WATER LOSSES IN THE PATAGONIAN STEPPE: A MODELLING APPROACH[1]

JOSÉ M. PARUELO[2] AND OSVALDO E. SALA
*Departamento de Ecología, Facultad de Agronomía, Universidad de Buenos Aires,
Avenida San Martín 4453, 1417 Buenos Aires, Argentina*

Abstract. In this paper we sought to answer questions related to the long-term soil water dynamics of the Patagonian steppe: What are the magnitude and seasonal dynamics of transpiration, evaporation, and deep percolation? How do these fluxes respond to fluctuations in annual precipitation? What is the pattern of soil water availability? We developed a soil water model for the steppe with a daily time step. The model gives weekly cumulative values of transpiration, evaporation, and drainage, maximum and minimum water content for the different soil layers in each week, and the weekly frequency of days with soil water potential higher than -1 MPa for each layer. The model was tested against three sets of experimental data. Simulated data of total water losses were significantly correlated with observed data, and the slope did not differ significantly from 1 nor the y-intercept from 0.

On a long term basis, evaporation accounted for 56% of total water loss, transpiration 34%, and deep percolation the remaining 10%. Transpiration and evaporation had asynchronic dynamics. Evaporation was high during the coldest and wettest months of the year (mainly winter months). Transpiration, on the contrary, reached maximum values when energy and water availability were simultaneously high in late spring–early summer. Drainage took place during the coldest months, when most of precipitation occurred, and the soil remained near field capacity.

Both evaporation and transpiration had a positive response to an increase in precipitation. However, the proportion of total water loss following these pathways decreased with increasing precipitation. Drainage had a positive exponential relationship with winter precipitation. Probabilities of soil water potential higher than -1 MPa in the upper soil layer were very low during most of the warm season ($P < 0.15$). At the beginning of the growing season the wettest layer was located at an intermediate depth (10–20 and 20–40 cm), and moved downward so at the end, only deep roots had high soil water availability.

Key words: Argentina; drainage; ecosystems; evaporation; functional types; long term studies; modelling; Patagonia; steppes; transpiration; water dynamics.

INTRODUCTION

The close relationship between carbon gain and water loss results in annual net primary production of arid environments being controlled mainly by water availability (Noy Meir 1973). Annual precipitation accounted for most of the temporal and spatial variability in productivity across a broad range of grasslands (Lauenroth 1979, Sala et al. 1988, Lauenroth and Sala 1992). Schimel and Parton (1986) pointed out the close coupling of the dynamics of nitrogen and soil water through the effects of water availability on mineralization and on movement of nitrogen in the soil profile. These references highlighted the importance of characterizing the water economy to understand the functioning of ecosystems in arid and semiarid regions.

Several field studies characterized the magnitude and dynamics of water losses in arid and semiarid ecosys-

tems (see e.g., Ng and Miller 1980, Floret et al. 1982, Wight et al. 1986). Sala et al. (1992) using a simulation approach, performed the first long term characterization of the soil water dynamics in a water limited environment, the shortgrass steppe in North America. The characterization of the responses of different functional groups of plants to the spatial and temporal heterogeneity in resource availability is a critical point to understand the structural and functional modifications that may result from global change (Steffen et al. 1992).

Most of the Patagonian region in the southernmost portion of Argentina is covered by steppes co-dominated by grasses and shrubs (Paruelo et al. 1991b). These functional types accounted for 95% of plant cover in the most typical plant community of the Occidental district of the Patagonian Phytogeographic Province, defined by Golluscio et al. (1982) as the "*Adesmia campestris, Berberis heterophylla, Stipa speciosa, Stipa humilis,* and *Poa lanuginosa*" community. In these steppes, grasses and shrubs differ in several structural and functional aspects. Grasses concentrate their roots in the uppermost layer of the profile (Soriano et al. 1987). Shrubs, on the contrary, have most of their roots

in the deepest layers of the soil (Fernández and Paruelo 1988). Grasses have green leaves during the entire year; shrubs show a seasonal phenology with a dormant period during winter. Experimental evidence about the partitioning of resources between these two functional types indicates that grasses absorb water mainly from upper layers and shrubs from deepest layers (Sala et al. 1989).

Average annual rainfall for a typical site of the Patagonian steppe (Río Mayo, Chubut, 45°S and 70°W), was about 150 mm (19 yr average), and was concentrated during fall and winter months. Mean monthly temperature ranged from 2°C in July to almost 14°C in January. Soils are characterized by their coarse texture, their high gravel content, and the presence of a calcareous layer at 45–60 cm depth (Paruelo et al. 1988).

The objective of this work was to describe the long-term soil–water dynamics in the Patagonian steppe, characterizing the main pathways of water loss and their principal controls. The long-term water dynamics were described assuming the existence of two functional types of plants: shrubs and grasses.

Specifically, we sought answers to the following questions: 1) What are, on a long term basis, the magnitude of evaporation, transpiration, and deep percolation in the steppe?, 2) What are the seasonal dynamics of these fluxes?, 3) How do these fluxes respond to interannual variation in precipitation?, and 4) What is the pattern of water availability in the soil profile?

The questions stated above need probabilistic answers. An experimental approach to solve these questions would need to record the different fluxes of the water balance equation for long periods (>10 yr). The use of simulation models is a more attractive, less expensive, and faster way to assign probabilities to the above questions than the experimental one (Pomeroy et al. 1988, Shugart 1989). The use of a water dynamics model allows the long term evaluation not only of evaporation, and transpiration flows but also deep percolation, which is difficult to estimate in the field (Feddes et al. 1988).

MODEL DESCRIPTION

We developed a water balance model, DINAQUA, for the conditions of the Patagonian steppe with the aim of answering the questions stated above. Weather inputs were daily values of mean temperature, global radiation, and precipitation. The simulation time step was daily. The model output consisted of weekly values of transpiration, evaporation, frequency of soil water potential higher than −1 MPa, and maximum and minimum values of water content during each week for the six layers defined in the soil profile.

Structure and general assumptions

We assumed the existence of only two functional types of plants: grasses and shrubs. This level of organization seemed to be the proper one to answer the questions that guided our work. There is structural and functional evidence that justified this grouping of species (Soriano and Sala 1983). The patterns of water consumption and resource partitioning will be more generalizable at this level than at the species level (Sala et al. 1989).

Horizontal heterogeneity in soil and vegetation were neglected in this model. Runoff and runon were also discarded because the topography is flat and the soils are coarse textured. We did not take into account plant interception of rainfall, because of the low plant cover of the steppe. Considering that the average size rainfall event is 6 mm, the interception calculated using Parton's equation (1978) is <0.35 mm per event.

DINAQUA simulated the seasonal course of green biomass of grasses and shrubs, interpolating linearly between the minimum and maximum biomass values. To perform this calculation, the model needs the specification of the day of the year when the growing season starts and ends, and the date of maximum biomass for each functional type. We assumed that the seasonal course of green biomass of grasses has a minimum in winter and a maximum in late spring and that the green biomass of shrubs was equal to zero during winter and reached a maximum in late spring (Soriano and Sala 1983, Fernández et al. 1991). The seasonal course and magnitude of green biomass of both functional types was held constant for the entire simulation.

Evaporation

We calculated soil evaporation from Ritchie's (1972) model. During phase I, water loss was limited only by the energy availability (Phillip 1957), and therefore, it was equal to potential evaporation. We estimated daily potential evaporation from Priestley and Taylor's (1972) formula, using net radiation and mean air temperature. Net radiation was calculated from global radiation and sunshine data following the procedure described by Feddes et al. (1978). Duration of phase I was proportional to soil hydraulic conductivity at −0.01 MPa (Ritchie 1972).

During the decreasing phase (II), evaporation was related to the square root of time and to hydraulic conductivity at −0.01 MPa (Ritchie 1972). Paruelo et al. (1991a) showed the suitability of this procedure to estimate evaporation in the Patagonian steppe. Evaporation losses in DINAQUA took place only from the upper layer (0–10 cm) (Paruelo et al. 1991a).

Transpiration

Transpiration was computed in an analogous but independent way for grasses and shrubs. Actual transpiration was a function of the potential transpiration and the effective available water for each functional type. Effective available water of a functional type is the sum of the available water of each soil layer weighted by the root proportion of this functional type in each layer (Sala et al. 1981):

$$EAW_{ik} = \sum^{j} ROOTS_{jk}(AW_{ij}/THICK_j),$$

where EAW_{ik} is the effective available water at time i for functional type k, $ROOTS_{jk}$ is the relative root density of the k functional type in the j layer, AW_{ij} the available water in the j layer expressed in millimetres (AW being equal to the difference between the water content at time i and the water content at wilting point), and $THICK_j$ the thickness of the j layer. The subscript i indicates the day of the year.

Potential transpiration ($TPOT_{ik}$, in grams of water per gram of green biomass per day), for both grasses and shrubs, resulted from:

$$TPOT_{ik} = TPOTtest_k \cdot (PET_i/PETtest),$$

where TPOTtest is the maximum value of daily transpiration experimentally recorded during the growing season, PETtest is the evapotranspiration corresponding to the day when TPOTtest was recorded, and PET_i the potential evapotranspiration of day i. The k subscript corresponds to the functional plant type.

The actual transpiration (TREAL) was reduced relative to the potential transpiration as a linear function of the effective available water when it fell below a threshold ($LIMAW_k$):

If $EAW_{ki} > LIMAW_k$,
$$TREAL_{ik} = TPOT_{ik}.$$

If $EAW_{ki} \leq LIMAW_k$,
$$TREAL_{ik} = TPOT_{ik} - [SLOP_k \cdot (LIMAW_k - EAW_{ki})],$$

where $SLOP_k$ is the slope of the relationship between actual transpiration and available water.

TREAL (in grams of water per gram of green biomass per day) was transformed to millimetres of water per day by multiplying it by the green biomass of each functional type in day i. TREAL, for both grasses and shrubs, was partitioned among layers as a proportion of the effective available water (EAW_{ki}).

Soil water and deep percolation

We considered in the model only saturated flows because the unsaturated hydraulic conductivity of these soils is very low even when they are close to field capacity (Paruelo 1991). The unidirectional flow was computed at the beginning of each day after adding daily rainfall. The flow from the last soil layer downward corresponded to deep percolation.

The model updates the water content of each layer after computing evaporation and transpiration. Daily values of evaporation and transpiration were accumulated weekly to reduce the output volume. Maximum and minimum weekly water contents were transformed to water potential using the equations provided by Paruelo et al. (1988). Table 1 summarizes variables and parameters of the model. The model was imple-

TABLE 1. Parameters and variables of the model DINA-QUA.

Code	Description
AW_{ij}	Available water for the j layer in the i date
$DBEG_k$	Day of year corresponding to the start of the growing season for the k functional type
$DEND_k$	Day of year corresponding to the end of growing season for the k functional type
$DMAX_k$	Day of year when biomass was maximum for the k functional type
$ROOTS_{kj}$	Relative root density in the j layer for the k functional type
EAW_{kj}	Effective available water in the i date for the k functional type
THICK	Thickness of the soil layers
PET_i	Potential evaporation in the i date
FC_j	Water content at field capacity for the j layer
SUN	Relative sunshine
K	Unsaturated hydraulic conductivity at -0.01 MPa
$LIMAW_k$	Threshold below which TREAL decreases with EAW for the k growth form
WIP_j	Water content at wilting point for the j layer
$SLOP_k$	Slope of the TREAL–EAW relationship for the k functional type
$TREAL_{ijk}$	Transpiration from the j layer in the i date for the k functional type
$TPOT_{ik}$	Potential transpiration for the i date and the k functional type
$TPOTtest_k$	Maximum transpiration rate for the k functional type

mented in Qbasic 3.0 for IBM-compatible PC microcomputers and the code is available on request.[3]

Data sources

We obtained daily data of temperature and rainfall from the Experimental Station of INTA (Instituto Nacional de Tecnologia Agropecuaria) in Río Mayo (Chubut, Argentina), and global radiation data from tables of the Smithsonian Institution (1958). Because of the lack of sunshine data, we assumed a relative value of 100% of incident for no-rain days and of 0% for rainy days.

We calculated the relative root density of grasses and shrubs for each layer from data of Soriano et al. (1987) and Fernández and Paruelo (1988). To characterize the losses for conditions typical of ungrazed areas of the steppe, we considered for grasses a maximum green biomass of 56 g/m² and a minimum of 20 g/m² (Fernández et al. 1991). The green biomass of shrubs used was 20 g/m² for the growing season and 0 for winter months (Fernández et al. 1991).

Water content at field capacity corresponded to a water potential of -0.01 MPa. Water content at wilting

point was defined as the water content at a soil water potential of −5.9 MPa, which corresponded to the water potential of the wettest soil layer during the driest period (Noy Meir 1973, Campbell and Harris 1981). The water content at field capacity and wilting point were calculated from the soil water retention curves and gravel content values using the model presented by Paruelo et al. (1988).

The maximum transpiration of each plant functional type (TPOTtest) and the potential evapotranspiration corresponding to the day when this transpiration value was recorded (PETtest) were measured in the field (Paruelo 1991). The effective available water below which the actual transpiration becomes a linear function of the EAW (LIMAW) for grasses and shrubs was obtained by parameter estimation (Innis 1979). We used the SIMPLEX algorithm for function minimization (Spendley et al. 1962, Jacoby et al. 1972). This method allowed, by iteration, the minimization of the differences between the observed and simulated values. We performed parameter estimation with data of total water loss (evaporation and transpiration, in millimetres per day) for periods without deep percolation, calculated from a water balance constructed using soil water potential data measured for different soil depths for a period of 3 yr (Sala et al. 1989).

MODEL EVALUATION

We evaluated the model at the level of the predictions, analyzing the fit of model results to experimental data. Simulated water losses were matched against experimental data of daily total losses (evaporation, transpiration, and deep percolation) estimated from a time series of soil water potential data at several depths during 2 or 3 yr according to the treatment. Water potential data were recorded with thermocouple psychrometers (Spanner 1951) at 5, 15, 30, and 60 cm depth and they corresponded to the average of 4 plots of 20 × 20 m (Sala et al. 1989). We converted water potential data into water content using the water retention curves reported by Paruelo et al. (1988).

We used three data sets to perform the model evaluation, each one corresponding to a different vegetation structure of the steppe (Sala et al. 1989): intact structure, grasses experimentally removed, and shrubs experimentally removed. Data corresponding to no-grasses and no-shrubs structures were not used for parameter estimation. The intact-structure data set is the same used to estimate the parameter LIMAW. To test for circularity problems in this case, we performed a random partitioning of the intact-structure data set. One portion of the data set was used to estimate the parameters and the other to evaluate the model (Wegener and Malone 1983). We performed 50 independent partitionings. The correlation coefficient between observed and simulated water losses was statistically significant for >80% of the partitioning runs. These results support the use of the entire intact-structure data set to test the model, in spite of its being used in the calibration.

The model simulated water losses (evaporation, transpiration, and deep percolation, in millimetres per day), for the same period for which experimental data were available. Three runs were done, one considering the values of biomass of grasses and shrubs recorded in the study site for the years corresponding to water potential data (Fernández et al. 1991), and the other two assuming the biomass of grasses or shrubs to be zero.

Fit between simulated and observed data was evaluated by regression analysis (Dent and Blackie 1979, Wallach and Goffinet 1989). The acceptance criterion was that (1) the regression was significant ($P < 0.05$), and (2) simultaneously, the y-intercept and the slope of the regression between simulated and observed data were not significantly different from 0 and 1, respectively ($P < 0.05$). For the three data sets the above criteria were satisfied (Fig. 1).

SENSITIVITY ANALYSIS

We studied the effect of 9 parameters upon 4 output variables: annual evaporation, annual transpiration of grasses, annual transpiration of shrubs, and deep percolation. We performed a factorial analysis to evaluate the effect of a set of parameters and their interactions. We devised a Fractional Factorial Design (Box et al. 1978) to reduce the number of model runs. This method reduced the number of runs in such a way that we were able to estimate the main effects and two-factor interactions, discarding high-level factor interactions. This kind of analysis has been used successfully in sensitivity analyses of complex models (Coffin and Lauenroth 1990) and it has proved to be better than other alternatives (Rose 1983).

We studied the sensitivity of DINAQUA to the following parameters: maximum transpiration rate of grasses and shrubs (TPOTtest), effective available water value below which transpiration declined for grasses and shrubs (LIMAW), the soil hydraulic conductivity at −0.01 MPa (K), the relative sunshine (SUN), the day of the year when the growing season started and ended (DBEG and DEND), and the day of the year when biomass peaked (DMAX). We used a fractional factorial design with two levels of the factors. Levels used corresponded to variations of ±30% of parameter values (Fig. 2).

In order to calculate the main effect of each one of the nine parameters, we multiplied the values of each output variable by the level of each parameter (+1 or −1) and added them up for the total of 16 runs. The main effect values were normalized by dividing the original sums by the mean of the corresponding variable, which allowed for comparisons among variables. We plotted the magnitude and direction (+ or −) of the main effect of each of the 9 parameters studied, on the 4 output variables (Fig. 2).

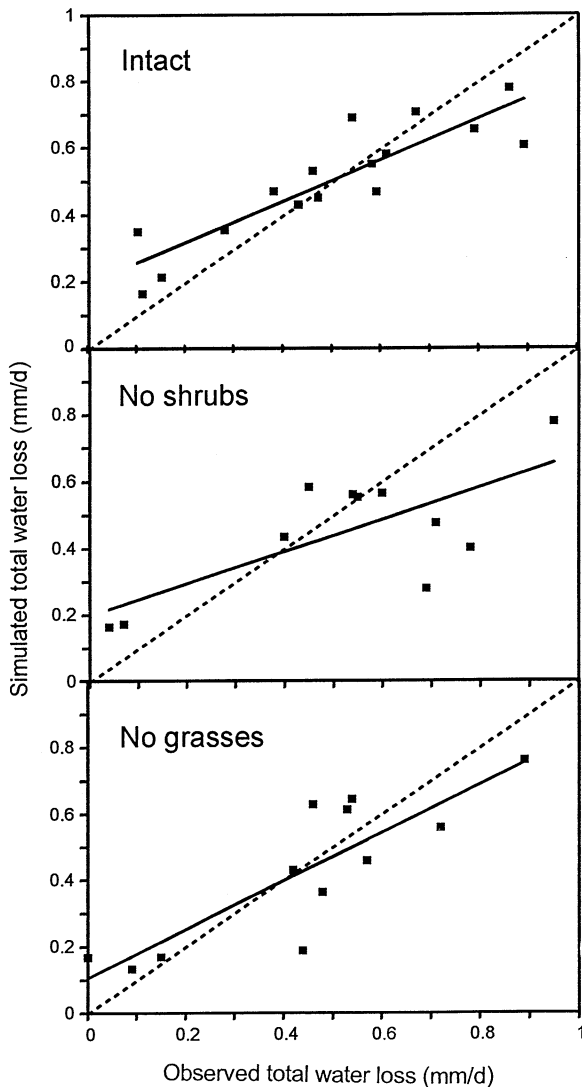The parameters related to plant characteristics: max-

FIG. 1. Observed vs. simulated total water loss for the control vegetation structure and for conditions where grasses or shrubs were experimentally removed in a Patagonian steppe. ——— the best fit regression line, and – – – the 1:1 relationship. Linear equations fitted were $y = 0.19\cdot0.62x$ ($n = 16, r = 0.88, P < 0.01$), $y = 0.10\cdot0.73x$ ($n = 11, r = 0.84, P < 0.01$), and $y = 0.19\cdot0.48x$ ($n = 11, r = 0.71, P < 0.01$) for intact, no-grasses, and no-shrubs structures respectively, where y corresponds to simulated losses and x to observed losses. The F test for $H_0 = y$-intercept $= 0$ and slope $= 1$ was nonsignificant ($P < 0.05$) for each of the three data sets.

imum potential transpiration (TPOTtest), the available water below which actual transpiration decreased (LIMAW), and the dates that define the growing season (DMAX, DEND, DBEG) did not affect evaporation losses markedly (Fig. 2). Only the value of relative sunshine determined a modification in the annual loss by evaporation. The parameters related to transpiration (TPOTtest and LIMAW) had the largest effect on the magnitude of annual transpiration. These parameters affected not only the losses of their own plant func-

tional type but also of the other one. Shrub transpiration suffered an important reduction when TPOTtest and/ or LIMAW of grasses increased (became more meso-phytic). The effect of TPOTtest and LIMAW of shrubs on grasses was less important. Grass transpiration was slightly affected by parameters related to the definition of the growing season. Shrub transpiration was sensitive to the time of maximum biomass (DMAX). The value of relative sunshine (SUN) affected the transpiration of both grasses and shrubs by reducing potential transpiration.

The parameter that modified deep percolation the most was relative sunshine, mainly by reducing transpiration losses. A high maximum rate of transpiration of grasses also reduced drainage losses. Two-way interactions did not show important features and we did not present these results.

We also analyzed the sensitivity of the four output variables (annual evaporation, annual transpiration of grasses, annual transpiration of shrubs, and deep percolation) to a change in root distribution. An even distribution of roots throughout the soil profile for both functional groups decreased deep percolation (38%) and shrub transpiration (24%), and increased grass transpiration (20%) and evaporation (9%), with respect to simulations based on the actual root profile.

RESULTS

The largest water losses in the Patagonian steppe during the 19-yr simulated period, occurred via evaporation (56%) (Fig. 3). Transpiration accounted for 34%, and deep percolation the remaining 10% of total water loss. Grasses accounted for 75% of transpiration losses.

Potential evapotranspiration had a clear seasonality, driven by the temperature pattern (Fig. 4). On the contrary, soil evaporation had a pattern (Fig. 3) related to the seasonality of the precipitation (Fig. 4). During the winter months, much of the water lost from the system followed the evaporation path. In contrast, during spring and summer <20% of water was lost by evaporation. Fluctuations superimposed on the general trend of evaporation losses were related to the episodic nature of evaporation pulses, which closely followed rainfall events (Fig. 3).

The seasonal course of transpiration had the opposite pattern of evaporation (Fig. 3). Transpiration had a maximum that occurred during early summer and a minimum that occurred during winter. The seasonal course of this flow was less variable than evaporation, because it was related to a bigger reservoir than evaporation. Evaporation occurs only from the uppermost soil horizon whereas the water lost via transpiration is absorbed from the entire soil profile. Deep percolation was constrained to winter and spring months, when most of the rainfall occurred and the profile was wet (Fig. 3). Drainage events occurred in 73% of the years
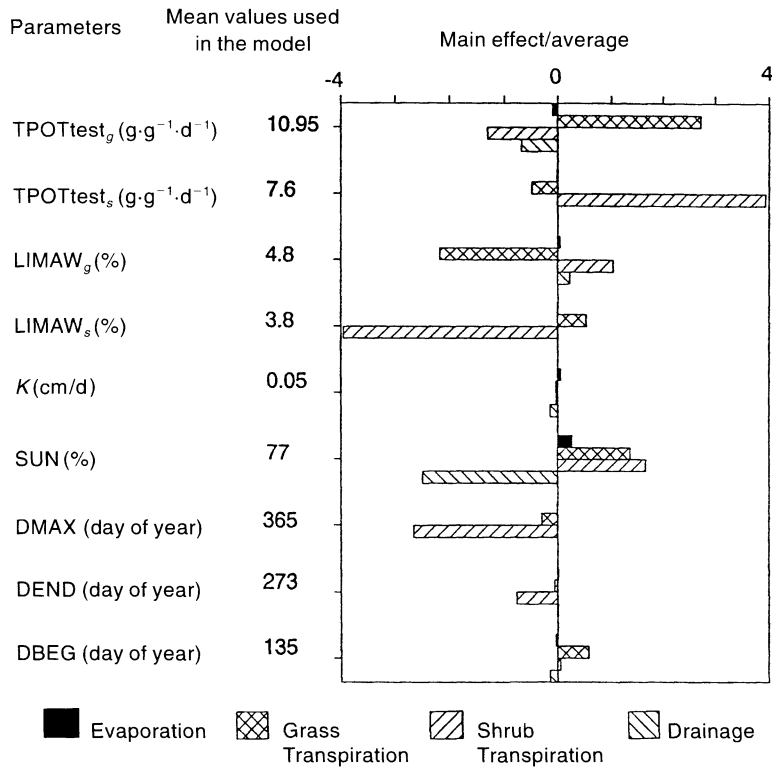
FIG. 2. Sensitivity analysis of DINAQUA. The relative effect of increasing or decreasing by 30% the value of each parameter used in the model, upon evaporation, transpiration of grasses, transpiration of shrubs, and drainage. Subscripts g and s mean grasses and shrubs, respectively. The meanings of acronyms are given in Table 1. The main effect of each parameter was calculated as the sum of the products of the output variables of each run, multiplied by the level of each factor (1 or -1). Main effects were normalized by dividing by the corresponding mean to allow comparisons among variables. We did not assign probabilities to the effects because these experiments did not satisfy the assumptions of the ANOVA (Rose 1983).

and they accounted for ≤20% of the total precipitation or ≤42% of winter precipitation.

The relationship between annual soil evaporation and annual rainfall had a slightly curvilinear shape ($r^2 = 0.71$, $P < 0.01$) (Fig. 5). During wet years a smaller proportion of total water loss occurred via evaporation than in dry years. During years with precipitation below average, evaporation accounted for 64% of total losses, whereas during above-average years evaporation accounted for only 53%. In contrast, drainage losses increased exponentially with fall-winter precipitation ($r^2 = 0.59$, $P < 0.01$) (Fig. 6).

Variability in total transpiration was accounted for almost completely by fall plus winter (FWPP) and spring plus summer (SSPP) precipitation ($r^2 = 0.92$, $P < 0.01$; Fig. 7A). Transpiration showed a curvilinear relationship with fall-winter precipitation and a linear relationship with spring-summer precipitation. Using single-variable models it could be seen that fall plus winter precipitation accounted for a higher portion of the total transpiration variance than spring plus summer precipitation ($r^2 = 0.62$ and $r^2 = 0.45$ respectively, $P < 0.01$).
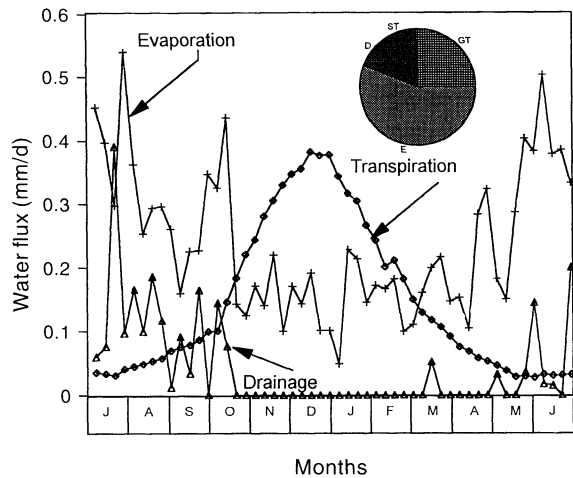

FIG. 3. Annual course of evaporation, transpiration, and drainage in a Patagonian steppe site. Each point corresponds to the weekly average of 19 yr. The pie chart indicates the relative losses on a yearly basis (E: evaporation, GT: grass transpiration, ST: shrub transpiration, and D: drainage).
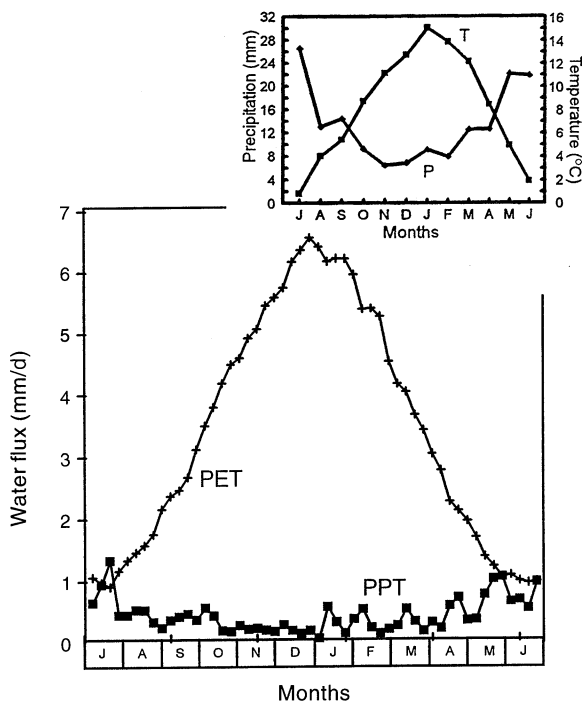
FIG. 4. Annual course of weekly potential evapotranspiration (PET) and precipitation (PPT) at a Patagonian steppe site. Each data point is the average of 19 yr. The inset figure shows the average monthly course of temperature (T) and precipitation (P).

FIG. 5. Relationship between annual precipitation and annual soil evaporation as estimated by DINAQUA for a 19-yr period.

Models similar to these used for total transpiration data were fitted to grass and shrub transpiration (Fig. 7B, C; $r^2 = 0.93$ and $r^2 = 0.85$, $P < 0.01$, for grasses and shrubs respectively). The portion of the variability accounted for by fall-winter and spring-summer precipitation in one variable models, differed between functional types. For grass transpiration, 58% ($P < 0.01$) of the variance was accounted for by spring-summer precipitation, while fall and winter precipitation explained 48% ($P < 0.01$). For shrubs 80% ($P < 0.01$) of transpiration variability was accounted for by fall and winter precipitation while spring and summer precipitation accounted for 13% (NS). Grasses absorb water mainly from the upper layers of the soil (Sala et al. 1989) and therefore are able to use summer rains, which wet only these layers. On the contrary, shrubs absorb water mainly from the deepest layers of the soil, and they are not very efficient in using summer rainfalls.

The deepest layer of the profile was the wettest and the uppermost the driest (Fig. 8). On an annual basis the probability of being wet (water potential higher than −1 MPa) was, on average, 0.25 for the upper layer and higher than 0.67 for the remaining layers (Fig. 8). The deepest layer was the most variable on an annual basis (Fig. 8).

During late winter and early spring, intermediate layers (10–20 and 20–40 cm) had the highest probability of being wet (Fig. 9). For the deepest layer, the
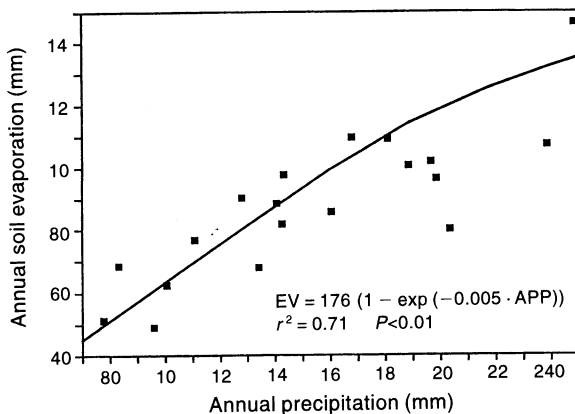
probability of water potential higher than −1 MPa was also high, but did not reach 1. For the upper layer, the probability of water potentials higher than −1 MPa was, for any week, lower than 0.6. At the beginning of the warm season wettest layers were located at intermediate depths (10–20 and 20–40 cm), and moved downward so at the end of the season, only the deepest layer had high soil water potentials (Fig. 9). During late summer and early fall only the deepest layer of the profile had a high probability of being wet (Fig. 9).

DISCUSSION

In the Patagonian steppe most of the water was stored deep in the profile. Water availability was low and variable in the upper layer, mainly during the warm months. On an annual basis, deepest layers showed the highest probability of being wet (Fig. 8). At a finer temporal scale, we observed that the probability of water potentials higher than −1 MPa during winter months was
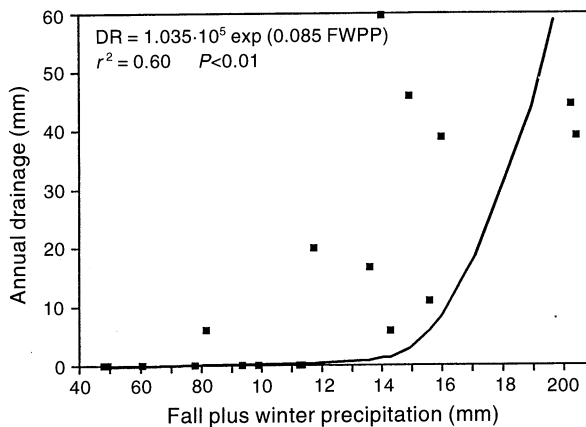

FIG. 6. Relationship between annual drainage and fall plus winter precipitation, as estimated by DINAQUA for a 19-yr period.
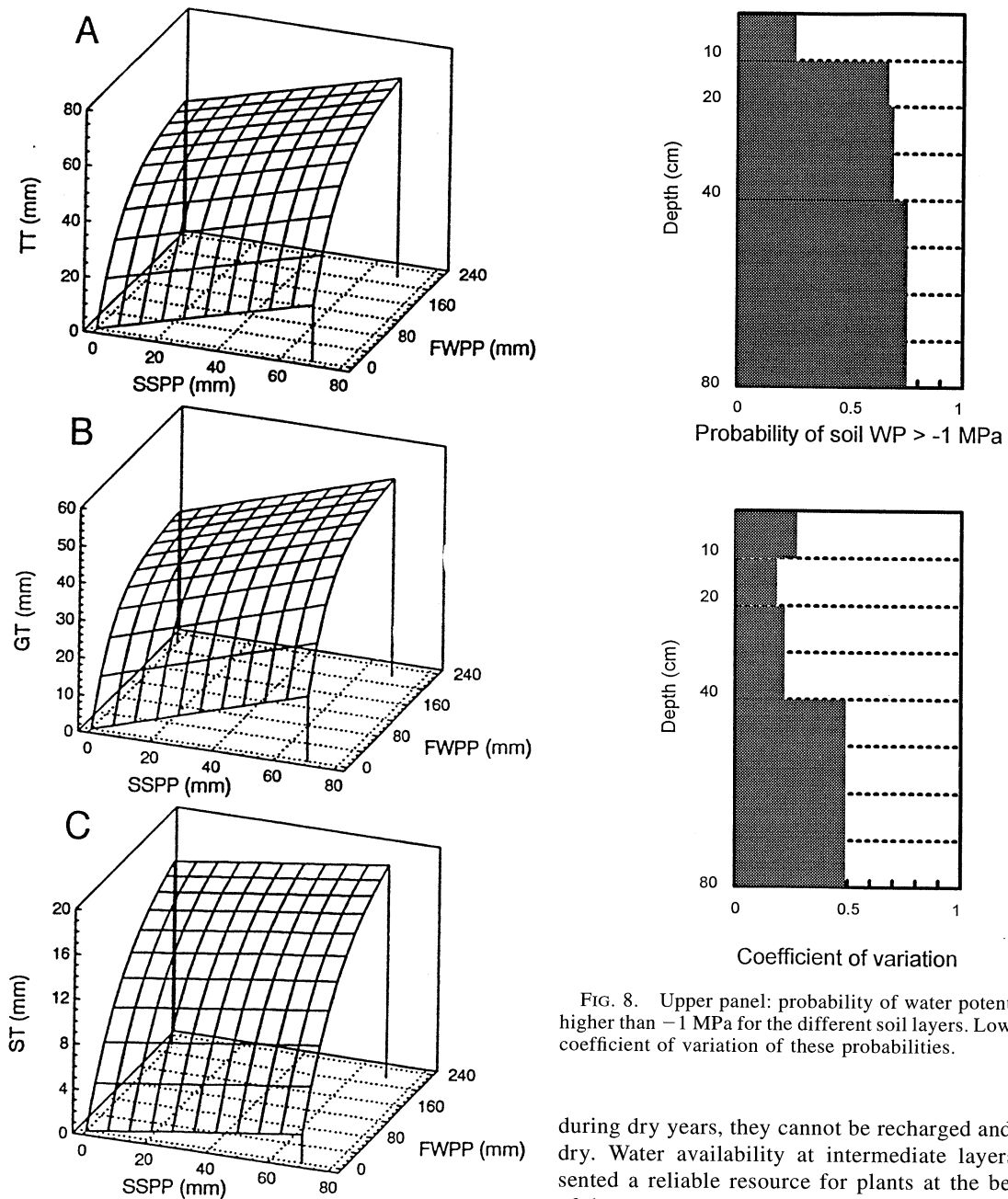
FIG. 7. (A) Relationship between fall plus winter (FWPP) and spring plus summer (SSPP) precipitation and total annual transpiration (TT) as estimated by DINAQUA for a 19-yr period {TT = 0.28·SSPP + 53.07·[1 − exp(−0.015·FWPP)], $r^2 = 0.92$, $P < 0.01$}. (B) Same for grasses {GT = 0.25·SSPP + 35.86·[1 − exp(−0.018·FWPP)], $r^2 = 0.92$, $P < 0.01$}. C) Same for shrubs {ST = 0.04·SSPP + 18.65·[1 − exp·(−0.009·FWPP)], $r^2 = 0.86$, $P < 0.01$}.

FIG. 8. Upper panel: probability of water potential (WP) higher than −1 MPa for the different soil layers. Lower panel: coefficient of variation of these probabilities.

higher at intermediate layers than at the deepest layer (Fig. 9). During dry winters, water reaches intermediate layers but not deeper ones. During average and wet years, deepest layers remain wet for long periods but during dry years, they cannot be recharged and remain dry. Water availability at intermediate layers represented a reliable resource for plants at the beginning of the warm season (spring and summer) (Fig. 8). The upper soil layer remained wet, on average, only during 10% of the days during the warm season. The moisture in upper layers also varied greatly among years (Fig. 8). This could be related to the low residence time of water in the soil during summer, and also to the high variability in the occurrence of summer precipitation events, which wet almost only the upper layer. Fall plus winter precipitation had a coefficient of variation of 45%, whereas spring and summer rainfall had a coefficient of variation of 64%. Only grasses seem to be able to use this short-lived resource (Sala et al. 1989). The pattern of water availability throughout the soil profile simulated by DINAQUA (Fig. 9) closely

matched the observed seasonal trends of water potential for different depths (Sala et al. 1989).

The distribution of water in the profile in the Patagonian steppe contrasts with that of a system with summer precipitation like the shortgrass steppe in North America (Sala et al. 1992). In the shortgrass steppe, the relative frequency of wet days was high in upper layers whereas in the Patagonian steppe it was high in lower layers. Differences in the distribution of water in the soil profile between the shortgrass steppe and the Patagonian steppe could explain the differences in functional type composition between these ecosystems. In the shortgrass, where water is located mainly in upper layers, grasses are the dominant functional type. In the Patagonian steppe, where a high proportion of water is stored in deep layers of the soil, deep-rooted shrubs are a quantitatively very important functional type. They account for 43% of primary production and 33% of basal cover.

Deep percolation is a frequent phenomenon in the Patagonian steppe and accounts for 10% of the total water loss. A high frequency of wet-soil days in upper layers during winter months is the result of the high concentration of precipitation, and the low potential evapotranspiration during this period. The depth of penetration of a precipitation event is a function of its size and of the water content of the soil (Hanks and Ashcroft 1980). Consequently, the wetting depth of a similar precipitation event is deeper, on average, during the cold season than during warm season. This and the tendency of precipitation events to be temporally clustered (Noy Meir 1973) may determine the high probability of occurrence of deep percolation events in the Patagonian steppe. For our study site, clusters of two or more sequential precipitation events accounted for 43% of the events and 46% of total annual precipitation.

A reduction in leaf area or temperature may result in an increase in deep percolation. Sensitivity analysis showed that the modification of parameters related to transpiration or potential evapotranspiration have a large effect on deep percolation. A change in transpiration or potential evapotranspiration modifies drainage losses through its effect on the soil water content at the beginning of fall. Simulated deep percolation losses decreased exponentially with an increase in biomass (Paruelo 1991). A 50% increase in biomass with respect to the average reduced drainage by 10%, whereas a 50% reduction in biomass increased deep percolation by 73%. It is important to highlight that the model predicts drainage to occur even for very large values of biomass (Paruelo 1991).

Drainage losses are generally negligible in arid and semiarid environments. For the shortgrass steppe, a system with predominantly summer rainfall, Sala et al. (1992) reported no drainage losses during a simulated 30-yr period. Deep percolation losses were negligible in the African system studied by Floret et al. (1982).
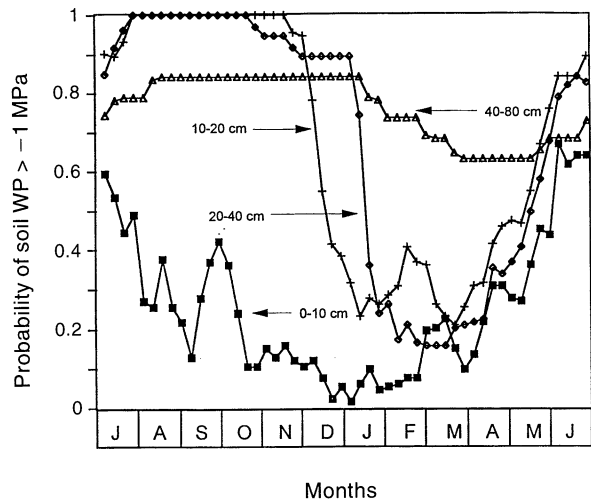

FIG. 9. Annual course of the probability of soil water potential being higher than −1 MPa in the upper four layers of the soil at a Patagonian steppe site. Each point corresponds to the average of the weekly frequency over a 19-yr period.

Ng and Miller (1980) observed for the Californian chaparral, which is a region with a rainfall distribution similar to that of the Patagonian steppe, drainage losses ranging between 4% and 15% for northern (with high plant cover) and southern (with low plant cover) slopes, respectively.

The precipitation/potential evapotranspiration ratio, on an annual basis, ranged between 0.06 and 0.20. An analysis of this relationship at a weekly scale showed that, on average, 10% of the weeks in a year had a PPT/PET > 0.8 and for 6% of the weeks this ratio was equal to 1. This would indicate the existence of an important period of the year for which water was not the limiting factor. Comparisons, on a annual basis, of water demand and water input are insufficient to characterize water availability in arid and semiarid environments. The evaluation of the extent to which water demand is matched by precipitation must take into account redistribution, storage, and losses. This assessment is largely dependent on the temporal scale (Sala et al. 1992).

The occurrence of higher precipitation during winter determined that the evaporation and transpiration flows were not in synchrony (Fig. 3). Evaporation was high during the coldest months, when the potential evapotranspiration was low. The asynchrony of transpiration and soil evaporation determines that, for the Patagonian steppe, the magnitude of evaporation is relatively independent of changes in vegetation characteristics. Sensitivity analysis (Fig. 2) showed that none of the parameters related to vegetation had a significant effect upon evaporation losses.

Annual average transpiration in the Patagonian steppe (34%) is close to the lowest limits referred in the literature for arid and semiarid ecosystems. Floret

et al. (1982), for a Tunisian mediterranean grassland (with a rainfall of 170 mm), reported transpiration losses between 31 and 60%. Ng and Miller (1980) found for the Californian chaparral that transpiration accounted for 8% of losses in southern slopes and 59% in northern ones. De Jong and Hayhoe (1984), for Canadian grasslands, found that transpiration was 67% of evapotranspiration losses. Simulated annual transpiration in Idaho (USA) ranged from 32 to 52% of the evapotranspiration (Wight et al. 1986). In a long term analysis of water dynamics in the shortgrass steppe, Sala et al. (1992) found that transpiration accounted for 64% of the precipitation. Differences in the relative magnitude of transpiration losses between Patagonia and the shortgrass steppe may be related to the differences in the seasonal precipitation patterns. In the shortgrass steppe, the growing season coincides with the wet season. In the Patagonian steppe, the growing season and the wet season occur during different parts of the year.

In that steppe, transpiration occurred mainly during a short period when temperature was favorable and the probability of high water availability in the upper layers was still great (end of spring and beginning of summer) (Fig. 3). Total transpiration losses were related, mainly, to the water accumulated in the profile during the winter. When fall and winter precipitation exceeded the water-holding capacity of the profile the surplus water drained and could not be transferred to the warm season. This determines the curvilinear response of transpiration to fall and winter precipitation. In contrast, transpiration showed a linear response to spring and summer precipitation. The system always responded to higher summer precipitation with higher transpiration, and this response never saturated for the range of conditions explored during this 19-yr simulated period. Grasses showed a higher response to summer rainfall than shrubs. This may be related to the distribution of roots, which is shallower for grasses than for shrubs. Evaporation showed a curvilinear response to precipitation because during wet years a high proportion of the precipitation penetrates deep into the profile where water cannot be evaporated (Fig. 5).

Plant functional types differed in their responses to fall-winter and spring-summer precipitation. Both functional types used the fall and winter precipitation stored at intermediate layers in the soil profile. This resource was the least variable, was the most reliable, and had the longest residence time. Spring and summer precipitation was used almost exclusively by grasses. This resource had a shorter residence time and was more variable than fall-winter precipitation. The partitioning of water between shrubs and grasses simulated by DINAQUA was similar to the partitioning resulting from a manipulative experiment performed in the same ecosystem (Sala et al. 1989). Grasses used mostly water from upper layers whereas shrubs absorbed exclusively from the deepest layers of the soil profile.

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