



Long-term dynamics of water and carbon in semi-arid ecosystems: a gradient analysis in the Patagonian steppe

Jose M. Paruelo¹, Osvaldo E. Sala¹ & Adriana B. Beltrán

Depto. Ecología and IFEVA¹, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, 1417 Buenos Aires, Argentina (E-mail: paruelo@ifeva.edu.ar)

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Abstract

We used a soil water simulation model and remotely sensed data to study the long-term dynamics of transpiration, evaporation, drainage and net primary production across a precipitation gradient in Northwestern Patagonia (Argentina). The proportion of precipitation transpired, the precipitation use efficiency and the transpiration use efficiency were constant across the gradient that covered a range of 150 to 600 mm. The proportion of water evaporated was higher than the proportion drained at the driest extreme of the gradient. The opposite relationship was observed at the wet extreme.

Two important characteristics of arid-semiarid systems dominated by winter precipitation emerged from our analyses: the importance of drainage losses and the asynchrony between evaporation and transpiration fluxes. These characteristics of the water dynamics influence the relative abundance of plant functional types and are crucial to generate heterogeneity at the landscape level. The coefficient of variation (CV) of transpiration, evaporation and ANPP was, in general, lower than the CV of annual precipitation. This pattern suggests a buffering capacity of the ecosystem. The ecosystem would be able to damp at the functional level inter-annual changes in the availability of resources.

Introduction

Desertification is one of the many faces of the global change process (Schlesinger et al. 1990) and a major environmental concern for society. Many international agencies are devoting an important amount of resources to study and control desertification all over the world. The definition of desertification and its assessment generate, however, many controversies. One of the most useful definitions of this process states that it is a human induced process leading to a reduction in the water use efficiency of the ecosystem (Le Houérou 1996), where water use efficiency (WUE) is defined as the ratio between net primary production and precipitation or transpiration. Based on this definition, to assess the magnitude of desertification in a particular place it is necessary to know the water use efficiency of the degraded and non degraded states of the system. The WUE of the reference or not de-

graded state will vary both in space and time. A change associated with the impact of external variables (i.e., overgrazing, changes in atmospheric composition or climate alteration) on ecosystem functioning will be detected if the effect of these forcing variables becomes larger than the variability of the natural system. Consequently, water fluxes and primary production have to be characterized not just by 'one site-one year' estimate but from long term records of both water and carbon fluxes.

Climate, and particularly precipitation, is the main driving variable of both water and primary production in semi-arid ecosystems (Noy Meir 1973; Sala et al. 1988; Epstein et al. 1997). The relative variability of precipitation, temperature, and evapotranspiration decreases exponentially with increases in mean annual precipitation (Goudie & Wilkinson 1977; Frank & Inouye 1994; Jobbágy et al. 1995; Lauenroth & Burke 1995). Paruelo & Lauenroth (1998) found that the

interannual variability of different aspects of above-ground net primary production was also negatively related to mean annual precipitation.

Patagonia is a cold temperate region (aprox. 700 000 km²) located in the southernmost portion of South America, east of the Andes. The area is dominated by grass and shrub steppes and semideserts. Most of the region can be characterized as arid or semi-arid (Paruelo et al. 1998). Carbon and water fluxes are connected in arid and semi-arid areas, but in some cases these two fluxes respond independently to environmental variables. In a simulation study, Aguiar et al. (1996) found that primary production and herbivore biomass had a larger response than transpiration to the structural changes associated with overgrazing in the Patagonian steppe. In this context, to characterize the temporal and spatial variability of water and carbon dynamics becomes particularly important both for theoretical and applied reasons.

In this article we analyzed the spatial and temporal patterns of carbon and water dynamics across an arid-emi-arid region of Patagonia (Argentina) that displays a steep precipitation gradient. An experimental approach to characterize the long-term dynamics of primary production and water across a precipitation gradient presents obvious logistic problems. Our study combined the use of simulation models and remote sensing data to estimate the dynamics of primary production and water. We used a water-balance model developed and tested for the Patagonian steppe (DINAQUA, Paruelo & Sala 1995). We incorporated simple algorithms into the model to calculate some of the plant parameters for the different sites of the precipitation gradient. DINAQUA simulates the dynamics of transpiration, evaporation, and drainage on a daily time step. We characterized carbon fluxes by the Aboveground Net Primary Production (ANPP). ANPP estimates were derived from the annual integral of the Normalized Difference Vegetation Index (NDVI) calculated from the NOAA/AVHRR satellites. The NDVI integral showed a high correlation with ANPP for grassland areas (Prince 1991; Paruelo et al. 1997).

Our objectives were to describe the spatial patterns and the inter-annual variability of water and carbon fluxes across a precipitation gradient. Specifically we characterized:

- Patterns of annual transpiration, bare soil evaporation, drainage, aboveground net primary production, and water use efficiency.
- The seasonal dynamics of transpiration, evaporation and drainage.

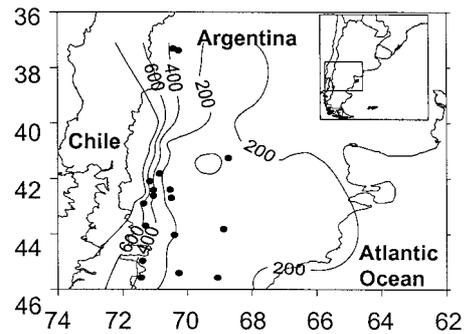


Figure 1. Map of mean annual precipitation of the study area. Dots corresponds to the study sites (see Table 1).

- The inter-annual variability of transpiration, bare soil evaporation, drainage, and aboveground net primary production (ANPP).

Materials and methods

The study area was located in the rain shadow of the Andes between 38° and 46°S and covers more than 150 000 km² in northwest Patagonia (Argentina) (Figure 1). This portion of the continent is dominated by Pacific air masses and strong westerly winds (Paruelo et al. 1998). Most of the moisture of these air masses precipitates on the western side of the Andes. On the eastern side of the mountains, precipitation is concentrated during winter and decreases eastward from 600 mm to 150 mm per year on a distance of 50–60 km (Jobbágy et al. 1995). Mean annual temperature ranges between 5 and 8 °C and is mainly controlled by altitude. Annual thermal amplitude is in general lower than 15 °C (Paruelo et al., 1998a). Associated with the mean annual precipitation gradient there is a gradual change in vegetation (León & Facelli 1981; Jobbágy et al. 1996). The main change in vegetation is an eastward decrease of total plant cover, and an increase in the relative abundance of shrubs.

We selected 17 sites spread across the study area based on the availability of daily data of precipitation (Table 1). For some of the sites the records were not continuous. Daily data of temperature were available for only three of the sites. Daily temperature data for the remaining sites was estimated from the nearest site with available data and mean annual temperature data. Data were obtained from the Servicio Meteorológico Nacional, INTA, EVARSA and private ranches.

Water dynamics was simulated using a water-balance model developed for the Patagonian steppe

Table 1. List of the study sites included in the analyses.

Site	Latitude (S)	Longitude (W)	Period	Years	Mean annual
EL Alamito	37°18'	70°26'	77–96	12	295
Chos Malal	37°22'	70°16'	80–96	10	224
Maquinchao*	41°25'	68°44'	39–72	33	158
Ñorquinco*	41°49'	70°52'	81–96	11	189
El Manten*	42°06'	71°10'	55–96	34	424
Fofocahuel*	42°24'	70°32'	69–96	27	137
Leleque*	42°25'	71°03'	69–96	27	459
Lepa	42°37'	71°03'	69–96	27	348
Gualjaina	42°42'	70°30'	63–96	41	117
Esquel*	42°54'	71°21'	71–95	15	282
La elena	43°42'	71°18'	56–96	37	597
Paso de Indios	43°49'	68°53'	68–90	22	188
Gobernador Costa	44°02'	70°24'	53–77	45	177
La Paulina	44°58'	71°24'	53–96	13	289
Rio Mayo*	45°25'	70°16'	37–95	24	154
Sarmiento*	45°35'	69°04'	59–96	21	147
Ea Media Luna*	45°35'	71°26'	81–95	14	325

*Sites with ANPP data available.

(DINAQUA) (Paruelo & Sala 1995). The model simulated on a daily basis evaporation, transpiration of grasses and shrubs, and drainage. Soil is divided into six layers and each layer was characterized by its thickness, water content at field capacity (FC) and wilting point (WP). Layers were 10, 10, 20, 40, 40 and 80 cm thick. Only one soil type was considered in the simulations (sandy-loam, INTA, 1990) (FC = 16%, WP = 5%) (Goto et al. 1994).

The model considers only saturated fluxes and the flow from the bottom layer corresponds to drainage. Downward fluxes are calculated daily after adding precipitation. Water content of each layer is updated after computing evaporation and transpiration. Bare soil evaporation was calculated from Ritchie's (1972) model. This model divided the drying cycle into two phases. During phase I evaporation was equal to potential evaporation. Duration of phase I depends on soil hydraulic conductivity at -1 Mpa. Phase II evaporation was proportional to the square root of time and to hydraulic conductivity at -1 Mpa. Potential evaporation was calculated from temperature and net radiation which in turn was calculated from global radiation and sunshine data. Based on Ritchie (1972) we set a reduction of 50% in net radiation for a leaf area index (LAI) of 2. Assuming a mean specific leaf area for the dominant species of the steppe of $40 \text{ cm}^2 \text{ g}^{-1}$ (del Pino, unpublished) the biomass that corresponds

to a LAI = 2 is 500 g m^{-2} . Evaporation took place from the upper layer (0–10 cm). Paruelo et al. (1991) tested Ritchie's model for the Patagonian steppe.

Transpiration is calculated independently for grasses and shrubs, the two main plant functional types of the steppe. Actual transpiration ($\text{g water g}^{-1} \text{ biomass}^{-1} \text{ day}^{-1}$) was a function of the potential transpiration and the effective available water for each functional type. Potential transpiration depends on species physiology and atmospheric demand. The effective available water of each plant functional type depends on the available water of each layer and on the proportion of roots in each layer.

The seasonal dynamics of green biomass of grasses and shrubs was simulated by interpolating between minimum and maximum biomass. The days of peak biomass, start and end of the growing season need to be specified. The model was successfully tested by comparing simulated and observed data of water losses and water content for different structural conditions of the steppe (Paruelo & Sala 1995) and for annual grasslands of California (Jackson et al. 1998). The code of the model is available at <http://www.ifeva.edu.ar/DAQ>. More details on the structure and performance of the model are available in Paruelo & Sala (1995), Aguiar et al. (1996) and Jackson et al. (1998).

We incorporated 4 new algorithms to the original version of DINAQUA to calculate some of the parameters of the model along a precipitation gradient. These simple algorithms were derived from regional analysis of the relationship between ecosystems or plant attributes and climatic variables. Peak biomass was calculated from the Sala et al. (1988) relationship between primary production and mean annual precipitation (MAP) ($\text{Peak Biomass or ANPP (g m}^{-2} \text{ year}^{-1}) = 0.6 * \text{MAP (mm year}^{-1}) - 34$). The proportion of grasses and shrubs was calculated based on a modification of (Paruelo & Lauenroth 1996) equations as a function of mean annual precipitation ($\text{SHRUB Prop.} = e^{(-.00462 * \text{MAP})}$, $\text{GRASS Prop.} = 1 - \text{SHRUB Prop.}$). The performance of these empirical models was previously tested for the temperate areas of South America (Paruelo et al. 1998b).

The seasonal dynamics of biomass was derived from (Jobbágy et al., in press) from mean annual precipitation (MAP) and mean annual temperature (MAT):

$$\begin{aligned} \text{Day of Maximum Biomass} &= \\ &335 + .0371 * \text{MAP} [\text{Day 1} = \text{January 1st}] \\ \text{Day of end of the growing season} &= \\ &119.7 + 15.07 * (1 - \text{EXP}(-.00251 * \text{MAP})) \\ \text{Day of start of the growing season} &= \\ &304 - 4.6 * \text{MAT} \end{aligned}$$

Maximum transpiration of each plant functional type was calculated as a function of MAP based on changes in maximum conductance. Not enough data were available in the literature to derive an empirical relationship between maximum conductance and MAP. The rationale of the relationship that we used is based on: (1) a linear relationship between specific leaf area (SLA) and xerophytism (and hence MAP) (Solbrig & Orians 1977; del Pino, unpublished $r = 0.68$), (2) a positive relationship between maximum conductance and maximum transpiration rates or maximum net carbon exchange rates (Schulze et al. 1994), and (3) a positive relationship between specific leaf area (SLA) and maximum conductance and SLA and Net photosynthesis (Schulze et al. 1994; Reiche et al. 1997). The relationships between maximum transpiration and MAP were based on estimates for xerophytic plants (Paruelo 1991) and mesophytic plants (Jackson et al. 1994).

Aboveground Net Primary Production (ANPP) summarizes essential features of ecosystem functioning (McNaughton et al. 1989) and is tightly coupled

to water dynamics in arid and semi-arid ecosystems (Noy Meir 1973). To estimate ANPP on a regional scale we used the seasonal integral of the Normalized Difference Vegetation Index (NDVI-I) derived from the NOAA/AVHRR satellites. Many studies showed a strong correlation between NDVI-I and ANPP for rangelands (i.e., Tucker et al. 1985; Prince 1991; Paruelo et al. 1997).

We used 10-day composite images of NDVI from the Pathfinder AVHRR Land database (James & Kalluri 1994) for the period 1981–1991. The spatial resolution of these data is 8×8 km (6400 ha). The 36 images available for each year were integrated using a triangular approach (see Paruelo & Lauenroth 1995). The data on the NDVI integral (NDVI-I) were converted into ANPP values using:

$$\begin{aligned} \text{ANPP} &= 3803 \cdot \text{NDVI} - 1^{.9028} \\ &(\text{Paruelo et al., 1997}) \end{aligned}$$

Only a subset of the 17 sites was used to characterize aboveground net primary production (ANPP). We discarded seven sites due to the presence of riparian areas, the degradation status, or the complexity of the landscape. The model calculates water fluxes for the typical non-degraded status of the steppe. The use of sites that include areas not representative of the typical conditions of the steppe will not provide comparable ANPP data. We analyzed the relationship between carbon and water dynamics by looking at two descriptors of water use efficiency: transpiration use efficiency (mean ANPP/mean annual transpiration) and precipitation use efficiency (mean ANPP/mean annual precipitation). Because the series of NDVI and precipitation do not match for the whole period for most of the sites, we did not perform a temporal analysis of water use efficiency.

Results and discussion

Total transpiration increased linearly with precipitation (Figure 2). A linear relationship between transpiration and precipitation indicate that transpiration losses were a constant proportion of total water inputs. On average, 38% of mean annual precipitation was transpired. Reynolds et al. (2000) found that transpiration accounted for by 32% of total losses in the Chihuahuan desert. The proportion of annual precipitation which was transpired showed a different temporal variability across the precipitation gradient (Figure 3). For the driest sites, the transpiration/annual

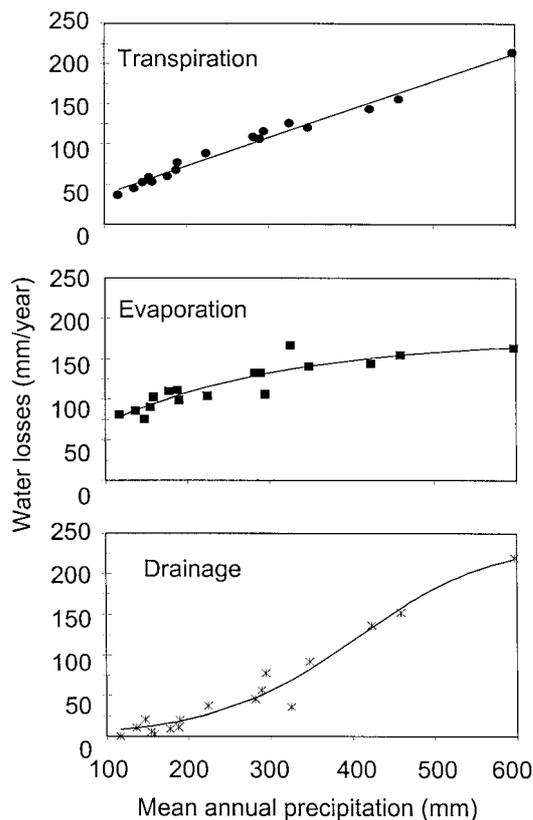


Figure 2. Relationship between mean annual precipitation (MAP) and mean annual transpiration (TR), evaporation (EV) and drainage (DR) for the 17 sites studied. $TR = 1.44 + 0.35 \times MAP$ ($r^2 = 0.98$, $n = 17$, $p < 0.001$), $EV = 175 - 164 \times e^{-0.0045 \times MAP}$ ($r^2 = 0.82$, $n = 17$, $p < 0.001$), $DR = 242 / (1 + 109.6 \times e^{-0.0116 \times MAP})$ ($r^2 = 0.96$, $n = 17$, $p < 0.001$).

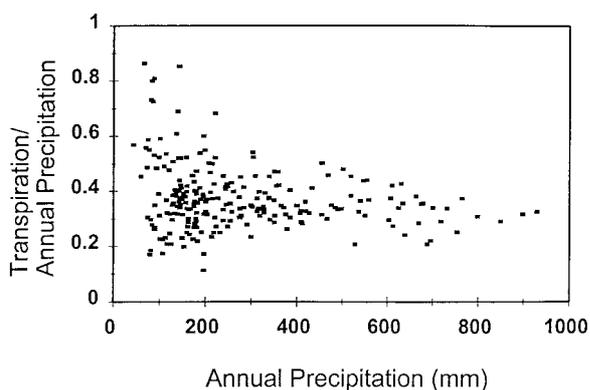


Figure 3. Annual transpiration/precipitation ratio for the 17 sites and the total numbers of years considered across the precipitation gradient.

precipitation ratio varied from almost 0.2 up to 0.9. Wet sites showed a lower variability among years in the proportion of precipitation which was transpired. Grasses accounted for most of water transpired (89%) at the wet extreme of the gradient. At the dry end, shrubs are the main path for transpiration (59%).

Bare soil evaporation increased with precipitation with a decreasing slope (Figure 2). Evaporation became a smaller fraction of total losses as mean annual precipitation increased. Evaporation losses depend mainly on the water held by the upper layer of the soil. The size of the average precipitation event increases as precipitation increases (Golluscio et al. 1998), consequently, more water moves downward reaching layers not subjected to evaporative losses. The ratio evaporation/precipitation decreased from 0.70 at the driest site, to 0.27 at the wettest extreme of the gradient. Drainage showed the opposite pattern, with the proportion of water drained increasing from 0 at the dry extreme of the gradient up to 0.36 at the wettest site (Figure 2). A sigmoidal curve described the changes in drainage across the precipitation gradient. As more water moved downward, the deepest layers of the soil reach field capacity and surplus water left the system. Drainage losses are particularly important in systems where precipitation is concentrated in winter (Paruelo and Sala 1995, Jackson et al. 1998).

For a particular site total annual precipitation was a poor predictor of total fluxes. The percentage of the interannual variance of transpiration, evaporation, and drainage accounted for precipitation was on average 39%, 53% and 51%, respectively. The proportion of the variance of the different fluxes accounted for precipitation was, however, quite variable among sites. It ranged from 0.13 to 0.88.

As has been shown for many grassland and shrubland areas of the world ANPP increased linearly with MAP (Walter 1939, Lauenroth 1979, Sala et al. 1988) (Figure 4). MAP accounted for most of the regional variability in mean ANPP ($r^2 = 0.90$, $n = 10$, $F = 71$). The linear relationship indicates a constant mean precipitation use efficiency across the precipitation gradient. On average the precipitation use efficiency (PUE) of the patagonian steppe is 0.37 g mm^{-1} (Figure 5). Transpiration use efficiency was also constant across the precipitation gradient and averaged $1.04 \text{ g mm of transpiration}^{-1}$ (Figure 5). Jobbàgy et al. (In press) showed for five sites located in the same area, that the annual integral of NDVI, an estimate of ANPP, was not related to annual precipitation. Changes in the seasonal distribution of precipitation

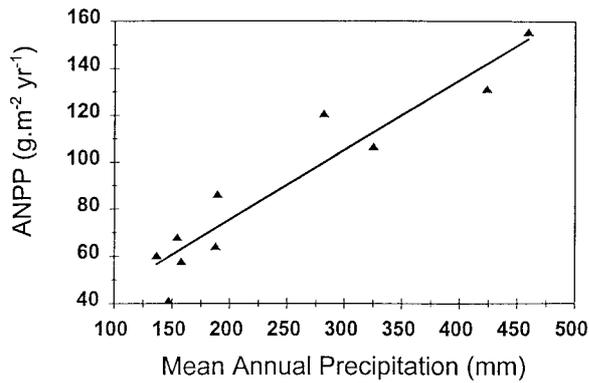


Figure 4. Relationship between mean annual precipitation (MAP) and aboveground net primary production (ANPP) for the sites studied along the gradient. ANPP was estimated from the Pathfinder Land AVHRR dataset using Paruelo et al. (1997) equation. $ANPP = 16 + 0.30 \times MAP$ ($r^2 = 0.90$, $n = 10$, $p < 0.001$).

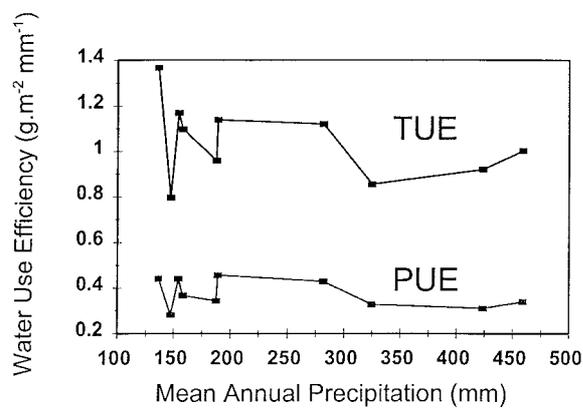


Figure 5. Average transpiration use efficiency (TUE=mean ANPP/mean annual transpiration) and precipitation use efficiency (PUE=mean ANPP/mean annual precipitation) across the precipitation gradient.

or water transferred from one year to the next account for the poor relationship between transpiration and annual precipitation. From a functional viewpoint transpiration losses and carbon gains are positively related (Noy Meir 1973). However, the correlation between aboveground net primary production (ANPP) and transpiration on an annual scale was in general low (data not shown). Intra-annual changes in transpiration use efficiency may account for the lack of correlation at the annual scale.

The average values of transpiration and precipitation use efficiency at the annual scale were relatively constant across the precipitation gradient. Transpiration use efficiency (TUE) was constant despite the changes in the maximum transpiration rate of the dominant species that may determine in itself, a reduction

in TUE. At the ecosystem level this effect was not evident. The key to understand why changes in maximum transpiration do not affect the TUE or the fraction of total precipitation which is transpired is the asynchrony of evaporation and transpiration. Evaporation and transpiration do not represent alternative pathways for water loss in the Patagonian steppe because they basically occur in different times of the year, when it rains (evaporation) or when it is warm and still wet (transpiration). Therefore, an increase in conductance and maximum transpiration does not affect total transpiration but it may anticipate the occurrence of the time of maximum transpiration. In synthesis, in the Patagonian steppe, an increase in conductance does not modify total transpiration or evaporation but may modify their seasonality. In fact we observed a delay in peak transpiration as precipitation decreased (Figure 6).

Water losses showed a characteristic pattern at the seasonal scale (Figure 6). Transpiration increased from early spring and reached a peak in late spring. Peak transpiration showed a delay from wet to dry sites associated to the changes in grass/shrub proportion. Transpiration was the main water loss for a longer portion of the year in wet sites than in dry sites. During the coldest month of the year evaporation, and drainage, accounted for most of water losses. Transpiration and evaporation showed a negative correlation throughout the year. The asynchrony between transpiration and drainage was evident all across the precipitation gradient (Figure 7). The correlation of evaporation and transpiration fluxes for periods of 10 days was negative and statistically significant for all the sites.

Bare soil evaporation was high during winter months when the water content of the upper layer of the soil was high, despite the low evaporative demand. At this time transpiration losses were constrained by the low leaf area index of the plant community. Even though evaporative demand is the major control of the evaporation rate at a daily scale (Ritchie 1972), over 10 days period soil water availability seemed to exert the greatest influence. Transpiration losses were maximum at spring when simultaneously water availability throughout the profile and leaf area index were high.

The interannual variability of annual values of transpiration, and evaporation decreased along the precipitation gradient (Figure 8). The same pattern has been described in many systems for the relative variability of precipitation (Goudie & Wilkinson 1977; Jobbágy et al. 1995; Lauenroth & Burke 1995). The

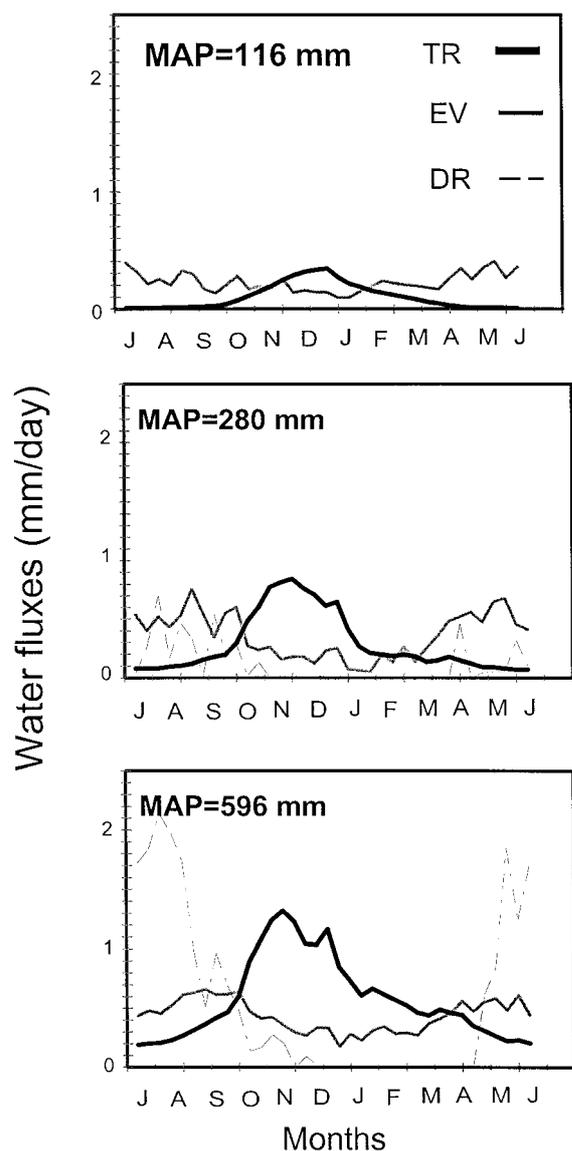


Figure 6. Average seasonal dynamics of transpiration, bare soil evaporation, and drainage for three sites across the precipitation gradient.

coefficient of variation of precipitation and ANPP did not show significant changes across the precipitation gradient (Figure 8). Drainage variability also decreased with MAP but it was an order of magnitude more variable than the others fluxes (Figure 9). Evaporation and transpiration showed a similar inter-annual variability for the whole range of sites studied. ANPP variability was lower than transpiration and evaporation variability at the driest extreme of the gradient.

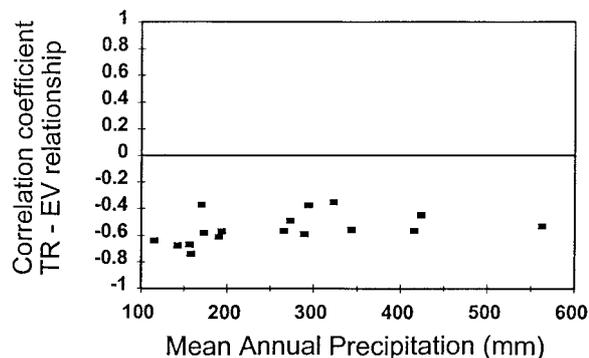


Figure 7. Correlation coefficient between transpiration and evaporation for periods of 10 days for the 17 sites analyzed across the precipitation gradient.

For most of the sites, the coefficient of variation (CV) of transpiration, evaporation and ANPP was lower than the CV of annual precipitation (Figure 10). This pattern suggests a buffering capacity of the ecosystem. The ecosystem may be able to damp fluctuations in the availability of resources. Paruelo & Lauenroth (1998) report a similar effect for North American grasslands and shrublands. Several reasons may account for this buffering capacity of the ecosystem, for example the soil may act as a water capacitor mainly in regions with winter precipitations; or the dominant species may have a moderate response to changes in resource availability.

The coefficient of variation (CV) of transpiration for periods of 10 days showed a distinct seasonal pattern for shrubs and grasses and it changed along the precipitation gradient (Figure 11). The seasonal changes of CV were also different along the precipitation gradient. During winter and early spring the coefficient of variation of transpiration losses was higher in dry areas than in wet areas (Figure 11). In the humid extreme of the gradient, winter precipitation is sufficient to refill the profile every year. In fact, a substantial proportion of the precipitation falling in these areas is loss as drainage (Figure 2). Drainage was a rare event in sites with low precipitation but it occurred every year in sites with high MAP. Consequently, water is a very reliable resource in winter and early spring at the humid extreme of the gradient for both grasses and shrubs. During late spring and summer, grass transpiration in wet sites was highly variable among years. Variability peaked during late summer in wet sites and in late fall in the dry site. Precipitation and water availability are always low in summer in dry sites but may fluctuate greatly for sites located in the most

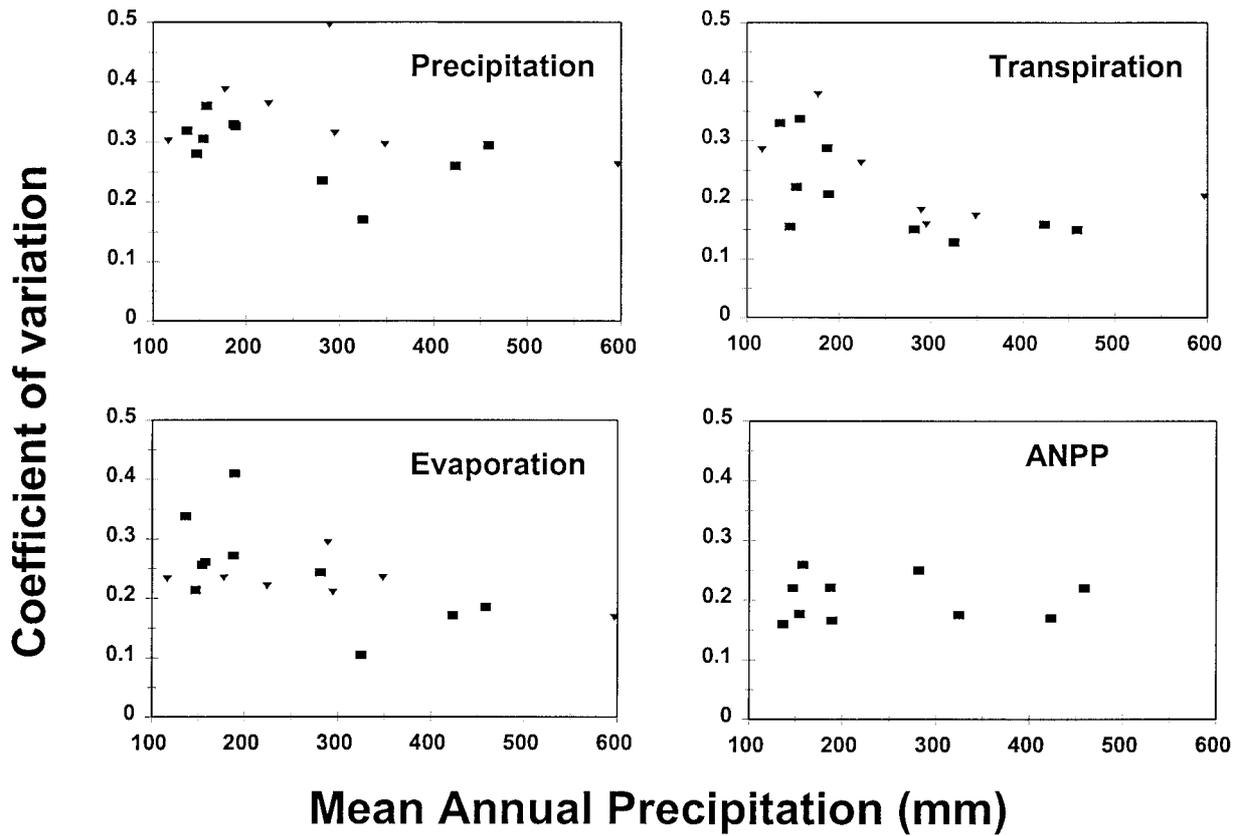


Figure 8. Changes in the coefficient of variation of annual precipitation ($r = -0.31, n = 17, n.s.$), transpiration ($r = -0.55, n = 17, p < 0.05$) bare soil evaporation ($r = -0.55, n = 17, p < 0.05$), and ANPP ($r = -0.03, n = 17, n.s.$) across the precipitation gradient. Squares correspond to sites with ANPP and water fluxes data and triangles to those sites with only water fluxes data.

humid areas. Inter-annual variability of shrub transpiration for periods of 10 days also increased through the growing season (Figure 11). However the peak of CV occurred later than for grasses. As well as for grass transpiration, the peak of relative variability of seasonal precipitation was lower at the driest extreme of the gradient.

Conclusions

The temporal and spatial extend of our analysis allow us to identify important features of the long-term dynamics of water and carbon in arid and semiarid systems that were not evident from single site studies. A particular characteristic of systems dominated by winter precipitation is the importance of drainage losses. Reynolds et al. (2000) showed that in systems with rainfall concentrated in summer water did not penetrate below 40 cm. In contrast drainage, defined

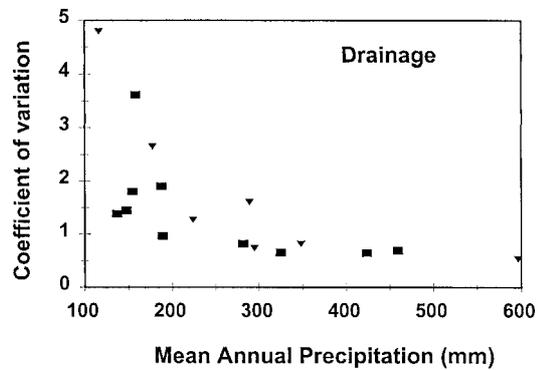


Figure 9. Changes in the coefficient of variation of annual drainage ($r = -0.63, n = 17, p < 0.05$) across the precipitation gradient. Squares correspond to sites with ANPP and water fluxes data and triangles to those sites with only water fluxes data.

here as water reaching a depth of 200 cm, accounted for up to 36% of total water inputs in the Patagonian steppe.

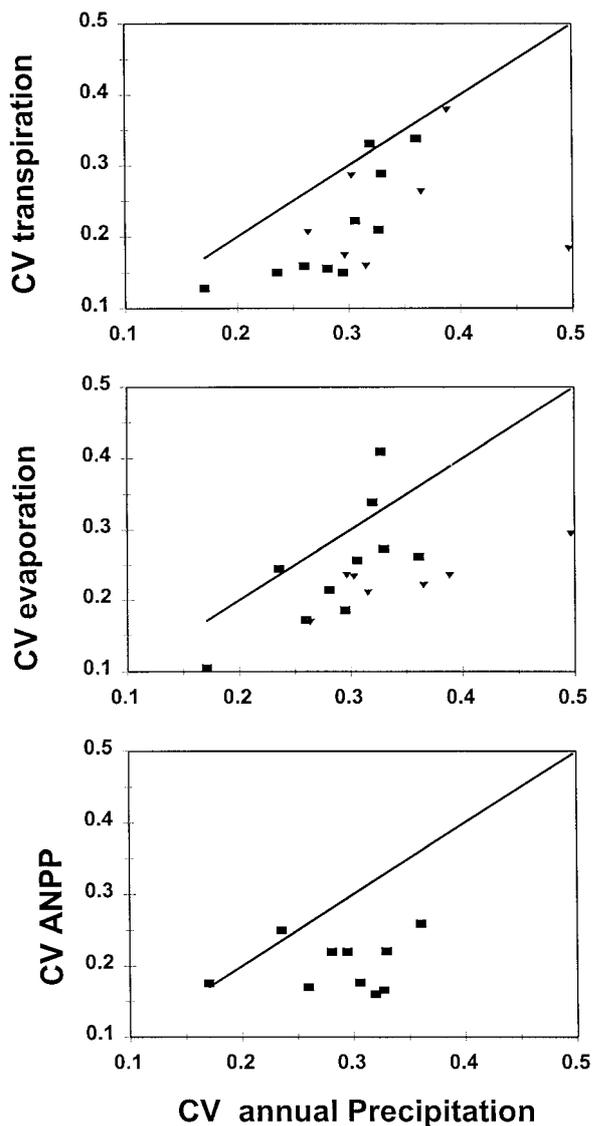


Figure 10. Relationship between the coefficient of variation of annual precipitation and the coefficient of variation of transpiration, evaporation, and ANPP. The line corresponds to the 1:1 relationship. Squares correspond to sites with ANPP and water fluxes data and triangles to those sites with only water fluxes data.

Another particular characteristics of ecosystems with a winter distribution of precipitation is the asynchrony between evaporation and transpiration. To a great extent evaporation and transpiration are not alternative pathways for soil water in these ecosystems. If transpiration is low, surplus water will mainly drain. At the landscape level the consequence of an increase in drainage versus an increases in evaporation should be quite different in terms of total production. Drained

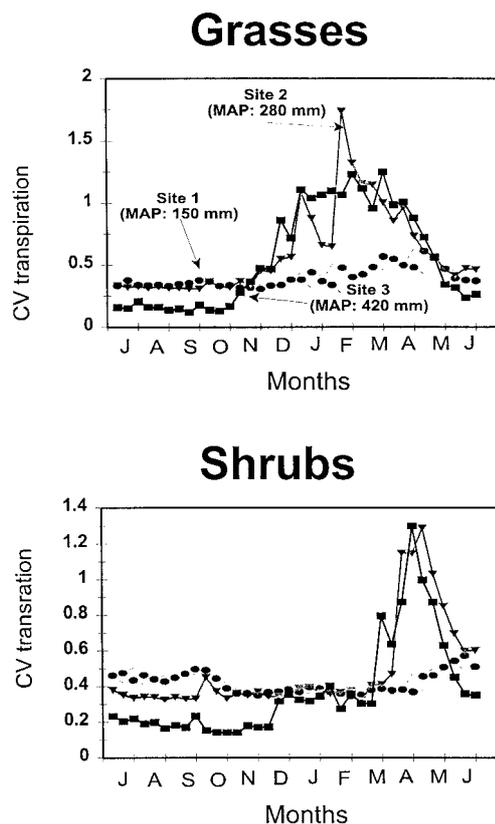


Figure 11. Seasonal changes of the coefficient of variation of grass and shrub transpiration for three sites located in different positions of the precipitation gradient. Each point corresponds to the CV of the transpiration for a period of 10 days.

water may be transpired in a different landscape position due to lateral flow, increasing total carbon gains of this unit. Drainage water may be the main source of water for meadows located in small valleys, locally named 'mallines' which are very important in supporting both wild and domestic animal populations. Although the 'mallines' occupied less than 5% of the area, they make a disproportionate contribution to the landscape primary production (Parelo & Golluscio 1994). Water redistribution generate a matrix of high and low production areas that may increase the production at the landscape level (Noy Meir 1981; Sala and Aguiar 1995).

The relative importance of drainage losses and the asynchrony between transpiration and evaporation are two critical difference between systems dominated by summer and winter precipitation. These characteristics of the long-term water dynamics will influence the relative abundance of plant functional types and the partitioning of resources among plant functional

types (i.e., grasses and shrubs). The higher availability of deep water in systems with winter precipitation will favor deep rooted plant functional types (i.e., shrubs). In fact, given the same amount of precipitation and temperature the relative abundance of shrubs increases with the proportion of total precipitation falling in winter (Paruelo & Lauenroth 1996). A winter distribution of the precipitation concentrate grass transpiration losses in a relative small portion of the year (spring and early summer) (Figure 6). Carbon gains will occur, then, in a relatively cool period favoring species with a C₃ syndrome. In areas with winter precipitation, such as Patagonia or the Great Basin in North America, no C₄ grasses are present. C₄ grasses are dominant in areas with the same temperature and total precipitation than Patagonia but with summer rainfall (Paruelo & Lauenroth 1996; Paruelo et al. 1998b).

Transpiration and ANPP are two key functional attributes of the ecosystems. Both are tightly related to the exchange of water, energy and carbon between the land-surface and the atmosphere. Our results support previous evidences (Fernández et al. 1991; Lauenroth & Sala 1992; Paruelo & Lauenroth 1998) that the ecosystem should be able to damp at the functional level inter-annual changes in water inputs. The 'buffer' capacity of the ecosystem should be associated with structural constrains related to the magnitude of the change in plant functional type composition, to biogeochemical constrains, to the role of the soil as a temporary reservoir of water or to redistribution of resources at the landscape level. This 'buffering' capacity of the ecosystem will be responsible of the weak relationship between long-term data of precipitation and ANPP (Lauenroth & Sala 1992; Jobbágy et al. in press) or transpiration (this study).

Desertification assessment often faces the problem of estimating the values of attributes that correspond to the non-degraded condition. We focus our study on the non-degraded state of the steppe. In such a way our results provided estimates of 'potential' values for some key attributes to study desertification (transpiration and precipitation use efficiency, Le Houérou (1996), Prince et al. (1998)). A combination of modeling and remotely sensed data provide a useful alternative to derive at a regional scale either potential or actual values of water use efficiency for arid and semi-arid steppes.

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