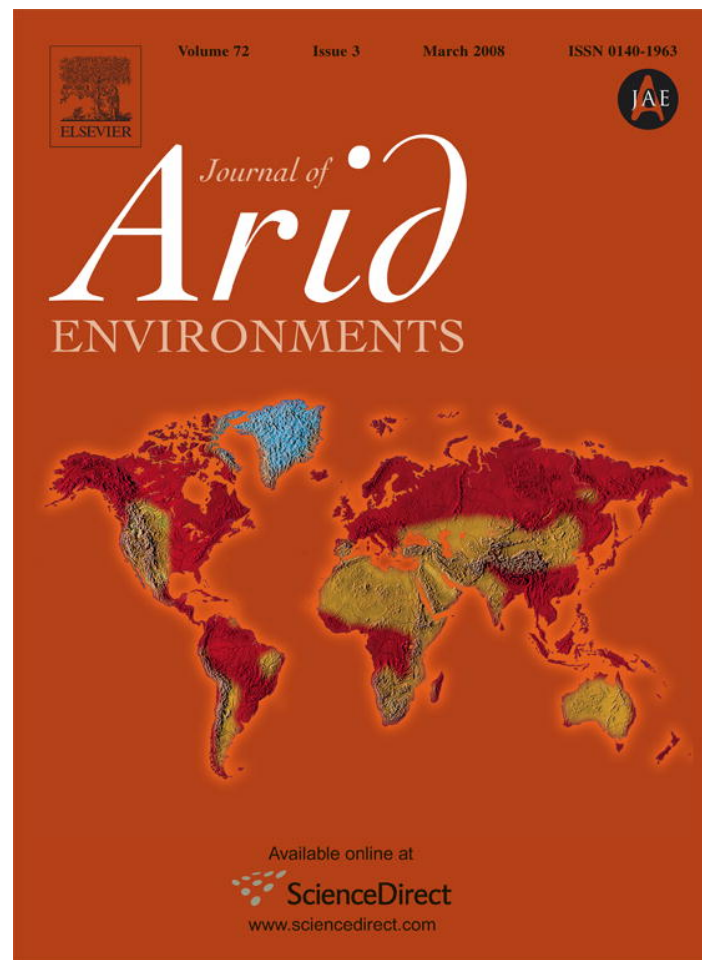


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Journal of Arid Environments 72 (2008) 162–174

Journal of
Arid
Environments

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Does drought control emergence and survival of grass seedlings in semi-arid rangelands?

An example with a Patagonian species

P.A. Cipriotti^{a,*}, P. Flombaum^b, O.E. Sala^b, M.R. Aguiar^c

^a*Cátedra de Métodos Cuantitativos Aplicados, Departamento de Producción Animal, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, Buenos Aires C1417DSE, Argentina*

^b*Ecology and Evolutionary Biology, Brown University, USA*

^c*Cátedra de Ecología-IFEVA, Departamento de Recursos Naturales y Ambiente, Facultad de Agronomía, Universidad de Buenos Aires/CONICET, Argentina*

Received 9 August 2006; received in revised form 31 May 2007; accepted 7 June 2007

Available online 30 July 2007

Abstract

Current climate change models for arid ecosystems challenge our ability to understand the effects of droughts on plant population dynamics. In a sandy soil plant community from the Patagonian steppe, we studied soil water dynamics and its effects on grass regeneration. Our hypothesis was that a decrease in precipitation would not change soil water dynamics of the top soil layer where most of the seeds and seedling roots are located. First, we simulated soil water dynamics with a balance model (DINAQUA) for different years and soil layers, in two different periods related to the emergence and survival of plants. Then, we performed a manipulative field experiment in which we generated a drought gradient by intercepting 0%, 25%, 50%, and 80% of the precipitation for two different microsites (vegetated and bare soil). We quantified drought effects on emergence, survival, and biomass of seedlings using a native grass (*Bromus pictus* Hook). Soil water content in the top soil layer at the end of growing season was a 61% less than mid and bottom soil layers, independently of the climatic condition of the year. The simulations suggested that drought reduces the maximum depth of water infiltration, but available water for plants in the top layer where seedlings have their roots, was not modified, in agreement with our field experiment measurements. Consistently, the emergence (51%), survival (65%), and biomass (15 g/ind) of seedlings were not affected by drought levels. However, there is a positive microsite effect on biomass (36%), indicating a facilitative role of adult plants on grass seedlings. We interpreted these results as indicative that seed germination and seedling recruitment will not be heavily impacted by increasing water deficit in the Patagonian steppe. © 2007 Elsevier Ltd. All rights reserved.

Keywords: Climate change; Microsites; Rain-out shelter; Recruitment; Top soil; Water stress

*Corresponding author. Tel.: + 54 11 4524 8000x8077.

E-mail address: cipriott@agro.uba.ar (P.A. Cipriotti).

URL: <http://www.agro.uba.ar/users/cipriott/myweb/> (P.A. Cipriotti).

1. Introduction

Water availability is the main control of plant population processes in arid and semi-arid rangelands (Fair et al., 1999; Fowler, 1986; Lauenroth et al., 1994; Sala et al., 1992; Schwinning et al., 2005). Recent climate change models challenge our ability to understand the consequences of precipitation reduction in arid ecosystems. In the Southern Hemisphere, arid ecosystems are supposed to experience a 20% reduction in annual precipitation and an increase of ca. 0.5 °C in mean annual temperature (Gian-Reto et al., 2002). As we move toward an era in which it is essential to take decisions regarding the management of natural resources, it is necessary to develop ecological forecasts about the probable impacts of global climate changes on population processes (Clark et al., 2001). Progress in ecological forecast can be achieved through a mix of environmental database analyses, field studies and modeling approaches (Clark et al., 2001). In this paper, we studied the effect of decreased rainfall on the emergence and survival of seedlings in arid ecosystems by a mix approach.

Emergence and survival of seedlings, both key processes for the maintenance of plant density (Lauenroth et al., 1994), are mainly controlled by water availability in the top soil layer and the micro-environment close to the soil surface (Bertiller et al., 1996; Defosse et al., 1997; Lauenroth et al., 1994; Novoplansky and Goldberg, 2001a). In the top soil layer, water availability depends on the balance between inputs by rainfall and outputs by evaporation, percolation, and plant absorption, whereas in deep soil layers, water availability depends on inputs by drainage from upper layers and outputs by plant absorption and drainage to lower layers. Water infiltration in the soil depends on rainfall amount, the water content of the soil layer, and soil texture. When water content in upper soil layers reaches field capacity, the excess infiltrates to lower soil layers. In other words, whatever the size of the events, upper soil layer will refill first and only the exceeding water will percolate to deeper soil layers. Reductions in water amount infiltrated will therefore have a lesser impact in the upper soil layer compared to bottom soil layers. In addition to the vertical heterogeneity of soil water, scarce water availability promotes horizontal heterogeneity of vegetation. Arid ecosystems typically have a two-phase mosaic structure, with high-cover vegetation microsites interspersed in a low-cover matrix (Aguar and Sala, 1999). This spatial structure promotes differences in ecosystem functioning, especially in the water balance of different microsites due to changes in evaporation and transpiration rates (Cornet et al., 1988).

In many arid ecosystems, small rainfalls (<5 mm) represent the highest fraction of precipitation events (Golluscio et al., 1998; Sala and Lauenroth, 1982), and are important for the maintenance of plant and population growth (Novoplansky and Goldberg, 2001b; Schwinning and Sala, 2004). However, small rainfall events differ in their effects on species and ecological process depending on soil texture (Sala and Lauenroth, 1985; Soriano and Sala, 1986). Because of the soil water refill dynamics, we hypothesize that a reduction in precipitation does not affect water availability for plant germination and seedling growth in arid ecosystems with coarse sandy soils. To evaluate this hypothesis, first we used a simulation model—DINAQUA—(Paruelo and Sala, 1995) to study the dynamic of water in the soil under different climatic conditions. We predicted that extreme dry years constrain seedling dynamics by lowering soil water potential. Second, we performed a manipulative field experiment in which we reduced the amount of precipitation for two different microsites where we sowed seeds of a native grass. Finally, we used DINAQUA again to simulate soil water conditions during the field experiment.

2. Materials and methods

2.1. Study site

The study was done in South Central Patagonia, Province of Chubut, Argentina, in the Experimental Field INTA Rio Mayo at 45°41'S, 70°16'W, 500 m above sea level. The annual mean precipitation is 152 mm ($n = 37$ years) ranging from 47 to 230 mm. More than 70% of total precipitation occurs during autumn and winter (Jobbágy et al., 1995). The annual mean temperature is 8.1 °C with a monthly mean that ranges from 2 °C in July to 14 °C in January. The landscape is flat and the soil is of coarse texture (sandy), with 50% of cobbles and pebbles in the soil mass (Paruelo et al., 1988). The vegetation

in the area corresponds to the dominant community of the Occidental District of the Patagonian steppe (Soriano, 1956). In this community, bare ground represents more than 50% of the cover, and grasses and shrubs cover 25% and 12%, respectively (Golluscio et al., 1982). The dominant grass species are: *Stipa speciosa* Trin. Et Rupr., *Poa ligularis* Nees ap. Steud., and *Stipa humilis* Vahl. The dominant shrub species are: *Senecio filaginoides* AD., *Mulinum spinosum* (Cav.) Pers., and *Adesmia campestris* (Rendle) Skottsbo. *Bromus pictus* Hook is a native and palatable grass species, and is particularly important in the region because it is a favorite of sheep (Golluscio et al., 1999) and has good attributes for regeneration (Rotundo and Aguiar, 2004). Currently, this species is completely absent from several grazed and overgrazed rangelands (Aguiar, unpublished data).

2.2. Simulation experiments

We used DINAQUA (Paruelo and Sala, 1995), a soil water dynamic model developed, calibrated, and verified for the Patagonian steppe, to simulate soil water content of soil layers explored by grass roots (Soriano et al., 1987). We divided the first 30 cm in three 10 cm intervals and we called them top, mid, and bottom layers (0–10, 10–20, and 20–30 cm, respectively). Inputs to the model were grass and shrub parameters (biomass, phenology, root distribution, and transpiration rate), soil parameters (layer thickness, field capacity, and wilting point), and meteorological data recorded at the study site by an automated standard met station with a data logger Campbell SCI 21X (daily values of precipitation, mean temperature, and radiation). The daily rainfall (mm) was recorded by a standard precipitation gauge. The daily mean air temperature (°C) was calculated as a simple average from the maximum and minimum recorded by the met station. The global radiation (kW/m²) is integrated in a daily value from records at 5-min intervals. DINAQUA simulates transpiration, evaporation, drainage, and soil water content for each soil layer based on a water balance model with a daily time step. Water evaporation from soil was calculated according to Ritchie (1972) model. The model mostly considered saturated flows because the unsaturated hydraulic conductivity of these soils is very low, even when they are close to field capacity (Paruelo and Sala, 1995). DINAQUA does not account for horizontal spatial heterogeneity. We ignored run-off and run-on because of the flat landscape and the sandy soil. Further details about DINAQUA are provided in Paruelo and Sala (1995).

We ran DINAQUA for years with different climatic conditions: dry, average, and wet. We used a 20-year climatic data set to define dry, average, and wet years. Dry years had less precipitation than the 1st quartile (133 mm), average years had precipitation between the 1st and 3rd quartile (190 mm), and wet years had more precipitation than the 3rd quartile. We selected years with full climatic records, which constrained to three replicates (years) per climatic condition. We also used DINAQUA to model soil water content after rainfall interception produced by the rain-out shelters during the experiment growing season (2000/01; see Section 2.3).

The main output variable of simulations was the daily soil water content per soil layer (0–10, 10–20, and 20–30 cm). With the modeled soil water content, we calculated soil water potential using an equation developed for the study site (Paruelo et al., 1988). Also, we calculated the water residence time defined as the number of days with soil water potential between 0 and –5.9 MPa, which represents the range of water potential for which water is available for plants in Patagonia (Paruelo et al., 1988; Sala et al., 1992) for two critical periods for the life cycle of most grasses in the Patagonia steppe: emergence (1 April–31 August) and survival (1 September–31 December). These two periods were defined because of more than 70% of total precipitation in Patagonian steppes occurs during autumn and winter (Jobbágy et al., 1995). This aspect clearly determines two different periods according to the water availability and temperature, key controls of grass recruitment. During autumn and late winter, the water soil conditions are adequate to germination and emergence of grass seedlings, but the low temperatures slow down the growth of seedlings up to spring (Paruelo et al., 1998; Paruelo and Sala, 1995; Rotundo and Aguiar, 2004; Walter and Box, 1983). Then, from spring up to early summer, rainfalls are rare and scarce. Hence, the water recharge of soil during cold season and the temperatures of warm season determine the soil water deficit and the extent of growing season, defining the survival and recruitment of seedlings.

2.3. Manipulative field experiment

We evaluated the emergence and survival of *B. pictus* with a field experiment in which we generated a drought gradient for vegetated and bare soil microsites. The experiment had a factorial design with two factors: drought and microsite. The drought factor had four levels (0%, 25%, 50%, and 80% of rain interception), and seven replicates. To intercept rainfall we used rainout shelters made with transparent acrylic bands, which delivered water to a plastic container. The device to intercept rainfall is described in detail in [Yahdjian and Sala \(2002\)](#). The number of plastic bands determined the amount of water intercepted. The device reduced incoming rainfall effectively for all interception levels, since soil water content varied accordingly to the drought treatments, while other environmental variables (e.g., radiation, temperature) were minimally affected (<10% variation) ([Yahdjian and Sala, 2002](#)). The area of each experimental plot was 3.76 m², and we considered non-significant surface or sub-surface lateral movement of moisture because of the flat terrain and coarse soil. We also corroborated the effectiveness of the shelters in inducing changes in soil water by measuring soil water content at two depths in winter and summer, with the time domain reflectometry (TDR) technique ([Reeves and Smith, 1992](#)) employing a Tektronix 1502C. We recorded the soil water content in May 2000 and December 2000 by burying two pairs of TDR probes of 10 and 20 cm height in each plot from control and drought treatments. Also, we compared our measures with those performed by [Yahdjian and Sala \(2002\)](#) in the same experimental setup and respective dates.

We incorporated a microsite factor as a variation source in the experimental design because of the partial and spatial heterogeneity of vegetation cover in the Patagonian steppe ([Cipriotti and Aguiar, 2005](#)). In this way, we quantified differences in plant performance related to vegetated and bare soil patches. We defined vegetated microsite as soil beside a *S. speciosa* adult (touching canopies), and the bare soil microsite as the center of an unvegetated area larger than 0.35 m in diameter. The experiment was designed as a split plot, with drought plots split into two subplots for microsite treatments.

We sowed 10 seeds of *B. pictus* in each replicate of the eight treatments (10 seeds × 4 drought levels × 2 microsites × 7 replicates = 560 seeds) at a depth of 1.5 cm in May 2000. We used the palatable grass *B. pictus* because of its high forage quality, good regeneration properties, and high local extinction risk in overgrazed fields ([Bonvissuto et al., 1983](#); [Rotundo and Aguiar, 2004](#); [Somlo et al., 1997](#)). Seeds were collected on the same study site during January 2000. The germination percentage in growth chambers under wet conditions during 15 days was more than 90% ([Rotundo and Aguiar, 2004](#)). The response variables were emergence, survival, and aerial biomass. We measured emergence as the number of seedlings for the first sampling date (September 2000). We marked emerged seedlings with a colored toothpick, and at the end of growing season (July 2001), we calculated the survival as the difference in living individuals between the first and the final sampling date. Finally, we harvested all individuals on July 2001 to quantify aerial biomass.

2.4. Data analysis

We analyzed the precipitation data for each critical period (emergence and survival) with a one-way ANOVA with three levels for the main factor “year type” (dry, average, and wet). We compared water residence time for each period with a two-way ANOVA with “year type” (dry, average, and wet) and “soil layer” (top, mid, and bottom) as the main factors. Similarly, the field measures of soil water content were analyzed by a two-way ANOVA with “drought level” (0%, 25%, 50%, and 80%) and “date” (May 2000 and December 2000) as the main factors. Finally, we analyzed the emergence, survival, and aerial biomass with a split-plot ANOVA, being “drought” the whole plot and “microsite type” the subplot. Furthermore, we calculated power of tests when needed. We employed the program G-power ([Erdfelder et al., 1996](#)) for a one-way ANOVA design with eight different treatments (4 drought levels × 2 microsites) and we tested the general hypothesis as a post-hoc test ([Cohen, 1988](#)).

3. Results

3.1. Database analyses of precipitation

We found that the amount of precipitation in the survival period was similar independently of the total year rainfall, whereas in the emergence period there were major differences among year types ([Fig. 1](#)). During the

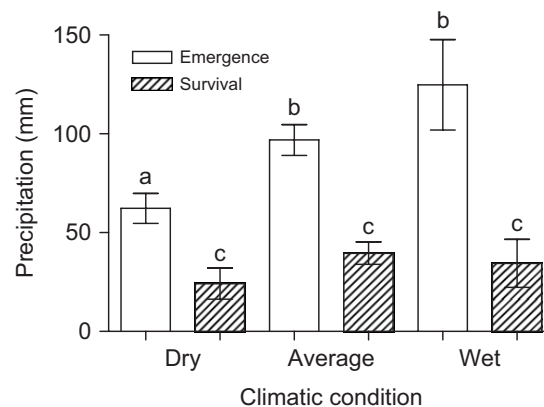


Fig. 1. Mean \pm SE rainfall recorded during the emergence (04/01 to 08/31) and the survival (09/01 to 12/31) period for three climatic conditions (dry, average, and wet). Different letters indicate significant differences ($p < 5\%$) among climatic conditions within each period ($n = 3$ years for each climatic condition).

period 1980–2000, 15 years fell into average or wet classes (> 133 mm/year). The probability of two consecutive dry, average or wet years was 9%, 23%, and 15%, respectively. In the three climatic conditions, about 60% of annual precipitation occurred during the emergence period, whereas only 20% occurred during the survival period.

3.2. Historical soil water content simulation

During the emergence period, soil water content and soil water residence time were influenced by annual precipitation, but values varied among soil layers (Figs. 2a–c and 3a). In the top soil layer, water residence time was similar among year types (Fig. 3a), whereas in the mid and bottom soil layers water residence time decreased with decreasing precipitation (Fig. 3a). In contrast, during the survival period, soil water residence time was similar among dry, average, and wet years, and only differed among soil layers (Fig. 3b).

3.3. Manipulative field experiment

3.3.1. Plant response variables

Emergence and survival of seedlings were not statistically different among drought treatments or microsite types (Fig. 4). The mean emergence was 51% and mean survival at the end of the experiment was 65% (Fig. 4a, b). However, seedling aerial biomass was higher in the proximity of other grasses and this was valid in all drought treatments (Fig. 4c).

3.3.2. Soil water content analysis

Simulations with the precipitation records of the year of field experiment indicated that soil water content simulated by DINAQUA varied among drought treatments, and for the growth period, and soil layers considered (Fig. 2d–f). The soil water content simulated with DINAQUA partially agrees with the field measures of soil water content. During winter (May 2000), simulated top soil water content quietly agree with field measures for control, 25% and 50% of rainfall interception treatments, with differences around 6% (Figs. 2d, e and 5a, b). However, for the 80% rainfall interception treatment, the model clearly sub-estimated the soil water content from the top soil, with differences larger than 100%. For the same season and mid soil layer, the differences between simulations and field measures were larger than top soil and especially important (300%) in the treatments for extreme droughts (50% and 80%). During summer, there is a clear agreement between simulated and field measures of soil water content from top soil layer for all drought treatments (Figs. 2d, e and 5a, b). The differences between the model outputs and field measures were around 5%. However, for the mid soil layer and extreme drought treatments (50% and 80%), again the simulated values sub-estimated the real soil water content, with differences around 130%. In summary, the DINAQUA model generates good predictions for top or mid soil layers, but in absence of extreme rainfall interceptions (50–80%).

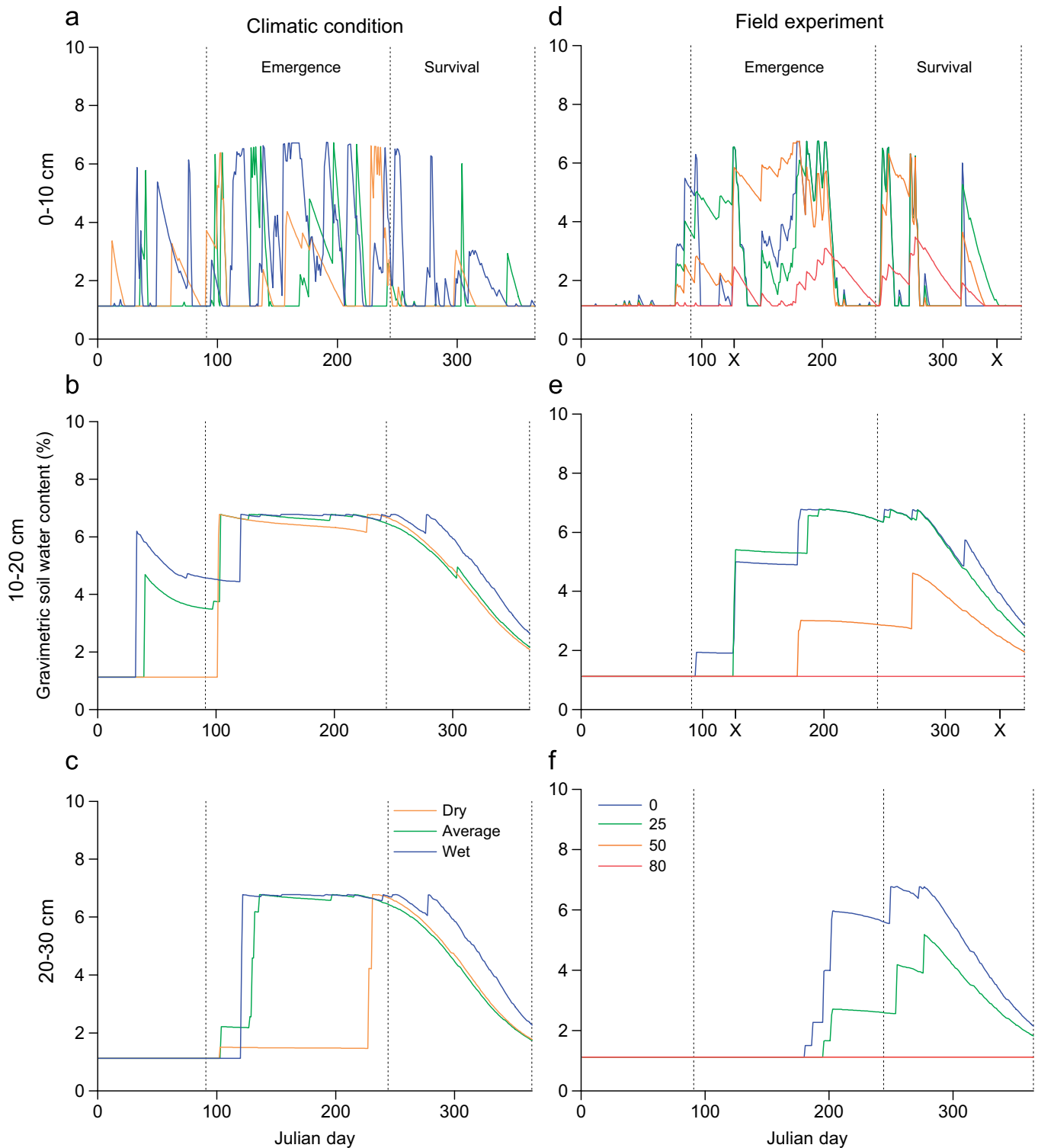


Fig. 2. Daily gravimetric soil water content simulated with DINAQUA for three soil layers (0–10, 10–20, and 20–30 cm) under: (a–c) three climatic conditions (dry, average, and wet years); and (d–f) four interception levels of precipitation (0%, 25%, 50%, 80%) during growing season of field experiment. The X indicates two dates of field measures of soil water content during winter (May 2000) and summer (December 2000).

During the emergence period 2000/01, in the top soil layer, water residence time was 15 days on the extreme drought treatment (80%; Fig. 3c) compared to water residence times higher than 75 days on the 0%, 25%, and 50% treatments (Fig. 3c). This last value was similar to the one simulated for dry, average, and wet years (Fig. 3a). In the

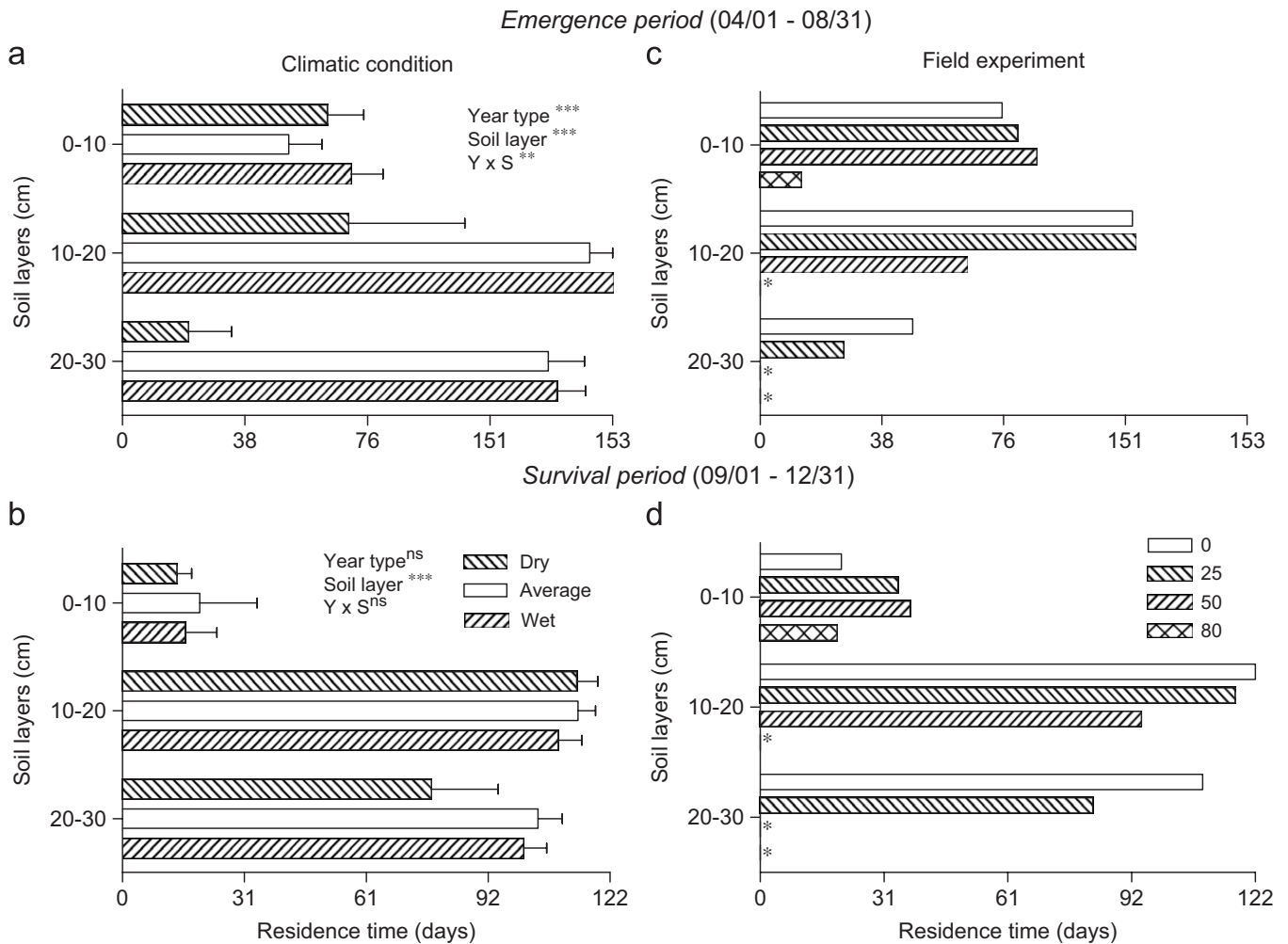


Fig. 3. Residence time of water for three soil layers (0–10, 10–20, and 20–30 cm) under: (a, b) three climatic conditions (dry, average, and wet years); and (c, d) four interception levels of precipitation (0%, 25%, 50%, 80%) during growing season of field experiment for emergence (04/01 to 08/31) and survival (09/01 to 12/31) period, respectively. The residence time of water was calculated as the number of days with soil water potentials higher than -5.9 MPa. To calculate it, we used the soil water content simulated with DINAQUA. These values represent the water available for plants in the Patagonian steppe. Asterisks (*) indicate no days with soil water potentials higher than -5.9 MPa.

mid soil layer, water residence time was the same for 0% and 25% treatment, but it decreased for 50% which had a similar value to the one estimated for dry years (Fig. 3a, c). The 80% treatment had no single day with water potential above -5.9 MPa (Fig. 3c). In the bottom soil layer, only 0% and 25% treatments registered soil water potential higher than -5.9 MPa, but water residence time was below the predicted for average years and similar to dry years of the 20-year record (Fig. 3a, c).

Similarly, during the survival period 2000/01 in the top soil layer, all drought treatments had higher values of water residence times compared to that estimated for dry, average, or wet years (Fig. 3b, d). In the mid soil layer, 0% and 25% treatments had the same water residence time and were comparable to the average or wet years (Fig. 3b, d). But, the 50% treatment showed a reduction in water residence time, and 80% treatment did not have a single day with water potential above -5.9 MPa (Fig. 3d). In the bottom soil layer, water residence time was similar for the 0% treatment and average or wet years (Fig. 3d, b), and for the 25% treatment and dry years (Fig. 3d, b). The 50% and 80% treatments had no single days above -5.9 MPa (Fig. 3d).

4. Discussion

Despite of the reduction in the incoming precipitation and water availability imposed by the rain-out shelters, seedlings emergence, survival, and aerial biomass were not affected. We performed a power analysis

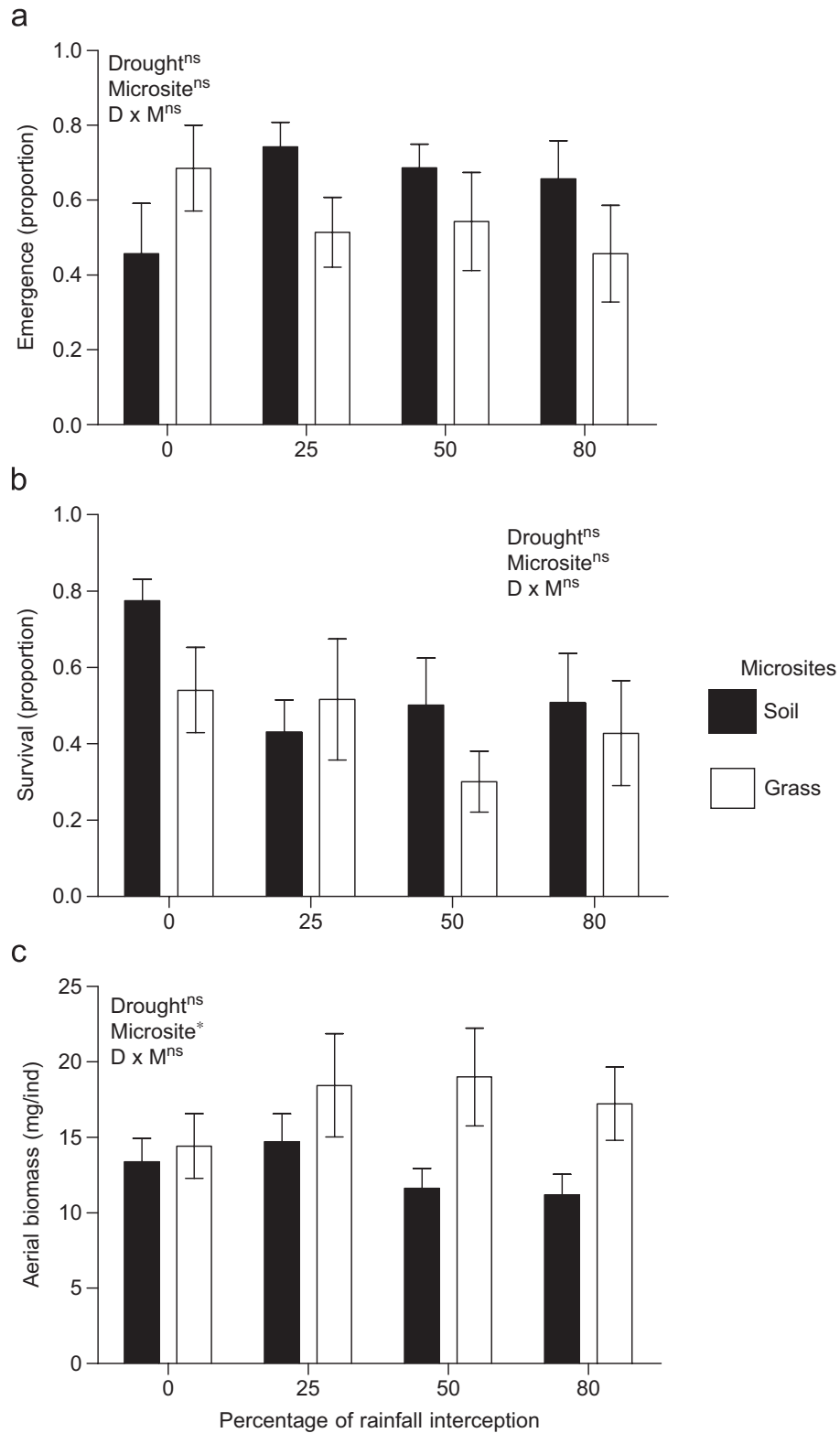


Fig. 4. (a) Emergence, (b) survival, and (c) aerial biomass of *Bromus pictus* seedlings for four different levels of rain interception (D: 0%, 25%, 50%, 80%) in two microsite types (M): bare soil (black bars) and grasses (white bars). The vertical bars indicate mean \pm SE.

to evaluate with which probability we would accept the null hypothesis of no difference among drought treatments. We found moderate power values (50–70%) on seedlings emergence, survival, and biomass probably because the test is highly sensitive to the error term and number of replicates (Zschokke and Lüdin,

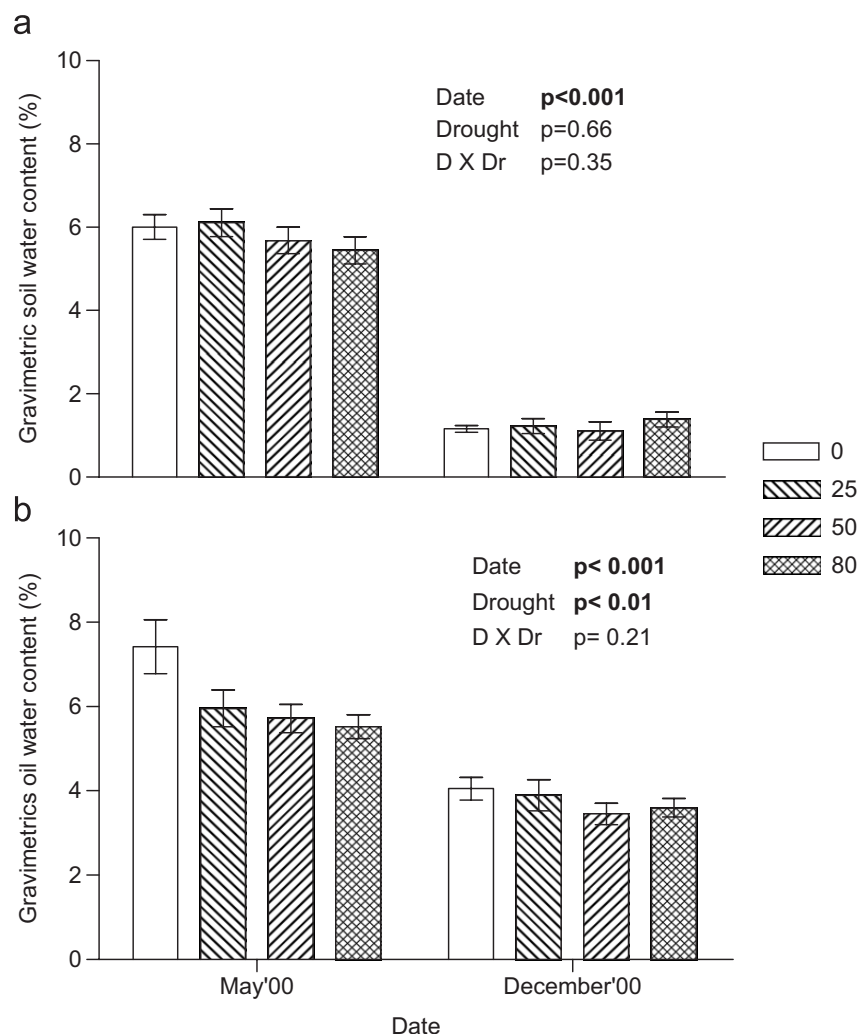


Fig. 5. Mean \pm SE gravimetric soil water content measured at two depths: (a) 0–10 cm and (b) 10–20 cm. Values were obtained from a field experiment with four interception levels of precipitation (Dr: 0%, 25%, 50%, 80%) in two dates (D: May 2000 and December 2000).

2001). The absence of differences in seedling response to drought treatments could be related to the lack of differences among treatments in water dynamics of the top soil layer and the species traits related to water stress resistance.

In the Patagonian steppe, where rainfall mainly occurs during the cold season, water availability decreases from mid-spring to summer (November–January) independently of climatic year condition. Our simulations based on the historic climatic record showed that there were no differences in water availability between dry and wet years in the top soil layer. However, the mid and bottom layers (10–30 cm) showed differences in soil water content between dry and wet years. For the emergence period of the experiment-growing season, our simulations showed a drastic reduction in water residence time in the top soil layer only at the extreme drought level (80%). Other major effects of drought treatments were registered on mid and bottom layers. In the survival period, water residence time was not clearly affected by drought treatments in the top soil layer, but again appeared differences at mid and bottom layers. In both periods, drought effects by experimental or natural conditions increased with depth.

The highest soil water contents simulated by DINAQUA in drought treatments from top soil and specially times were probably related to changes in the water movement across the soil profile because of changes in the hydraulic conductivity as naturally occur in Patagonian steppe ecosystem. High hydraulic conductivity in the Patagonian steppe soils is more probable to occur in winter (rainy season) and/or after large rainfall events under the control treatment. In summer (dry season) or under drought treatments, it is more probable to occur

low hydraulic conductivity. Low hydraulic conductivity is the most common situation from this ecosystem, even at field capacity (Paruelo and Sala, 1995), and therefore the vertical down water movement across soil profile is constrained. Only in exceptional cases, gravimetric forces are more important than tension forces and hence, the water descendent occurs. The water content in the top soil layer under control was lower than in drought treatments during the emergence period after two large rainfall events for Patagonia (> 10 mm/day; see Golluscio et al., 1998; Sala and Lauenroth, 1982, 1985), and during the survival period after three large rainfall events (> 11 mm/day).

We think that the absence of seedling responses to drought treatments were also related to specific abilities of *B. pictus* to cope with water stressful conditions, mainly during the emergence period where marked differences in the water residence among treatments appeared. Root length of 1-year-old *B. pictus* seedling is less than 10 cm (Aguiar, unpublished data), and is constrained to the scarce water availability on the top soil layer. *B. pictus* may have adaptive mechanisms that make possible emergence, survival, and growth under water stress conditions. For example, *B. pictus* presented the lowest water potential that impede germination [$\psi_{a(50)} = -1.14 \pm 0.27$ MPa at 10°C (mean \pm SD)], compared to other dominant grass species which had values above -0.70 MPa (Rotundo, 2005). The germination threshold for *B. pictus* is equivalent to 7.5 mm of soil water content (approximately half field capacity) for the top soil layer in Patagonia. With such low germination water potential, *B. pictus* could germinate at very low water availability. We suggest that *B. pictus* population dynamics is controlled by adult vital rates, especially tillering, seed production, and/or adult survival rather than on the emergence or survival of seedlings. We based our assertion on the facts that: (a) the good performance of seedlings in spite of extreme dry conditions, (b) the specific eco-physiological traits related to germination–emergence processes (Rotundo, 2005; Rotundo et al., 2006), and (c) the major drought effects on deep soil layers (10–30 cm). However, our results may not directly extrapolate to other species in arid ecosystems with finer-textured soils, because these soils have a different water dynamic (Fair et al., 1999; Lauenroth et al., 1994). For example, in the shortgrass steppe clay soils, a modeling exercise indicated that recruitment of *Bouteloua gracilis* is highly infrequent under the rainfall reduction scenarios (Peters, 2000).

We found that aerial biomass of seedlings was affected by microsite treatment, even in the absence of drought effect. Seedling biomass was almost double in the vegetated microsite compared to the bare soil microsite. Adult grasses can simultaneously facilitate and compete with new seedlings. Adult grasses can facilitate seedling recruitment by increasing the shaded area, the height of soil boundary layer, and soil water infiltration. Combined, these actions result in a decrease radiation, temperature, evaporation, and water stress (Breshears et al., 1998; Hamilton et al., 1999; Maestre et al., 2001; Novoplansky and Goldberg, 2001a). Our results provided evidence for net facilitation in the seedling recruitment period. Other authors reported an improvement in micro-environmental conditions and net facilitation effect for the recruitment of seedlings related with the presence of vegetation (Aguiar et al., 1992; Brittingham and Walker, 2000; Li and Wilson, 1998; Pugnaire and Luque, 2001). However, competition can replace facilitation interactions between seedling and adult grasses, when seedlings roots grow into deep soil layers (Aguiar et al., 1992).

Our approach to evaluate drought effects by modeling and field experiments represent a good opportunity to verify the DINAQUA model behavior developed and validated for our study site (Paruelo and Sala, 1995). We found that soil water content simulated in control and 25% of rainfall interception treatment for top and mid soil layers were correctly predicted by the model during winter and summer. However, there are differences when we considered the extreme rainfall interceptions (50–80%), with a clear sub-estimation by DINAQUA of the field soil water content for both seasons. In the DINAQUA model, the reduction of effective rainfall translates directly to the water content of the soil profile, without incorporating any stochastic process (Paruelo and Sala, 1995). However, in the field experimental setup, the reduction of effective rainfall did not translate directly to the soil water content, and also incorporate the experimental error as a random variation source. Yahdjian and Sala (2002) found that in spite of the large differences in the rainfall excluded from the plots by the rain-out shelters, there were no differences in soil water contents, among plots with 25%, 50%, and 80% interception. Also, the current version of DINAQUA model does not take account the spatial vegetation heterogeneity, that probably influences the soil water content, specially at top and mid soil layers where most of root grasses concentrate. Furthermore, the differences in the temporal resolution between soil water content simulated by DINAQUA (day) and field measures (season), and the difficult to take daily field measures of soil water content at different depths and microsities, preclude a more deep

analysis. From the experimental setup, edge effects for instance by oblique rainfalls due to wind, could also hindered differences in soil water content among drought treatments in spite of the effective rainfall interception. Probably, a combination of these issues could explain the differences observed between simulations and field measures of soil water content.

As climate change forecasts propose an increase in the frequency of dry climate for Patagonia, it is necessary to address possible effects on ecological processes. Recruitment is a critical phase in the life cycle of species in different ecosystems (Eriksson and Ehrlén, 1992; Grubb, 1977; Turnbull et al., 2000), and particularly from arid regions (Bertiller et al., 1996; Lauenroth et al., 1994; Milton, 1995; Soriano and Sala, 1986; Veenendaal et al., 1996). Our study contributes to the knowledge of plant responses at population level to climatic changes. In our field experiment, we reduced the total incoming rainfall without changing the rainfall seasonal dynamic. In contrast, in our modeling approach, we also used recorded dry, average and wet years that reflect the natural water seasonal dynamic in Patagonia. Hence, our study approach explored two potentially different modifications of rainfall regime. The use of historic data is considered to be a more realistic approach of climate change (Easterling et al., 2002), even though in our study soil water content in the top soil layer was the same for both experimental approaches. According to our simulations, differences in annual rainfall among years did not translate into differences in water content in the top soil layer where seeds and seedling roots concentrate. Similarly, in the field experiment, the emergence and survival of seedlings was not affected by severe drought levels. Both results supported our original hypothesis about the small impact of rainfall decrease in the grass regeneration.

Acknowledgments

We are particularly grateful to María L. Yahdjian for offering us the possibility to use the rain out shelters for our experiment, to José M. Paruelo for his advice and comments on DINAQUA v1.4, and to two anonymous reviewers who greatly improved the manuscript. We acknowledge National Institute of Agricultural Technology (INTA) for its permission to use facilities at Experimental Field Rio Mayo, Chubut, Argentina. Research was funded by the National Agency of Scientific and Technological Promotion (ANPCyT, PICT 01-06641 and PICT Redes 331 to M.R.A., PICT 6850 and PICT 774 to O.E.S.), Inter American Institute for Global Change Research (CRN 12) to O.E.S., National Council of Scientific and Technical Research (CONICET), and the University of Buenos Aires (UBA). This work complies with the ethics guidelines and current laws of Argentina. P.A.C. and P.F. were supported by doctoral fellowship from CONICET. M.R.A. and O.E.S. are members of CONICET.

References

- Aguiar, M.R., Sala, O.E., 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends in Ecology and Evolution* 14, 273–277.
- Aguiar, M.R., Soriano, A., Sala, O.E., 1992. Competition and facilitation in the recruitment of seedlings in Patagonian steppe. *Functional Ecology* 6, 66–70.
- Bertiller, M.B., Zaixso, P., Irisarri, M.P., Brevedan, E.R., 1996. The establishment of *Festuca pallese* in arid grasslands in Patagonia (Argentina): the effect of soil water stress. *Journal of Arid Environment* 32, 161–171.
- Bonvissuto, G., Moricz de Tecso, O., Astibia, O., Anchorena, J., 1983. Resultados preliminares sobre los hábitos dietarios de ovinos en un pastizal semidesértico de Patagonia. *Informe de Investigaciones Agropecuarias (INTA)* 36, 243–253.
- Breshears, D.D., Nyhan, J.W., Heil, C.E., Wilcox, B.P., 1998. Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy patches. *International Journal of Plant Science* 159, 1010–1017.
- Brittingham, S., Walker, L.R., 2000. Facilitation of *Yucca brevifolia* recruitment by Mojave desert shrubs. *Western North American Naturalist* 60, 374–383.
- Cipriotti, P.A., Aguiar, M.R., 2005. Effects of grazing on patch structure in a semi-arid two-phase vegetation mosaic. *Journal of Vegetation Science* 16, 57–66.
- Clark, J.S., Carpenter, S.R., Barber, M., Collins, S., Dobson, A., Foley, J., Lodge, D., Pascual, M., Pielke, R., Pizer Jr., W., Pringle, C., Reid, W., Rose, K., Sala, O., Schlesinger, W., Wall, D., Wear, D., 2001. Ecological forecasting: an emerging imperative. *Science* 293, 657–660.
- Cohen, J., 1988. *Statistical Power Analysis for the Behavioral Sciences*, second ed. Erlbaum, Hillsdale, NJ.

- Cornet, A.F., Delhoume, J.P., Montaña, C., 1988. Dynamics of striped vegetation pattern and water balance in the Chihuahuan desert. In: During, H.J., Werger, M.J.A., Willems, J.H. (Eds.), *Diversity and Pattern in Plant Communities*. SPB Academic, The Hague, The Netherlands, pp. 221–231.
- Defosse, G.E., Robberecht, R., Bertiller, M.B., 1997. Seedling dynamics of *Festuca* spp. in a grassland of Patagonia, Argentina, as affected by competition, microsites and grazing. *Journal of Range Management* 50, 73–79.
- Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R., Mearns, L.O., 2002. Climate extremes: observations, modeling, and impacts. *Science* 289, 2068–2074.
- Erdfelder, E., Faul, F., Buchner, A., 1996. GPOWER: a general power analysis program. *Behaviour Research Methods, Instruments and Computers* 28, 1–11.
- Eriksson, O., Ehrlén, J., 1992. Seed and microsite limitation of recruitment in plant populations. *Oecologia* 91, 360–364.
- Fair, J., Lauenroth, W.K., Coffin, D.P., 1999. Demography of *Bouteloua gracilis* in a mixed prairie: analysis of genets and individuals. *Journal of Ecology* 87, 233–243.
- Fowler, N.B., 1986. The role of competition in plants communities in arid and semiarid regions. *Annual Review of Ecology and Systematics* 17, 89–110.
- Gian-Reto, W., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389–395.
- Golluscio, R.A., León, R.J.C., Perelman, S.B., 1982. Caracterización fitosociológica de la estepa del oeste de Chubut, su relación con el gradiente ambiental. *Boletín de la Sociedad Argentina de Botánica* 21, 299–324.
- Golluscio, R.A., Sala, O.E., Lauenroth, W.K., 1998. Differential use of large summer rainfall events by shrubs and grasses: a manipulative experiment in the Patagonian steppe. *Oecologia* 115, 17–25.
- Golluscio, R.A., Paruelo, J.M., Deregius, V.A., 1999. Pastoreo con descansos en la Patagonia: desarrollo de un paquete tecnológico. *Revista Argentina de Producción Animal* 19, 89–102.
- Grubb, P.J., 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Reviews of the Cambridge Philosophical Society* 55, 107–145.
- Hamilton, J.G., Holzapfel, C., Mahall, B.E., 1999. Coexistence and interference between a native perennial grass and non-native annual grasses in California. *Oecologia* 121, 518–526.
- Jobbágy, E.G., Paruelo, J.M., León, R.J.C., 1995. Estimación del régimen de precipitación a partir de la distancia a la cordillera en el noroeste de la Patagonia. *Ecología Austral* 5, 47–53.
- Lauenroth, W.K., Sala, O.E., Coffin, D.P., Kirchner, T.B., 1994. The importance of soil water in the recruitment of *Bouteloua gracilis* in the shortgrass steppe. *Ecological Applications* 4, 741–749.
- Li, X., Wilson, S.D., 1998. Facilitation among woody plants establishing in an old field. *Ecology* 79, 2694–2705.
- Maestre, F.T., Bautista, S., Cortina, J., Bellot, J., 2001. Potential for using facilitation by grasses to establish shrubs on a semiarid degraded steppe. *Ecological Applications* 11, 1641–1655.
- Milton, S.J., 1995. Spatial and temporal patterns in the emergence and survival of seedlings in arid Karoo shrubland. *Journal of Applied Ecology* 32, 145–156.
- Novoplansky, A., Goldberg, D.E., 2001a. Interactions between neighbour environments and drought resistance. *Journal of Arid Environments* 47, 11–32.
- Novoplansky, A., Goldberg, D.E., 2001b. Effects of water pulsing on individual performance and competitive hierarchies in plants. *Journal of Vegetation Science* 12, 199–208.
- Paruelo, J.M., Sala, O.E., 1995. Water losses in the Patagonian steppe: a modeling approach. *Ecology* 76, 510–520.
- Paruelo, J.M., Aguiar, M.R., Golluscio, R.A., 1988. Soil water availability in the Patagonian arid steppe: gravel content effect. *Arid Soil Research and Rehabilitation* 2, 67–74.
- Paruelo, J.M., Beltrán, A.B., Sala, O.E., Jobbágy, E.G., Golluscio, R.A., 1998. The climate of Patagonia: general patterns and controls on biotic processes. *Ecología Austral* 8, 85–104.
- Peters, D.P.C., 2000. Climatic variation and simulated patterns in seedling establishment of two dominant grasses at a semi-arid–arid grassland ecotone. *Journal of Vegetation Science* 11, 493–504.
- Pugnaire, F.I., Luque, M.T., 2001. Changes in plant interactions along a gradient of environmental stress. *Oikos* 93, 42–49.
- Reeves, T.L., Smith, M.A., 1992. Time domain reflectometry for measuring soil water content in range surveys. *Journal of Range Management* 45, 412–414.
- Ritchie, J.T., 1972. Model for predicting evaporation from a row crop with incomplete cover. *Water Resources Research* 8, 1204–1213.
- Rotundo, J.L., 2005. Estudios poblacionales de *Poa ligularis*, una gramínea de zonas áridas amenazada por sobrepastoreo. Thesis to M.Sc. degree, Universidad de Buenos Aires.
- Rotundo, J.L., Aguiar, M.R., 2004. Vertical seed distribution in soil constrains regeneration processes of *Bromus pictus* in a Patagonian steppe. *Journal of Vegetation Science* 15, 514–522.
- Rotundo, J.L., Cipriotti, P.A., Gundel, P.E., 2006. Morphological and growth responses to water stress of two sub-populations of *Bromus pictus* from soils with contrasting water availability. *Revista Chilena de Historia Natural* 79, 65–74.
- Sala, O.E., Lauenroth, W.K., 1982. Small rainfall events: an ecological role in semiarid regions. *Oecologia* 53, 301–304.
- Sala, O.E., Lauenroth, W.K., 1985. Root profiles and the ecological effect of light rainshowers in arid and semiarid regions. *American Midland Naturalist* 114, 406–408.
- Sala, O.E., Lauenroth, W.K., Parton, W.J., 1992. Long-term soil water dynamics in the shortgrass steppe. *Ecology* 73, 1175–1181.
- Schwinning, S., Sala, O.E., 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia* 141, 211–220.

- Schwinning, S., Starr, B.I., Ehleringer, J.R., 2005. Summer and winter drought in a cold desert ecosystem (Colorado Plateau) Part I: effects on soil water and plant water uptake. *Journal of Arid Environments* 60, 547–566.
- Somlo, R., Pelliza, A., Willems, P., Nakamatsu, V., Manero, A., 1997. Atlas dietario de herbívoros patagónicos. Chubut, Prodesar GTZ-INTA, FAO, 109pp.
- Soriano, A., 1956. Los distritos florísticos de la provincia Patagónica. *Revista de Investigación Agropecuaria* 10, 349–367.
- Soriano, A., Sala, O.E., 1986. Emergence and survival of *Bromus setifolius* seedlings in different microsites of a Patagonian arid steppe. *Israel Journal of Botany* 35, 91–100.
- Soriano, A., Golluscio, R.A., Satorre, E., 1987. Spatial heterogeneity of the root system of grasses in the Patagonian arid steppe. *Bulletin of the Torrey Botanical Club* 114, 103–108.
- Turnbull, L.A., Crawley, M.J., Rees, M., 2000. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* 88, 225–238.
- Veenendaal, E.M., Ernst, W.H.O., Modise, G.S., 1996. Effect of seasonal rainfall pattern on seedling emergence and establishment of grasses in a savanna in south-eastern Botswana. *Journal of Arid Environment* 32, 305–317.
- Walter, H., Box, E.O., 1983. Climate of Patagonia. In: West, N.E. (Ed.), *Deserts and Semideserts of Patagonia*. Temperate Deserts and Semideserts. Elsevier, Amsterdam, pp. 440–453.
- Yahdjian, L., Sala, O.E., 2002. A rainout shelter design for intercepting different amounts of rainfall. *Oecologia* 133, 95–101.
- Zschokke, S., Lüdin, E., 2001. Measurement accuracy: how much is necessary? *Bulletin of the Ecological Society of America* 82, 237–243.