R.A. Golluscio · O.E. Sala · W.K. Lauenroth

Differential use of large summer rainfall events by shrubs and grasses: a manipulative experiment in the Patagonian steppe

Abstract In the Patagonian steppe, years with above-average precipitation (wet years) are characterized by the occurrence of large rainfall events. The objective of this paper was to analyze the ability of shrubs and grasses to use these large events. Shrubs absorb water from the lower layers, grasses from the upper layers, intercepting water that would otherwise reach the layers exploited by shrubs. We hypothesized that both life-forms could use the large rainfalls and that the response of shrubs could be more affected by the presence of grasses than vice versa. We performed a field experiment using a factorial combination of water addition and life-form removal, and repeated it during the warm season of three successive years. The response variables were leaf growth, and soil and plant water potential. Grasses always responded to experimental large rainfall events, and their response was greater in dry than in wet years. Shrubs only used large rainfalls in the driest year, when the soil water potential in the deep layers was low. The presence or absence of one life-form did not modify the response of the other. The magnitude of the increase in soil water potential was much higher in dry than in humid years, suggesting an explanation for the differences among years in the magnitude of the response of shrubs and grasses. We propose that the generally reported poor response of deep-rooted shrubs to summer rainfalls could be because (1) the water is insufficient to reach deep soil layers, (2) the plants are in a dormant phenological status, and/or (3) deep soil layers have a high water potential. The two last situations may result in high deep-drainage losses, one of the most likely explanations for the elsewhere-reported low response of aboveground net primary production to precipitation during wet years.
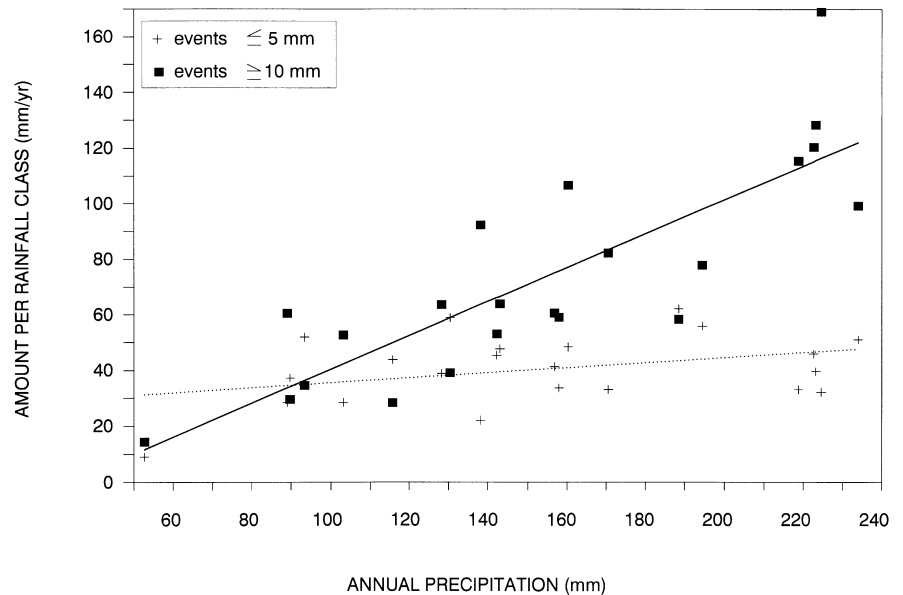
Introduction

Precipitation is the main limiting factor of primary production in arid and semiarid zones (Noy Meir 1973). Aboveground net primary production (ANPP) is linearly related to annual precipitation (PPT) from deserts to steppes and grasslands (Lauenroth 1979; Sala et al. 1988). However, the slope of the ANPP-PPT relationship changes if we consider only one site through time (temporal model), instead of several sites across a region (regional model) (Lauenroth and Sala 1992). The temporal model compares annual production and precipitation data for a given site, whereas the spatial model compares average production and average precipitation for different sites. In the shortgrass steppe of the United States of America (mean PPT = 321 mm), the temporal model has a lower slope than the regional model (Lauenroth and Sala 1992). In the Patagonian steppe (mean PPT = 137 mm), ANPP increases linearly with PPT until 150 mm, where it reaches a plateau (Fernández et al. 1991).

A hypothesis which accounts for the different slopes between the regional and temporal models is that ecosystems have limited ability to use the extraordinary water inputs which are characteristic of wet years. The response of ANPP to an increase in water availability can be accounted for by the response of several components: species composition, plant density, and production of individual plants. While these three components change from arid to subhumid sites, only the third variable can rapidly change from a dry to a wet year in one site. This hypothesis suggests that in arid and semiarid zones, rain use efficiency (RUE = ANPP/PPT; Le Houérou 1984) may be lower in wet years than

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Fig. 1 Amount of water received in events of less than or equal to 5 mm (+, ...) or of more than or equal to 10 mm (■, ___) as a function of annual precipitation for 22 years recorded in the Patagonian steppe at Río Mayo (45°41′S, 70°16′W)

in dry years, because of structural constraints which hamper the ability of plants to quickly respond to pulses of high water availability (Lauenroth and Sala 1992).

In the Patagonian steppe, the occurrence of a few large rainfall events is sufficient to generate a wet year. Annual rainfall is significantly correlated with the amount of water received in events larger than 10 mm ($r = 0.83$, $P < 0.01$, $n = 22$), but not with the amount of water received in events smaller than 5 mm, which is almost constant among years $r = 0.37$, $P > 0.05$, $n = 22$) (Fig. 1). The same pattern was found in the shortgrass steppe of Colorado (USA), suggesting that this could be a general phenomenon in arid and semiarid regions (Sala et al. 1992).

The Patagonian steppe is a cold semiarid system, with 70% of annual rainfall occurring during fall and winter, which results in a recharge of the soil profile during the cold season almost every year (Sala et al. 1989; Golluscio and Sala 1993). Shrubs and grasses, the dominant life-forms in the Patagonian steppe, have contrasting rooting patterns, resource utilization patterns, and phenologies. Shrubs concentrate most of their roots below 30 cm in the soil (Fernández and Paruelo 1988), use water from the lower layers (Sala et al. 1989), and remain dormant from late summer to early spring (Soriano 1983). Grasses concentrate most of their roots above 30 cm (Soriano et al. 1987), use water from the upper layers (Sala et al. 1989), and their tillers always have leaves capable of expanding when soil water availability and air temperature are favorable (Soriano 1983).

Our objective for this paper was to analyze the ability of shrubs and grasses to use large rainfall events. This study attempts to contribute to understanding the phenomenon of reduced RUE during wet years found by Lauenroth and Sala (1992). Based on the rooting and water use patterns of shrubs and grasses in the Patago-

nian steppe, we hypothesized that (1) both shrubs and grasses use the water provided by large events, which wet the whole soil profile, (2) the response of grasses does not depend on the presence of shrubs, but (3) the response of shrubs is larger in the absence of grasses.

To test these hypotheses, we simulated rainfall events of 30 mm on plots with both grasses and shrubs, and plots with only one of these life-forms. The experiment was repeated in three different years.

Materials and methods

We performed a two-way factorial experiment with two rainfall regimes (control vs. irrigated with 30 mm rainfall) × three life-form habitats (intact, shrub removal, and grass removal). We repeated the experiment in three different years. The response variables were leaf growth, leaf water potential, and soil water potential at 5, 15, 30, and 60 cm of depth. On the basis of available information and experience, we considered *Poa ligularis* and *Mulinum spinosum* as representatives of the grass and shrub life-forms, respectively (Sala et al. 1989).

The work was carried out at Río Mayo, southwest Chubut, Argentina (45°41′S, 70°16′W). Vegetation corresponds to the *Stipa speciosa* Trin. et Rupr., *S. humilis* Cav., *Adesmia campestris* (Rendle) Skottsb., *Berberis heterophylla* Jubb., and *P. lanuginosa* Poir. community, which predominates in the Patagonian Occidental District (Soriano 1956; Golluscio et al. 1982). This community has a mean aerial cover of 48% and two strata: an upper shrub layer (15% cover) and a lower grass-dominated herbaceous layer (33% cover) (Golluscio et al. 1982). The dominant species are the shrubs *M. spinosum* (Cav.) Pers., *A. campestris* and *Senecio filaginoides* DC., and the grasses *S. speciosa, S. humilis* and *P. ligularis* Nees ap. Steud. Mean annual rainfall is 137 mm ($n = 37$), and mean annual temperature is 8.4°C, with mean monthly temperature ranging between 2 and 14°C, in July and January, respectively (Fernández et al. 1991). Soils have an upper sandy layer 45–60 cm deep, and a lower calcareous stony layer (Paruelo et al. 1988).

The experiment was repeated in three consecutive years which were very similar in terms of overall precipitation: the amounts of rainfall during the 12 months prior to the simulation were 158, 171

and 158 mm in years I, II, and III respectively. However, initial conditions were different: the soil water potential in the profile was lowest in year I (dry), and was highest in year III (wet). The second year had dry initial conditions but a 18-mm natural rainfall event occurring 9 days after rainfall simulation turned it into the wettest year (year II, intermediate). Different initial conditions were reflected in the green grass biomass at the beginning of the experiment: in the wet year III, it was 42% higher than in the initially dry years I and II: 41.8 ± 8.2 versus 29.5 ± 4.7 and 29.4 ± 2.8 g m^{-2}, respectively (means $\pm$ SE, four 1-m^2 plots harvested each year). Experimental rainfalls were applied at the beginning of summer.

We randomly allocated four replications per treatment to 24 20×20 m plots, separated by 10-m-wide alleys and located within an exclosure for large animals. We manually removed grasses and shrubs every year, and we simulated rainfalls with water sprinklers. We compared only control and irrigated intact plots the first year. We performed analysis of variance on each response variable within each date, and considered differences as significant when $P < 0.05$.

Leaf elongation of *P. ligularis* was measured on expanding leaves following the technique described by Soriano et al. (1976): we first placed a 3-mm-diameter wire rod vertically near the tiller containing the leaf to be measured. Second, we attached the tiller and the leaf to the rod with two plastic rings. Third, we marked the location of the leaf tip on the rod with another plastic ring. We recorded periodically the difference between current and previous position of the leaf tip on the rod. The selected leaf was replaced by an other expanding leaf from the same tiller when the ligule was visible. Five subsamples, each from a different tussock, were measured in each plot with grasses.

We measured the length of the growth of the year in branches of five individuals of the shrub *M. spinosum* of modal height in each plot. Growth of the year is easy to identify in *M. spinosum* because their branches change color from green to gray during winter. At the end of each experiment, we harvested the growth of the year on 10×25 cm quadrats located at the top of five shrubs selected from each plot with shrubs.

We evaluated leaf water potential using the pressure chamber technique (Scholander et al. 1965), taking standard precautions to minimize errors (Turner 1988). We enclosed grass leaves in a plastic tube, 3 mm in diameter, prior to severing them from the plant. We transported shrub twigs from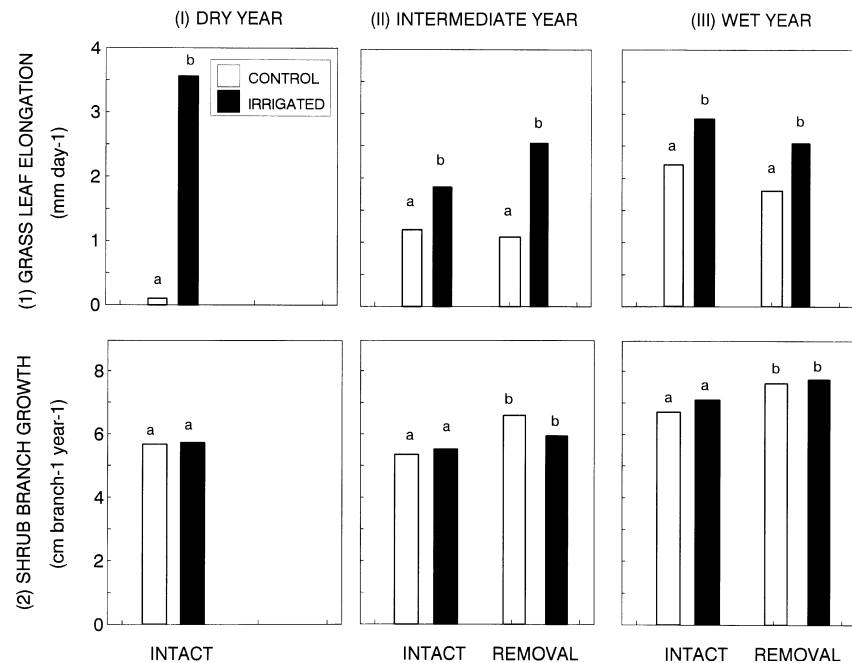 the plot to the pressure chamber, a few meters away, in a plastic container. We did not enclose the sample while it was in the chamber because condensation is unlikely to occur under dry Patagonian conditions. We never recut the portions of leaves and twigs external to the seal of the chamber. We accurately estimated the endpoint with a dissecting microscope. We utilized one new branch of *M. spinosum* and one expanding leaf of *P. ligularis* per replication. We made measurements at midday in the three years, and before dawn only in the first two years (dry and intermediate).

We measured soil water potential with PC55 Wescor thermocouple hygrometers (Spanner 1951) and a Wescor HR 33 dew point microvoltmeter. Hygrometers proved to be a reliable way of assessing soil water potential patterns in the Patagonian steppe (Soriano and Sala 1983, 1986; Sala et al. 1989). We buried one set of hygrometers at 5, 15, 30, and 60 cm depth in the center of each plot, which yielded a total of 96 hygrometers. We made the measurements on the same dates that we measured leaf water potential. We did not record soil temperature because it does not affect the estimate of soil water potential when using the dew point technique (Wescor 1979). We took precautions against temperature gradients which could cause errors in soil water potential measurements (Brown and Oosterhuis 1992). First, the geometry of the Wescor hygrometers minimizes the effect of temperature gradients between the soil and the thermocouple (Wiebe and Brown 1979; Brown and Bartos 1980). Second, we did not make comparisons among soil depths, and we located hygrometers horizontally because the main spatial gradient of soil temperature is vertical (Wiebe et al. 1977; Brown and Oosterhuis 1992). Third, given that the main temporal gradients of soil temperature are the daily and seasonal dynamics, we always measured soil water potential at the same time of the day (mid-morning), and only made comparisons among treatments within each date.

Results

Leaf elongation of grasses was always higher in irrigated than in control plants, and this response was unaffected by the presence of shrubs. The magnitude of the response was larger in the driest than in the wettest year (Fig. 2). Shrub growth did not show any response to

Fig. 2 Leaf elongation of the grass *Poa ligularis* during the first week after simulated rain and annual branch growth of the shrub *Mulinum spinosum* in response to 30-mm simulated rains in plots which remained intact and plots where the other life-form had been removed for three years. *White bars* are control treatments and *black bars* are irrigated treatments. *Different letters* indicate significant differences among treatments within each year ($P \leq 0.05$)
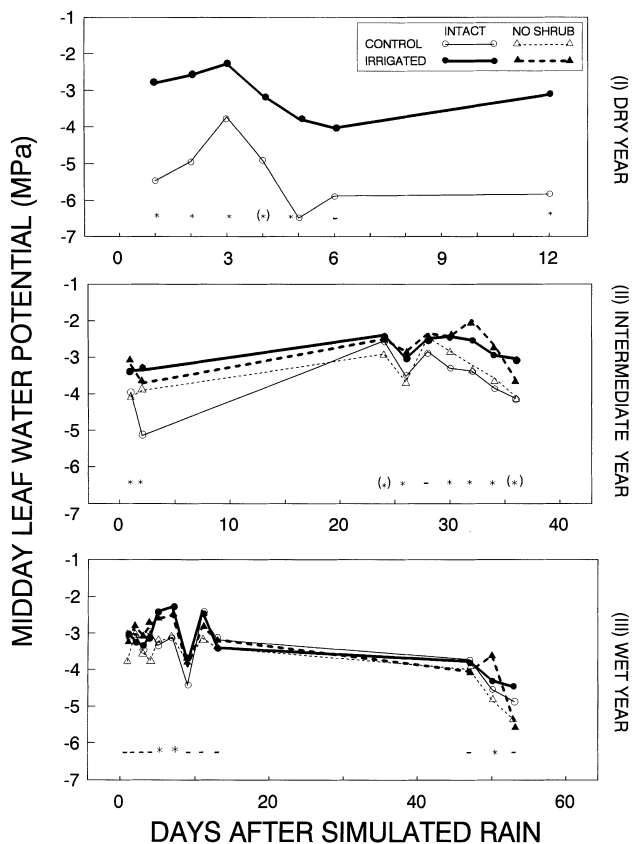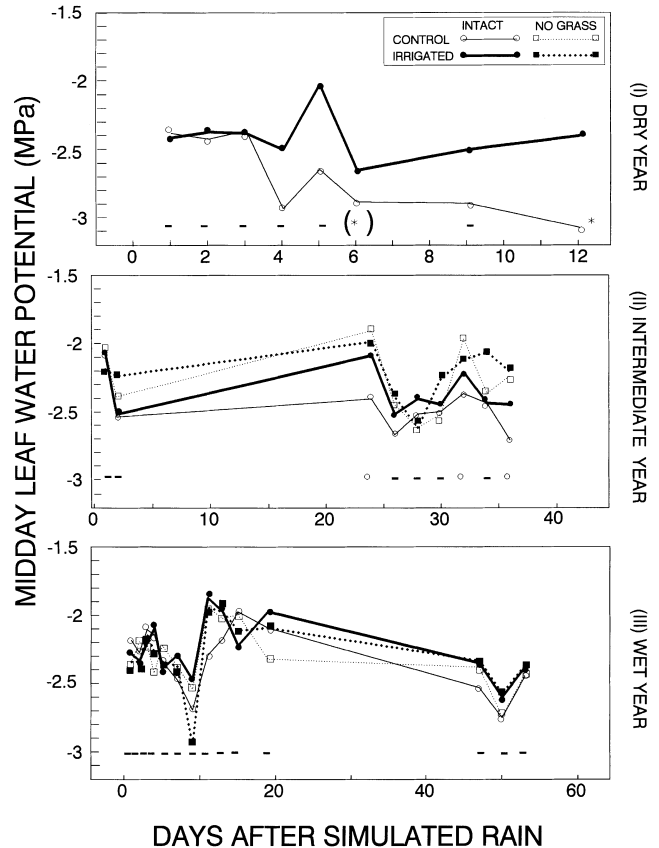
Fig. 3 Midday leaf water potential responses of the grass *P. ligularis* to 30-mm simulated rains for three years. *Thick lines* indicate irrigated treatments and *thin lines* indicate control treatments; ___ intact treatments, - - - - shrub removal treatments; * significant rain effect. Statistical comparisons within dates: $P \leq 0.05$, except when *symbol is between parentheses* ($P \leq 0.10$)

Fig. 4 Midday leaf water potential responses of the shrub *M. spinosum* to 30-mm simulated rains for three years. *Thick lines* indicate irrigated treatments and *thin lines* indicate control treatments; ___ intact treatments, ... grass removal treatments; * significant rain effect, ○ significant removal effect. Statistical comparisons within dates: $P \leq 0.05$, except when *symbol is between parentheses* ($P \leq 0.10$)

water addition, but showed an increment in response to grass removal (Fig. 2).

Leaf water potential of grasses rapidly increased in response to the large experimental rainfall events, and reached similar values in wet or dry years. As with leaf elongation, the response was unaffected by the presence of shrubs, and increased with the initial water stress (Fig. 3). The leaf water potential of shrubs increased as a response to simulated rainfall only in the driest year, and it increased as a result of grass removal only in the intermediate year (Fig. 4). Pre-dawn leaf water potential followed the midday patterns. The response of grasses was greater than that of shrubs, the response of both life-forms was greater in the dry than in the intermediate year, and the shrubs did not respond to rainfall simulation but to grass removal (Fig. 5).

Soil water potential increased immediately after rainfall simulation at 5 cm (Fig. 6a), and with a delay in deeper layers. Time delays were longer at 60 than at 30 cm in all three years. These time delays are well represented by the time after rainfall simulation at which significant rainfall effects begin to be observed in Fig. 6.

This lag was longer in the wet year (III) than in the initially dry years (I and II). The increase in soil water potential at 15 cm was immediate in the dry and the intermediate year, but it also showed a time delay in the wet year (Fig. 6b). The rain effect on soil water potential was observed both in control and removal treatments (Fig. 6a–d).

Grass removal resulted in an increase in soil water potential at 15 and 30 cm depth, both in irrigated and non-irrigated plots (Fig. 6b, c). At 5 cm, instead, grass removal effects were only observed on irrigated plots (see interaction effects on Fig. 6a). All these removal effects were observed at least 1 month after the rainfall simulation (Fig. 6a–c). No removal effects were recorded at 60 cm, where root density is very low (Soriano et al. 1987; Fernández and Paruelo 1988).

Discussion

Our results support the hypothesis about the response of grasses to large rainfall events, but only partially

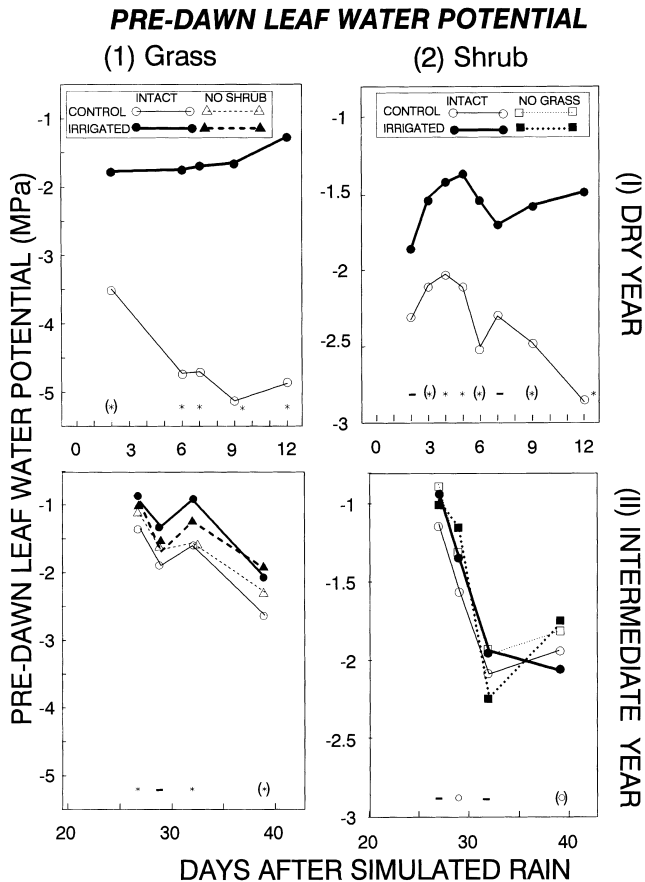## PRE-DAWN LEAF WATER POTENTIAL

Fig. 5 Pre-dawn leaf water potential responses of the grass *P. ligularis* and the shrub *M. spinosum* to 30-mm simulated rains for two of the three years. *Thick lines* indicate irrigated treatments and *thin lines* indicate control treatments; ___ intact treatments, ... grass removal treatments, - - - - shrub removal treatments; * significant rain effect, ○ significant removal effect. Statistical comparisons within dates: $P \leq 0.05$, except when *symbol is between parentheses* ($P \leq 0.10$)

support the hypothesis concerning the response of shrubs. As predicted, grasses used large rainfall events both in the presence or absence of shrubs. Shrubs only responded to them when the soil before the simulated rainfall was relatively dry at 30–60 cm, which is where their roots are concentrated (Fernández and Paruelo 1988). In contrast, shrubs did not respond in years when deep soil layers were already wet before watering. The absence of grasses did not improve the use by shrubs of the extra water supply.

The response of grasses and shrubs to large rainfall events increased with water stress, as found by Hodgkingson (1992) (Fig. 7). The smaller magnitude of the response in leaf growth and leaf water potential in wet years than in dry years may be the result of plants being closer to their maximum values (Ansley et al. 1992). The values of the irrigated plants, similar in wet or dry years, support this hypothesis and are in accordance with data shown by Sala et al. (1982) for the shortgrass steppe of North America.

Responses of shrubs to large rainfall events were never measurable in terms of leaf growth, and only in

the driest year in terms of leaf water potential. In this year, the increase in soil water potential at 30 and 60 cm as a result of the experimental rain was higher than in the other two years. The large events caused a very small increase in deep soil water potential during wet and intermediate years, because it was close to its maximum value (Sala et al. 1989).

The large events likely caused deep percolation losses in wet years. The depth of penetration of a rainfall event is inversely related to soil water content (Hanks and Ashcroft 1980). If the rainfall simulated in the intermediate year immediately reached 60 cm depth, it must have percolated beyond this depth in the wet year.

The depression of midday leaf water potential with respect to the pre-dawn leaf water potential (pre-dawn minus midday leaf water potential) was higher for grasses than for shrubs in the two years compared (Fig. 8). This could be the result of the different distribution of shrub and grass roots in the soil profile (Soriano et al. 1987; Fernández and Paruelo 1988). Grasses have their roots concentrated in the upper soil layers and shrubs in the lower layers, which in the Patagonian steppe are the wettest throughout most of the year (Sala et al. 1989; Paruelo and Sala 1995). The differential root location may account for the higher leaf water potential of shrubs and the lower amplitude between pre-dawn and midday. The interaction between the location of roots and the distribution of soil water in the profile can be quantified by the effective soil water potential which weights the soil water potential by the root biomass of each layer (Sala et al. 1981). The effective soil water potential for shrubs was, on average, higher than that of grasses (−2.4 MPa for shrubs vs. −6.2 MPa for grasses in the dry year, and −1.0 for shrubs vs. −3.7 MPa for grasses in the intermediate year).

Large rainfall events caused an increase in the soil water potential of the entire profile, but with a time delay which increased with soil depth because water enters the soil from the top. Lags should be shorter in wet than in dry soils because hydraulic conductivity increases with soil water potential. In fact, the lag was longer in the dry than in the intermediate year at every depth (Fig. 9). However, the lag was longer in the wet year than in the dry and intermediate years, suggesting that an additional process may cause the time delay in the wet soil. When soil is wet, water addition causes a smaller increase in soil water potential than in soil water content, because of the shape of water retention curves. Only after evaporation and/or plant absorption have significantly reduced soil water content does the effect of water addition become detectable in soil water potential. We suggest that in wet soils, the time delay increases with soil depth because both evaporation and plant absorption decrease with soil depth (Alizai and Hulbert 1969; Soriano et al. 1987; Fernández and Paruelo 1988).

Recent publications have reported the absence of response to summer rainfall of deep-rooted shrubs. Several of these papers found that the isotopic composition of xylem water of shrubs was closer to that of
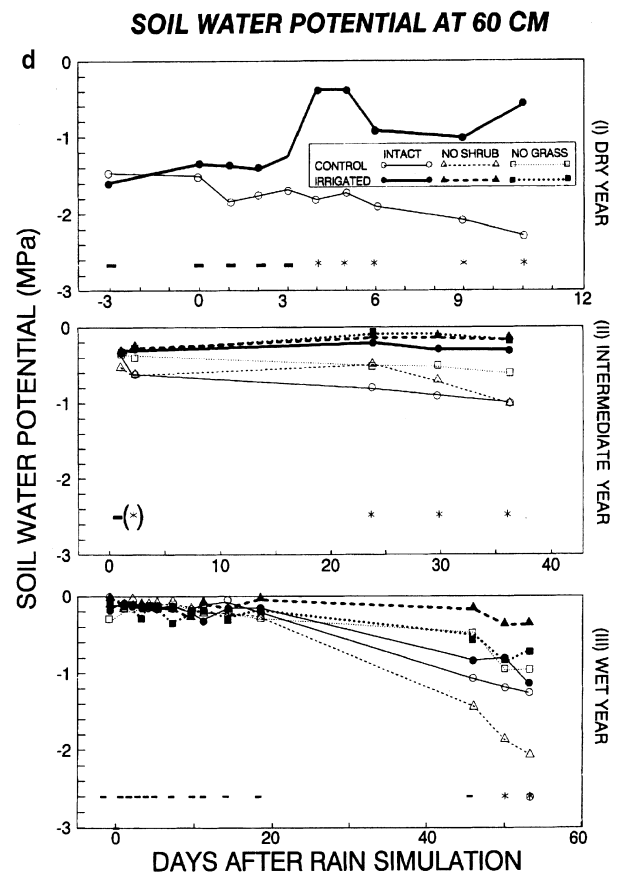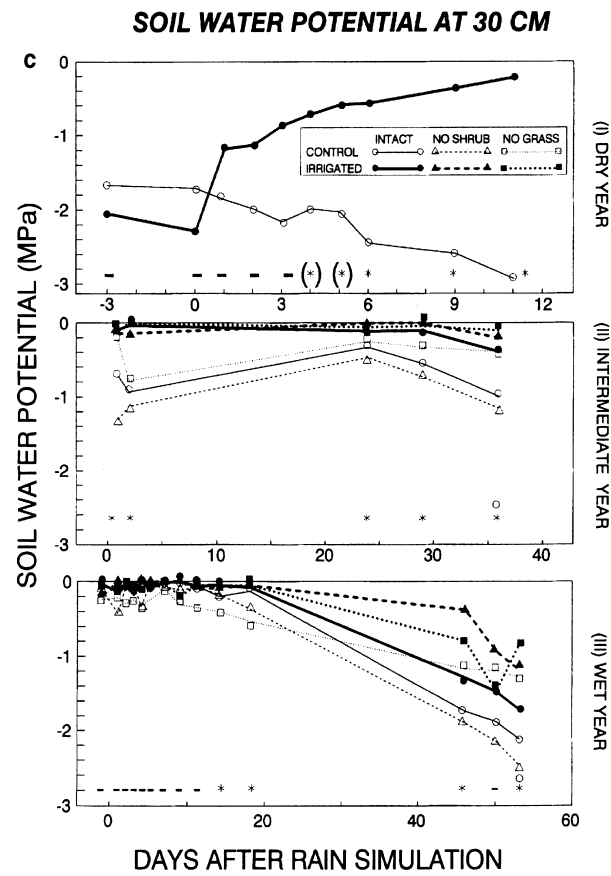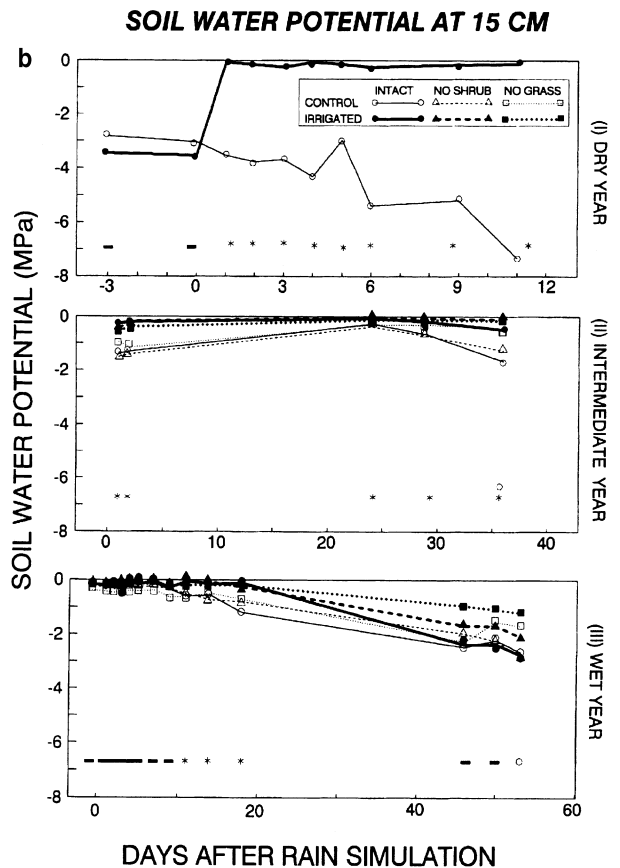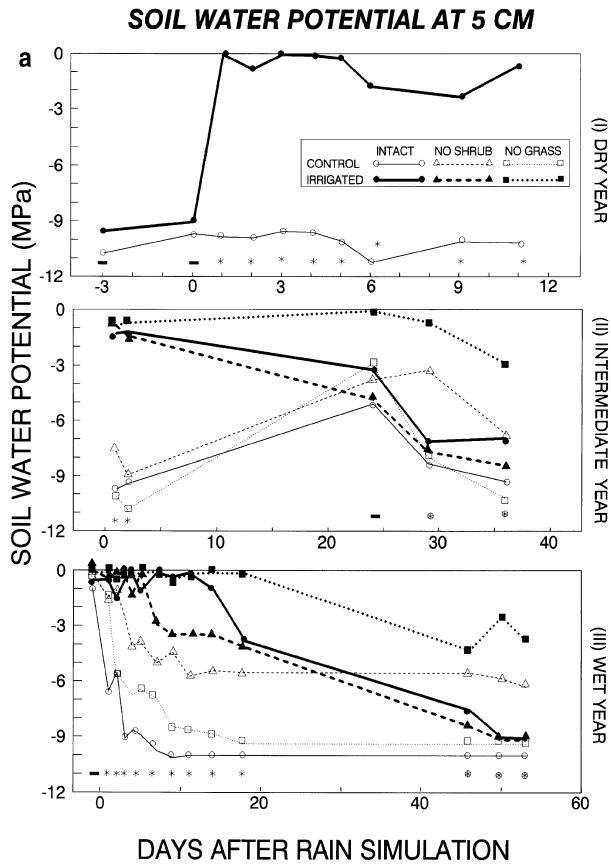
SOIL WATER POTENTIAL AT 5 CM

a

(I) DRY YEAR

(II) INTERMEDIATE YEAR

(III) WET YEAR

SOIL WATER POTENTIAL (MPa)

DAYS AFTER RAIN SIMULATION

SOIL WATER POTENTIAL AT 15 CM

b

(I) DRY YEAR

(II) INTERMEDIATE YEAR

(III) WET YEAR

SOIL WATER POTENTIAL (MPa)

DAYS AFTER RAIN SIMULATION

SOIL WATER POTENTIAL AT 30 CM

c

(I) DRY YEAR

(II) INTERMEDIATE YEAR

(III) WET YEAR

SOIL WATER POTENTIAL (MPa)

DAYS AFTER RAIN SIMULATION

SOIL WATER POTENTIAL AT 60 CM

d

(I) DRY YEAR

(II) INTERMEDIATE YEAR

(III) WET YEAR

SOIL WATER POTENTIAL (MPa)

DAYS AFTER RAIN SIMULATION

Legend: CONTROL — INTACT, NO SHRUB, NO GRASS; IRRIGATED — INTACT, NO SHRUB, NO GRASS

LEAF WATER POTENTIAL DEPRESSION

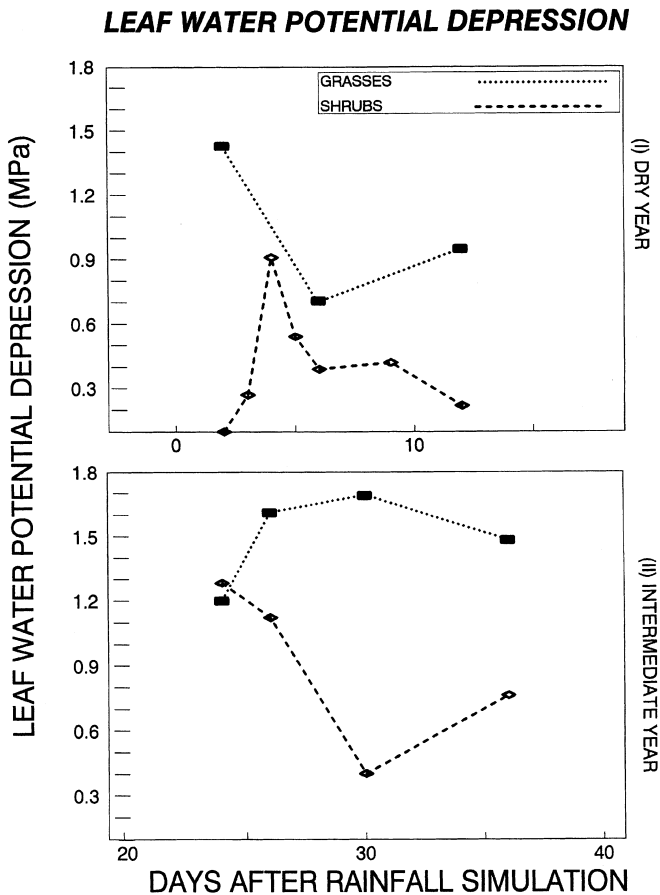**Fig. 9** Time delay in the response of soil water potential to rainfall simulation at each depth in dry, intermediate, and wet years. The delay is measured as the number of days between the rainfall simulation and the time of occurrence of a statistically significant difference in soil water potential between irrigated and control treatments

cannot use water supplied by extremely large rainfall events, which penetrate beyond their shallow rooting depth. Finally, shrubs can respond to large rainfalls which occur when the soil they explore (30–60 cm) is dry (i.e., after December; Sala et al. 1989), but while shrubs are still phenologically active (i.e., before April; Soriano 1983). This could explain a similar lack of response to large rainfalls found in a Niger arid steppe (Wylie et al. 1992), and in the shortgrass steppe of the USA (Lauenroth and Sala 1992), where rainfall events of more than 30 mm had only a minor influence on forage production.

Several global climate models predict that mean total rainfall will increase in the Patagonian steppe between 5 and 12%, depending on the model (GISS, Hansen et al. 1983; GFLD, Manabe and Wetherald 1987; UKMO, Wilson and Mitchell 1987). On a long time scale, structural changes in the plant communities could occur which would improve the response of the ecosystem to these large rainfall events. However, our results suggest that, for the current community structure, a larger increase in ANPP could be expected if this rainfall increase is caused by an increase in the number than by an increase in the size of the rainfall events.

the soil water potential of the layers the plants explore before they become dormant. As the soil water potential increases, the probability of a portion of a rainfall event being lost through deep drainage increases. As the size of the event increases, the probability of plant response would increase if the rain falls on dry soil, but would remain constant if it falls on wet soil.

The results of our rainfall simulation experiments suggest an explanation for the reported decrease in RUE in wet years, characterized by the occurrence of large rainfall events. This decrease in RUE in wet years would be responsible for the slope of the temporal ANPP versus PPT model being lower than that of the ANPP versus PPT spatial model (Lauenroth and Sala 1992). First, during fall and winter, when the activity of plants is minimal, all the water exceeding the water holding capacity (100 mm until 120 cm depth) is lost via deep drainage independent of the size of the event (Paruelo et al. 1988). Paruelo and Sala (1995) showed that the response of transpiration to increasing precipitation flattens out at lower values for fall-winter precipitation than for spring-summer precipitation. Second, grasses

References

Ansley RJ, Jacoby PW, Meadors CH, Lawrence BK (1992) Soil and leaf water relations of differentially moisture-stressed honey mesquite (*Prosopis glandulosa* Torr). J Arid Environ 22: 147–159

Alizai HU, Hulbert LC (1969) Effects of soil texture on evaporative loss and available water in semiarid climates. Soil Sci 110: 328–332

Brown RW, Bartos DL (1980) A calibration model for Peltier thermocouple psychrometers. INT 1600-12 (9/66). Intermountain Forest and Rangeland Experimental Station, Ogden, Utah

Brown RW, Oosterhuis DM (1992) Measuring plant and soil water potentials with thermocouple psychrometers: some concerns. Agron J 84: 78–86

Donovan LA, Ehleringer JR (1994) Water stress and use of summer precipitation in a Great Basin shrub community. Funct Ecol 8: 289–297

Ehleringer JR, Dawson TE (1992) Water uptake by plants: perspectives from stable isotope composition. Plant Cell Environ 15: 1073–1082

Ehleringer JR, Phillips SL, Schuster WSF, Sandquist DR (1991) Differential utilization of summer rains by desert plants. Oecologia 88: 430–434

Fernández RJ, Paruelo JM (1988) Root systems of two Patagonian shrubs: a quantitative description using a geometrical method. J Range Manage 41: 220–223

Fernández RJ, Sala OE, Golluscio RA (1991) Woody and herbaceous aboveground production of a Patagonian steppe. J Range Manage 44: 434–437

Flanagan LB, Ehleringer JR (1991) Stable isotope composition of stem and leaf water: applications to the study of plant water-use. Funct Ecol 5: 270–277

Flanagan LB, Ehleringer JR, Marshall JD (1992) Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland. Plant Cell Environ 15: 831–836

Golluscio RA, Sala OE (1993) Plant functional types and ecological strategies in Patagonian forbs. J Veg Sci 4: 839–846

Golluscio RA, León RJC, Perelman SB (1982) Caracterización fitosociológica de la estepa del Oeste de Chubut; su relación con el gradiente ambiental. Bol Soc Argentina Bot 21: 299–324

Hanks RJ, Ashcroft GL (1980) Water quantities. In Hanks RJ, Ashcroft GL (eds.). Applied soil physics. Soil water and temperature applications. Springer, Berlin Heidelberg New York, pp 1–19

Hansen J, Russell G, Rind D, Stone P, Lacis A, Lebedeff S, Ruedy R, Travis L (1983) Efficient three-dimensional global models for climate studies: models I and II. Mon Weather Rev 3: 609–612

Heitschmidt RK, Ansley RJ, Dowhower SL, Jacoby PW, Price DL (1988) Some observations from the excavation of mesquite root systems. J Range Manage 41: 227–231

Hodgkinson KC (1992) Water relations and growth of shrubs before and after fire in a semi-arid woodland. Oecologia 90: 467–473

Lauenroth WK (1979) Grassland primary production: North American grasslands in perspective. In: French NR (ed) Perspectives in grassland ecology. Ecological studies, vol 32. Springer, Berlin Heidelberg New York, pp 3–24

Lauenroth WK, Sala OE (1992) Long-term forage production of North American shortgrass steppe. Ecol Appl 2: 397–403

Le Houérou HN (1984) Rain use efficiency: a unifying concept in arid-land ecology. J Arid Environ 7: 213–247

Lin G, Phillips SL, Ehleringer JR (1996) Monsoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau. Oecologia 106: 8–17

Manabe S, Wetherald RT (1987) Large-scale changes in soil wetness induced by an increase in carbon dioxide. J Atmos Sci 44: 1211–1235

Montaña C, Cavagnaro B, Briones O (1995) Soil water use by coexisting shrubs and grasses in the Southern Chihuahuan Desert, México. J Arid Environ 31: 1–13

Noy Meir I (1973) Desert ecosystems: environment and producers. Ann Rev Ecol Syst 4: 23–51

Paruelo JM, Sala OE (1995) Water losses in the Patagonian steppe: a modeling approach. Ecology 76: 510–520

Paruelo JM, Aguiar MR, Golluscio RA (1988) Soil water availability in the Patagonian arid steppe: gravel content effect. Arid Soil Res Rehab 2: 67–74

Phillips SL, Ehleringer JR (1995) Limited uptake of summer precipitation by bigtooth maple (Acer grandidentatum Nutt) and Gambel's oak (Quercus gambelii Nutt). Trees 9: 214–219

Sala OE, Lauenroth WK, Parton WJ, Trlica MJ (1981) Water status of soil and vegetation in a shortgrass steppe. Oecologia 48: 327–331

Sala OE, Lauenroth WK, Parton WJ (1982) Plant recovery following prolonged drought in a shortgrass steppe. Agric Meteorol 27: 49–58

Sala OE, Parton WJ, Joyce LA, Lauenroth WK (1988) Primary production of the Central Grassland region of the United States. Ecology 69: 40–45

Sala OE, Golluscio RA, Lauenroth WK, Soriano A (1989) Resource partitioning between shrubs and grasses in the Patagonian steppe. Oecologia 81: 501–505

Sala OE, Lauenroth WK, Parton WJ (1992) Long-term soil water dynamics in the shortgrass steppe. Ecology 73: 1175–1181

Scholander PF, Hammel HT, Bradstreet ED, Hemmingeng EA (1965) Sap pressure in vascular plants. Science 148: 339–346

Soriano A (1956) Los distritos florísticos de la Provincia Patagónica. Rev Invest Agríc 10: 323–347

Soriano A (1983) Deserts and semideserts of Patagonia. In: West NE (ed) Temperate deserts and semideserts. Elsevier, Amsterdam, pp 423–460

Soriano A, Sala OE (1983) Ecological strategies in a Patagonian arid steppe. Vegetatio 56: 9–15

Soriano A, Sala OE (1986) Emergence and survival of Bromus setifolius seedlings in different microsites of a Patagonian arid steppe. Isr J Bot 35: 91–100

Soriano A, Alippe HA, Sala OE, Schlichter TM, Movia CP, León RJC, Trabucco R, Deregibus VA (1976) Ecología del pastizal de coirón amargo (Stipa spp.) del Sudoeste de Chubut. Ana Acad Nac Agron Vet 30: 1–13

Soriano A, Golluscio RA, Satorre EH (1987) Spatial heterogeneity of the root systems of grasses in the Patagonian arid steppe. Bull Torrey Bot Club 114: 103–108

Spanner SRJ (1951) The Peltier effect and its use in the measurement of suction pressure. J Exp Bot 2: 145–168

Toft CA (1995) A 10-year demographic study of rabbitbrush (Chrysothamnus nauseosus): growth, survival and water limitation. Oecologia 101: 1–12

Turner NC (1988) Measurement of the plant water status by the pressure chamber technique. Irrig Sci 9: 289–308

Valentini R, Scarascia Mugnozza GE, Ehleringer JR (1992) Hydrogen and carbon isotope ratios of selected species of a Mediterranean macchia ecosystem. Funct Ecol 6: 627–631

Wescor (1979) Instruction manual HR-33T Dew point microvolmeter Wescor, Logan, Utah

Wiebe HH, Brown RW (1979) Temperature gradient effects on in situ hygrometer measurements of water potential. II. Water movement. Agron J 71: 397–401

Wiebe HH, Brown RW, Barker J (1977) Temperature gradient effects on in situ hygrometer measurements of water potential. Agron J 69: 933–939

Wilson CA, Mitchell JFB (1987) A doubled CO_2 climate sensitivity experiment with a global model including a simple ocean. J Geophys Res 92: 13315–13343

Wylie BK, Pieper RD, Southward GM (1992) Estimating herbage standing crop from rainfall data in Niger. J Range Manage 45: 277–284