rising temperatures and reduced water availability (Usodomenech et al., 1995) and the expected increase in aridity and temperatures in regions already dry, such as the Mediterranean basin, will likely have serious consequences (IPCC, 2007). Rainfall predictions, however, are extremely complex at the regional level. Unlike the increase in CO₂, which occurs in

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a geographically uniform manner, climate change is strongly dependent on local conditions (IPCC, 2007).

In the Mediterranean basin rainfall has declined by 20% on average during the 20th century, although not uniformly in all locations (Esteban-Parra et al., 1998; Piñol et al., 1998). In the SE of the Iberian Peninsula it is expected that 21st century conditions will be significantly drier than the period 1961–1990 (Esteban-Parra et al., 1998). Several studies predict an increase in winter precipitation primarily in the form of high-intensity events (Frei et al., 1998) which, together with decreased spring and autumn rainfalls, can have important consequences for ecosystem function. For instance, it may speed up desertification processes (Rodrigo, 2002) and reduce ecosystem productivity. Seasonal changes in rainfall can affect population dynamics of certain species that might become locally extinct (Pugnaire et al., 2004). It can also have deep impact on plant–plant and plant–animal interactions leading to changes in the structure and composition of whole communities (Suttle et al., 2007). For example, seed germination in autumn could be dramatically reduced so that recruitment of some species will be threatened and may disappear in the mid term (Miranda et al., 2009a). Overall, changes may imply an alteration of the regeneration niche affecting population dynamics; they may also imply a loss of species richness as only species with broad environmental tolerance will be able to respond to new ecological situations (Cramer et al., 2001; Jump and Peñuelas, 2005).

Most climate change studies have been conducted in temperate ecosystems in the northern hemisphere and the Arctic, but responses may be very different in warmer and drier environments (Llorens et al., 2003). To our knowledge, very few experiments have addressed changing seasonal rainfall patterns, and none in the Mediterranean basin. Thus, our purpose in this manuscript is: 1) to review the most important long-term experiments that have manipulated rainfall patterns in arid and semi-arid environments worldwide; and, 2) to enshrine the only experiment set in a semi-arid Mediterranean environment, where the amount of precipitation as well as the seasonal distribution of rainfall were manipulated for more than 5 years. After a short description of the PSA experiment, the first and unpublished results of this pioneer trial are presented and discussed. The main objectives of this experiment were to study and understand the response of a grassland-shrubland community of Mediterranean semi-arid environments to reduced precipitation amount and changes on rainfall seasonal distribution. We hypothesized that annual rainfall reduction would reduce ANPP of annual species and would worsen the physiological status of woody species as a consequence of lower water availability for plants, while an increase in winter precipitation would not produce such negative effects.

2. Field experiments on altered rainfall patterns in dry ecosystems

Analyses of long-term datasets or natural climate gradients have been used to predict ecosystem responses to future climate (Alward et al., 1999; Dunne et al., 2004; Rastetter et al., 2003). These methods are an alternative to experimental approaches of climate change research that rely on highly manipulative experiments. Long-term datasets are expected to reveal patterns of ecosystem responses similar to those identified by short-term manipulations (Nippert et al., 2006); however, this assumption may only hold if predicted changes are similar in magnitude to those recorded in historic data (Nippert et al., 2006), which may not be the case.

Rainout shelters have been proposed as an alternative to long-term dataset analyses, as they are useful tools to manipulate precipitation (Fay et al., 2000) and give considerable flexibility to make experiments in a realistic manner. Simple shelters can

provide control over the timing of drought but more elaborate shelters can include irrigation systems able to control the daily, weekly, and seasonal timing and the extent of wet and dry periods, independently of natural rainfall patterns (Arkin et al., 1976; Miller et al., 1991; Ries and Zachmeier, 1985; Svejcar et al., 1999). Finally, the use of rainout shelters also allows for the selection of a particular experimental design and location, with the potential of long-term manipulations (Fay et al., 2000).

Fay et al. (2000) and, recently, Miranda and Pugnaire (2009) reviewed the different designs of fixed and mobile rainout shelters. Although still few, some of these shelters have been set up in dry and arid environments. We have included a short description and the main results of the most important long-term experiments set up in these environments on Table 1. One of the earliest designs was developed by Yahdjian and Sala (2002) in a semi-arid shrub steppe in Patagonia, Argentina. Using a fixed, partial shelter made of polycarbonate bands folded in V-form, these shelters reduced the amount of rain by 30, 55 and 80% on small plots (200 × 188 cm). These authors also compared plot responses to artificial watering that resembled dry and wet years, to find that recovery after watering was lower in plots that had experienced drought the previous year, which showed a link between time to recover and drought intensity (Yahdjian and Sala, 2006).

In the tallgrass prairie of Kansas (USA), a rainfall manipulation experiment that altered both mean rainfall and seasonal distribution of precipitation has been running since 1998 (Knapp et al., 2002) in one of the first experiments that manipulated precipitation frequency (Table 1). Results to date have shown that changes in the temporal distribution of rainfall had a negative effect on plant productivity, photosynthetic rates, and soil CO₂ flux whereas reducing precipitation by 30% had smaller effects (Fay et al., 2000, 2002, 2003).

In an arid sagebush steppe in Oregon (USA), 4 treatments or distributions (control, natural distribution, winter and spring distribution) were compared (Svejcar et al., 1999). The winter treatment received 80% of its water between October and March; in the spring treatment 80% of water was applied between April and July; and the natural distribution treatment received a precipitation matching the site's long-term (50 years) distribution pattern. Finally, a control outside the shelters received naturally occurring precipitation. The first significant changes in the extant plant community occurred 4 years after the beginning of the experiment, when productivity was greatest in the spring treatment, which concentrated 80% of the mean annual precipitation in that season (Bates et al., 2006). The delayed response evidences the strong resilience of this arid system to changes in precipitation (Bates et al., 2006).

Six rainout shelters were established in a semi-arid grassland in the Santa Rita Experimental Range (Arizona, USA) on two different soils; three on sandy-loam and three on clayish soils (Huxman et al., 2004a). Several responses were addressed in this system. English et al. (2005) analyzed the effect of soil type and grass species on soil moisture; Potts et al. (2006) measured net ecosystem exchange (NEE) of CO₂ and evapotranspiration (ET); Ignace et al. (2007) analyzed the dynamics of leaf photosynthesis and water status in native and non-native grass species, and Resco et al. (2009) analyzed constraints to leaf gas exchange after precipitation pulses.

In the Colorado Plateau (Southern Utah, USA), Schwinning et al. (2005a, 2005b) manipulated for two years summer and winter rainfall with a fixed shelter that excluded precipitation to cause droughts in summer and/or winter and comparing them with natural rainfall patterns. Rainout shelters were moved from summer to winter plots as drought treatments changed seasonally. Growth of all target species was far more sensitive to winter than to

Table 1
Main experiments that have manipulated rainfall patterns in arid and semi-arid environments worldwide.

Ecosystem/Location	Rainfall manipulations	Rainout shelter design	Main results	Main references
Semi-arid shrub steppe/ Patagonia (Argentina)	Amount reduction: –30, –55, –80%	Fixed, partial shelter made of polycarbonate bands folded in V-form	Seedling emergence, survival, and aboveground biomass were not affected. Aboveground productivity was linearly correlated to annual precipitation along the experimental precipitation gradient.	Yahdjian and Sala, 2002, 2006 Cipriotti et al., 2008
Tallgrass Prairie/Konza (Kansas, USA)	Amount reduction: –30% Longer drought periods (+50%)	Fixed shelter. Precipitation was fully excluded but collected in a container and redistributed to plots by sprinklers	Changes in the temporal distribution of rainfall had a negative effect on plant productivity, photosynthetic rates, and soil CO ₂ flux, but smaller than 30% reduction of rainfall.	Fay et al., 2000, 2002, 2003 Knapp et al., 2002
Arid Sagebrush steppe/Burns (Oregon, USA)	4 seasonal distributions	Fixed shelter. Precipitation was fully excluded but collected in a container and redistributed to plots by sprinklers	First significant changes in plant community occurred 4 years after the beginning of the experiment: productivity was greatest in the spring treatment (strong resilience of this arid system to changes in precipitation).	Svejcar et al., 1999 Bates et al., 2006
Semi-arid grasslands and shrublands/Colorado Plateau (Utah USA)	Drought: Yes/No During the summer, winter, all year long	Fixed shelter. Precipitation was fully excluded	Growth of all species was more sensitive to winter than to summer drought. A decreased summer rainfall will cause high mortality among shallow-rooted species, potentially leading to irreversible community changes.	Schwinning et al., 2005a, 2005b
Semi-arid grassland/Tucson (Arizona, USA)	Rainfall amount: +50% or –50%	Fixed shelter. Precipitation was fully excluded but collected in a container then redistributed to plots by sprinklers	Soil type did not always have an effect. Events in June led to improved plant water status and photosynthesis, whereas pulses in August did not. Recovery of photosynthesis was incomplete when the vascular system was severely impaired during the drought period.	Huxman et al., 2004a English et al., 2005 Potts et al., 2006 Ignace et al., 2007 Resco et al., 2009
Mediterranean shrublands/ NE Spain (+other 5 countries)	Amount reduction Temperature increase	Precipitation was fully excluded during the spring and autumn. Shelter covered the plots automatically when rainfall started.	Drought decreased the number of emerging seedlings and their respective species richness and reduced transpiration, stomatal conductance, and photosynthetic rates in the main shrub species. Plants growing under drought plots produced less total aboveground plant biomass relative to control plots and flower production also decreased.	Ecosystems (2004), 7: 583–671 Lloret et al., 2004, 2005 Llorens and Peñuelas, 2005 Sardans et al., 2008
Semi-arid grasslands and shrublands/Tabernas desert (SE Spain)	Amount reduction: –30% Changes on seasonal distribution	Partial shelter made of polycarbonate bands folded in V-form. Shelter covered the plots automatically when rainfall started.	Absence of significant response of plants and soil to short-term manipulations. First significant changes in woody species occurred 4 years after the beginning of the experiment. Great resilience of plant communities, adapted to high variability in precipitation regime.	Miranda, 2008

summer drought (Schwinning et al., 2005b). The authors concluded that a potential future variation in fall-to-spring precipitation would have strong effects on primary productivity, causing reversible fluctuations in community composition while decreased summer rainfall caused high mortality among shallow-rooted species, potentially leading to irreversible community changes (Schwinning et al., 2005a, 2005b).

Finally, Beier et al. (2004) and Peñuelas et al. (2004a) analyzed the impact of climate change on European shrublands. Although they did not include arid environments, there was a Mediterranean site seasonally dry located in NE Spain. In these systems, temperature was raised at night with a cover that blocked infrared radiation emitted from the soil surface. The warming treatment increased mean temperature by 0.5–2.0 °C (Beier et al., 2004). Rainfall was only excluded during spring and autumn with a mobile transparent plastic sheet that covered the entire plot, reducing annual rainfall by 72% and soil moisture by 33% in plots at the Mediterranean site (Beier et al., 2004). An extensive literature resulted from these experiments, addressing the effects of manipulations on e.g., diversity and seedling emergence (Lloret et al.,

2004, 2005), ecophysiology (Llorens et al., 2003; Peñuelas et al., 2004a), phenology (Llorens and Peñuelas, 2005; Peñuelas et al., 2004b), or nutrient cycling (Sardans et al., 2008).

The experiments described here share an interest to gather long-term data on the effects of rainfall manipulations on arid ecosystems. Other research addressed the relationship between rainfall and productivity in dry ecosystems but it was aimed either at short-term studies (e.g. Fay et al., 2008; Knapp et al., 2001; Miranda et al., 2009a,b; Reynolds et al., 1999; Xu et al., 2007), focused on the responses to pulsed water availability (Chesson et al., 2004; Jentsch et al., 2007; Kreyling et al., 2008; Novoplansky and Goldberg, 2001; Schwinning and Sala, 2004; Schwinning et al., 2004; Sher et al., 2004) or strictly focused on the relationship between annual productivity and precipitation (Huxman et al., 2004b; Sala et al., 1988).

3. The PSA experiment

The only experiment worldwide set in an arid environment that manipulated the amount of precipitation as well as the seasonal

distribution of rainfall was carried out in Tabernas (Almería), in the southeast corner of the Iberian Peninsula (Miranda, 2008). This set up was established in 2005 in the Plataforma Solar de Almería (PSA) grounds. Through an automated, mobile rain enclosure consisting of several polycarbonate bands of different size folded in V-shape, the amount of rainfall (natural or 30% reduction) and its seasonal distribution (normal or altered, 15% less in spring and autumn, 30% more in winter) were applied with a fully factorial design and 4 replicates. Both amount and seasonal distribution were altered in the MIX treatment. Shelters consisted of a steel frame (2 × 3 m) supporting a clear, 4 mm thick polycarbonate banded roof (1.10 m mean height, 20° inclination) anchored in the ground. Open sides maximized air movement and minimized temperature and relative humidity artefacts (Fig. 1). The polycarbonate bands were V-folded at a 120° angle and had a swivel on a metal shaft, so they were placed with the apex of the “V” pointing the ground during rainfall and horizontal when rain ceased; in this way disruptions were minimized and environmental conditions remained close to natural. Movement of polycarbonate bands was automatically driven by a rain detector. Shelters were installed with a north-south orientation to minimize shadow.

To exclude the desired amount of precipitation, the number (5–9) and width (6–16 cm) of polycarbonate bands were changed each season, adapting both magnitudes to experimental treatments (Table 2). Excluded water was diverted to a container (Fig. 1) and the actual percentage of rainwater excluded was later assessed (Fig. A1 in Appendices). To supplement rainfall in winter, a steel frame supported a 1.10 × 1.70 m polyester sheet (Uralita, Spain) representing 30% of plot surface was used. Water collected was then channeled to appropriate plots through 10 microtubes and uniformly distributed throughout the plot, thus imposing a larger rain event. This design does not alter microclimatic characteristics while supplies water as it falls; therefore, the conditions similar to natural rain are kept. There were no significant differences in PAR radiation and air or soil temperatures among treatments (Miranda, 2008), so together with the high effectiveness of the rainout shelter, these results clearly showed that the design was appropriate in

modifying rainfall quantity and distribution while not altering microclimatic conditions.

Shelters were established in Tabernas (SE Spain 37°5′ N, 2°21′ W, 500 m elevation), a semi-arid environment characterised by a mean annual precipitation of 242 mm and a drought period without rains from June to September. Mean annual temperature is near 18 °C, with a mean maximum temperature of 34.7 °C in August; frosts, although possible in winter are not common (Lázaro et al., 2001). Sandy soils derived from mica-schists and quartzite bedrock are most common and the vegetation community is dominated by dwarf shrubs such as *Andryala ragusina* L., *Artemisa barrelieri* Besser, *Artemisia hispanica* L., and *Phagnalon saxatile* (L.) Cass., and annual species like *Bromus rubens* L., *Medicago minima* L., *Reichardia tingitana* (L.) Roth, and *Stipa capensis* Thunb. At shelter set up, there was at least one individual of *A. ragusina*, *A. barrelieri*, *A. hispanica*, and *P. saxatile* under each shelter.

Soil water potential was measured using psychrometers installed at 30 cm depth in the centre of each plot. Due to the efficiency of rainfall exclusion (Fig. A1 in Appendices), soil water potential was different among rainfall treatments (Fig. 2). In wet winters (e.g., December 08–February 09) all plots showed soil water potentials values at –30 cm close to 0 MPa. However, in spring (March–May) and summer (June–August) control treatments displayed the highest water potentials, followed by plots where seasonal distribution was altered. Plots in the reduction and MIX treatments had the lowest soil water potentials (Fig. 2). Differences between control and 30% reduction treatments were higher as drought periods progressed.

From the beginning of rainfall exclusion several soil and plant community variables were measured, including soil nutrients, respiration, net primary productivity (NPP), relative water content (RWC), fruit and seed production of the most common annual species, as well as different plant functional traits (SLA and growth rate) and plant physiological measurements (Fv/Fm, carbon exchange rates) in the dominant woody species in the community (see Appendices, Table B1 for detailed descriptions of these measurements).



Fig. 1. An example of a rainout shelter installed in Tabernas (Almería, SE Spain). This rainout shelter belongs to MIX treatment during autumn. Polycarbonate bands are in position to intercept the rain.

Table 2
Rainfall manipulations and the number and size of polycarbonate bands used for each rainfall treatment and season. Please take into consideration that this size is the width of the band once the band has been folded (120°). The size of the plots is 2 m wide \times 3 m long. Experimental factors were: Amount of rainfall (natural or 30% reduction) and Seasonal distribution of precipitation (normal or altered, 15% less in spring and autumn, 30% more in winter) and the interaction between both.

Treatment (rainfall manipulation)	Autumn	Winter	Spring	Summer
	Rainfall manipulations/number (size) of polycarbonate bands			
30% Reduction	-30%/9 (11 cm)	-30%/9 (11 cm)	-30%/9 (11 cm)	-30%/9 (11 cm)
Altered seasonality	-15%/5 (10 cm)	+30%/0 + microtubes	-15%/5 (10 cm)	100%/0
MIX treatment	-40%/9 (14 cm)	-10%/5 (6.6 cm)	-40%/9 (14 cm)	-30%/7 (14 cm)
Control	100%/0	100%/0	100%/0	100%/0

Overall, there were no differences among treatments in any measured variable until May 2007, two years after the beginning of the rain exclusion. At that time soil nutrients and organic matter content slightly differed among treatments; the more severe the water reduction treatment applied, the lower these soil variables were (i.e., 30% reduction and MIX treatment; Table B2 in Appendices). However, this trend disappeared in winter. There were no differences in soil respiration among treatments in 2007; however, in 2009, i.e., four years after the beginning of rain exclusion, mean daily CO_2 flux was 50% lower in plots where rainfall was reduced by 30% (Table B2).

In 2007, growth of the annual grass *S. capensis* significantly differed among treatments, with 30% reduction in mean precipitation causing the highest decrease in biomass (Fig. 3; Table B2) as hypothesized. In 2009, productivity of *M. minima* also differed in response to rainfall manipulations; plants growing in plots under altered seasonal patterns displayed the highest values (Table B2). However, there were no changes in fruit and seed production in neither species, in *Medicago truncatula* nor in *Asphodelus fistulosus* in 2009; none of the annual species displayed significant differences in their relative water content (RWC) among rainfall manipulations and/or years (2007–2009, Table B2). Annual plant community growth was measured in 2006, 2007 and 2009 by different methodologies (please see Table B1), but only in 2009 there were significant differences, the lowest values found in plots subjected to rainfall reductions of 30% (1.95 ± 0.74 g) while control plots produced the highest ANPP (3.74 ± 0.44 g) (Fig. 4, Table B2). This result partially agrees with our first hypotheses.

While annual species growth patterns changed between years and were species-specific, woody species showed no response in growth, functional, or physiological parameters until May 2009, when the two *Artemisia* species (*A. barrelieri* and *A. hispanica*) had lower photosynthetic rates (A) in plots with rainfall reduction than in control plots, as hypothesized. *A. hispanica* showed higher carbon exchange rates (A and g_s) in altered seasonal precipitation plots (Fig. 5; Table B2). However in 2010, with an accumulated precipitation from October 2009 to June 2010 of 416 mm (almost two times the annual average), differences disappeared (Fig. 5; Table B2) and both species displayed higher values in 2010 than in 2009 likely due to higher water availability.

Other measured variables such as SLA, Fv/Fm, RWC, or woody species growth rate and water use efficiency did not differ among treatments or years.

4. Discussion

Shelters in the PSA experiment were efficient in excluding precipitation without altering microclimate characteristics. However, changes in rainfall quantity and seasonal rainfall distribution did not lead to consistent short-term responses although there were some isolated responses. Two years after the beginning of the rain exclusion we found that one of the most abundant annual species (*S. capensis*) had the lowest annual productivity in the 30% reduction treatment. By contrast, species like *Asphodelus fistulosus*, *Medicago truncatula* or *R. tingitana* did not show any changes, evidencing that plant responses to rainfall manipulations were species-specific. Neither community productivity nor growth of woody species significantly changed until four years after the onset of rainfall manipulations. Overall, these results suggest great resilience of the community adapted to high variability in precipitation regime, as this semi-arid ecosystem.

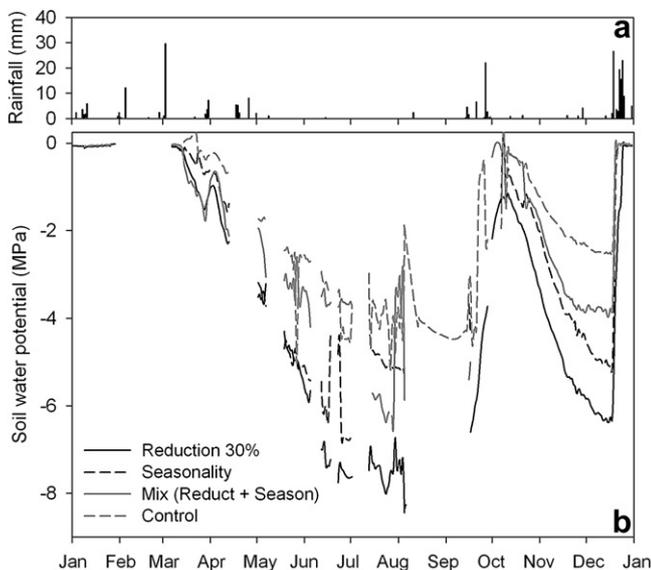


Fig. 2. Rainfall events (columns, panel a) recorded at a meteorological station close to the study site and daily mean soil water potential (b) measured at 30 cm depth for each rainfall treatment ($n = 4$) during 2009.

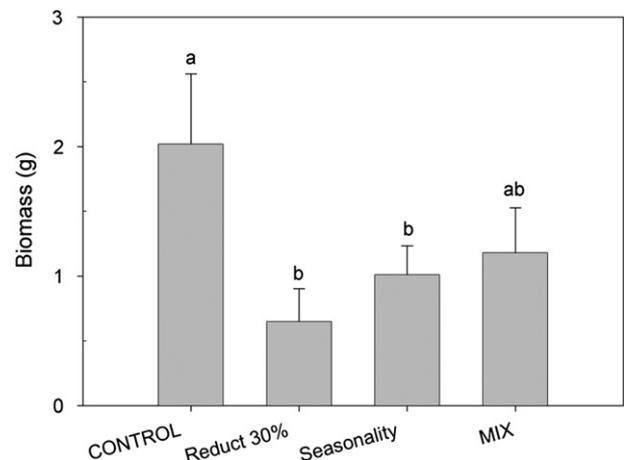


Fig. 3. Total biomass of *Stipa capensis* individuals harvested in two 10×10 cm subplots within the rainfall manipulation plots in May 2007. Columns show mean values ± 1 SE ($n = 4$). Different letters show significant differences ($p < 0.05$) among treatments.

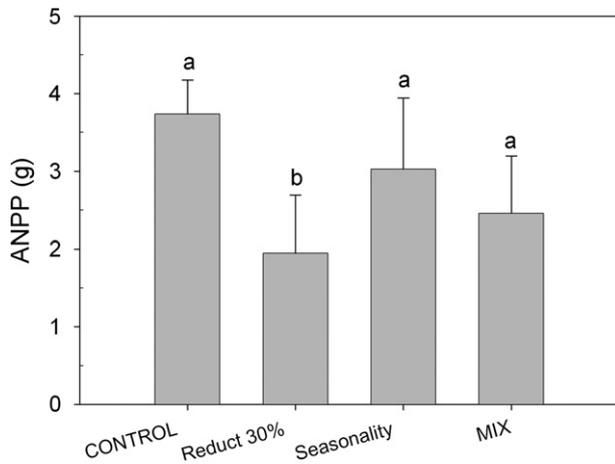


Fig. 4. ANPP (g) harvested in a subplot (Soil respiration PVC ring of 20.12 cm in diameter) inside the rainfall manipulations plots in May 2009. Columns show mean values \pm 1 SE ($n = 4$). Different letters show significant differences ($p < 0.05$) among treatments.

Two years after the beginning of rainfall manipulations soil nutrients and organic matter content slightly differed among treatments. It could be expected that such differences had direct effects on plant communities but also indirect effects through changes in soil and root microbial communities. However, they did not happen. Similarly, in an arid sagebush steppe in Oregon, USA the first significant change in vegetation responses occurred 4 years after the beginning of the experiment (Bates et al., 2006); community productivity was greatest in the treatment where 80% of the mean annual precipitation was distributed in spring (April to July). Such delayed responses show the strong resilience of arid systems (Bates et al., 2006). In our field site, neither a decrease in 30% rainfall nor changes in its seasonal distribution did yield significant differences, most likely because plants are adapted to the characteristic inter- and intra-annual climatic variability proper of semi-arid environments, where such variability is the norm (Jump and Peñuelas, 2005; Lázaro et al., 2001); in our field site, inter-annual variability may reach 36% and intra-annual variability up to 207% (Capel-Molina, 2000; Lázaro et al., 2001). Our interpretation is that most species can tolerate short-term variability through phenotypic plasticity (Jump and Peñuelas, 2005). Also, low and unpredictable rainfall has shaped communities adapted to such constraints, so that plants are able to use resources gained in favorable periods in order to persist during more critical periods (Cheson and Huntly, 1989). It is particularly significant, however,

that many woody species living in this arid environment are only moderately resistant to xylem embolism, and thus traits and mechanisms associated with fast and efficient recovery of physiological function after severe drought must be explored (Miranda et al., 2010). One such mechanism may be the ability of seedlings to respond to low water availability through higher root elongation and increased absorptive root surface (Padilla et al., 2007). Root growth can be interpreted as an adaptive strategy to deal with drying soils and decreasing soil moisture since larger roots enable to exploit larger volumes of soil, which may ensure recruitment success and survival because of higher access to permanent water sources (Padilla and Pugnaire, 2007).

It has also been shown that annual species in arid environments are able to resume rapid growth following rainfall events (Sala and Lauenroth, 1982; Williams et al., 1998), a behavior that could provide competitive advantage where rain is scarce and unpredictable, tending to stabilize biomass in highly variable climates (Williams et al., 1998). In this sense, Miranda et al. (2009b) found that a 50% reduction in watering during one year reduced plant productivity, cover, and diversity in three annual plant communities. However, neither a 25% reduction nor changes in the frequency of watering events seemed to affect these communities. Similarly, Yahdjian and Sala (2006) found that aboveground net primary productivity (ANPP) in a semi-arid steppe decreased as precipitation interception increased. This relationship was mostly due to the drought sensitivity of grasses and not to shrub species whose ANPP was unrelated to annual precipitation (Yahdjian and Sala, 2006).

The lack of plant responses to moderate water reductions could be due to the identity and resistance of the communities involved, highly adapted to rainfall variability so characteristic of arid environments. Primary productivity, physiology and plant diversity in more mesic grasslands are usually affected by lower rainfall and seasonal changes (Knapp et al., 2002; Fay et al., 2002). These changes, however, do not affect dominant and subdominant species in the same way because dominant species have greater tolerance to rainfall variability (Fay et al., 2003). In mesic ecosystems there were significant decreases in soil respiration due to increased drought periods, but such differences were only found after three years of rainfall manipulations (Fay et al., 2000; Harper et al., 2005).

In an experiment in NE Spain, the rainfall experiment closest to our study site, both temperature and precipitation were manipulated (Beier et al., 2004). There was no increase in total aboveground biomass due to warming, as temperature in this ecosystem is already close to the optimum for photosynthesis (Peñuelas et al., 2004a); this site presented instead the most negative response to drought treatments of four European sites included in the study;

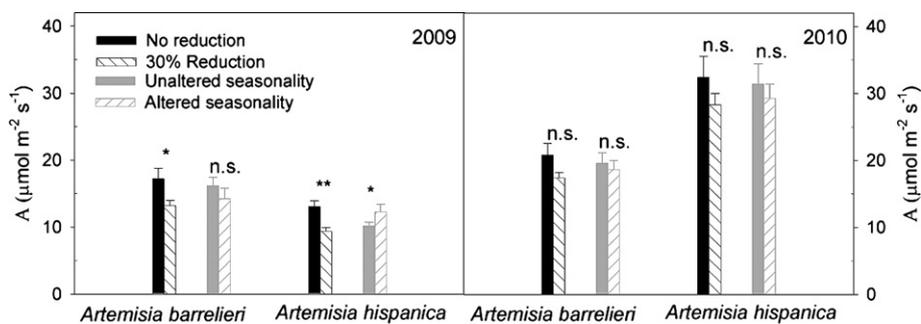


Fig. 5. Photosynthesis rates (A) measured in May 2009 and June 2010 for the two main woody species growing under rainfall manipulations. Columns show mean values \pm 1 SE ($n = 4$). As the interaction between the factors amount (A) and seasonality (S) was not significant in both years, differences between treatments correspond to differences between the two levels of each factor (A; amount: natural or 30% reduction; S; altered seasonality: normal or altered). Differences are denoted by ANOVA results shown as *, ** and *** for $p < 0.05$, $p < 0.01$ and $p < 0.001$ respectively; ns = not significant.

two years after the beginning of manipulations there was a 14% decrease in total aboveground plant biomass relative to control plots (Peñuelas et al., 2004a), flower production decreased by 40%, and the number of seedlings and species richness also decreased (Lloret et al., 2004). There was a reduction in transpiration, stomatal conductance, and photosynthetic rates in the main shrub species (Llorens et al., 2003). By contrast, in our semi-arid site there were almost no short-term changes in vegetation responses due to rainfall manipulations.

The inherent inter-annual rainfall variability in this area makes the study of long-term responses difficult, as years of exceptional precipitation could hinder the response of vegetation to rainfall manipulation, so long-term experiments are needed to see the response of arid ecosystems to changing rainfall patterns.

In summary, our results show that inherent inter-annual rainfall variability of arid ecosystems makes long-term experiments necessary, as years of high precipitation may restart the system canceling short-term differences among treatments. However, we were able to show that changes in rainfall patterns, including decreases in rainfall quantity and changes in seasonal distribution, affect semi-arid plant community and that short-term productivity and physiology may be affected only if there are strong decreases in precipitation or longer periods of rainfall manipulations. These responses, joined to the results found on different annual plant communities in the same semi-arid region, point to the highly resilience of these communities

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Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jaridenv.2011.04.022.

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