

Ecohydrological effects of grazing-induced degradation in the Patagonian Monte, Argentina

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Abstract Water-limited ecosystems have undergone rapid change as a consequence of changing land use and climate. The consequences of these changes on soil quality and vegetation dynamics have been documented in different regions of the world. In contrast, their effects on soil water, the most limiting resource in these environments, have received less attention, although in recent years increasing efforts have been made to relate grazing, soil water and vegetation functioning. In this paper, we present the results of field observations of plant phenology and soil water content carried out during two successive years at four sites along a degradation gradient caused by grazing in the Patagonian Monte, Argentina. We also developed a simplified soil water balance model to evaluate how changes in plant cover could affect water balance. Our field observations showed that the soil water content in the soil layer where roots of grasses are abundant (0–25 cm) was higher and the growing cycles were longer in degraded than in preserved sites. Similarly, our modelling approach showed that the deep soil (depth > 10 cm) was wetter in the degraded than in the preserved situation. Simulation also suggested a switch from transpiration to a direct evaporation dominance of water losses with degradation. Although reductions in plant cover related to grazing degradation were associated with a decrease in annual transpiration, the simulated soil water loss by transpiration was higher during summer in the degraded than in the well preserved situation. Thus, our field observations seem to be a consequence of ecohydrological changes causing an accumulation of water in the soil profile during the cold season and its transpiration during summer. In conclusion, our results showed that changes in plant cover caused by grazing disturbance can alter the soil water balance, which in turn can affect vegetation function.

Key words: desertification, Monte Desert, Patagonia, plant cover, soil water balance.

INTRODUCTION

Water-limited ecosystems occupy about half of the Earth's land surface (Newman *et al.* 2006). The main human use of these ecosystems is as rangelands, which have undergone rapid change as consequence of changing land use and climate (Wilcox & Thurow 2006). These changes (desertification, groundwater depletion, salinization, soil erosion and woody plant encroachment) have received increasing attention because of their detrimental effects on the ability of the ecosystem to provide goods and services (Van Jaarsveld *et al.* 2005). As a consequence, the effects of these processes on the soil nutrients and on vegetation have been documented in many different regions of the

globe (Milchunas & Lauenroth 1993; Schlesinger *et al.* 1996; Adler *et al.* 2001). In contrast, the consequences of these processes on soil water, perhaps the most limiting resource in those environments, have received less attention, although in recent years increasing efforts have been made to relate grazing, soil water and vegetation functioning (e.g. O'Connor *et al.* 2001; Snyman 2005; Swemmer *et al.* 2007).

As a consequence of these efforts, in recent years a new discipline called ecohydrology has received increasing interest by ecologists (Breshears 2005). According to Rodriguez-Iturbe (2000), ecohydrology may be defined as 'the science that seeks to explain the hydrologic mechanisms that underlie ecological patterns and processes'. Although during the last years some efforts have been made to evaluate the ecohydrological implications of arid land degradation (e.g. Huxman *et al.* 2005), many authors argued that we are far from a complete understanding of the issue (e.g. Huber-Sannwald *et al.* 2006) and identified the pursuit of ecohydrological feedbacks in rangeland

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degradation processes as one of the emerging issues in rangeland ecohydrology (Wilcox & Thurrow 2006).

The studies relating grazing induced degradation of rangelands and soil water have shown the influence of grazing on the water balance and have highlighted its effect on ecosystem functioning (Naeth *et al.* 1991; Naeth & Chanasyk 1995; Aguiar *et al.* 1996; Snyman 2000). Grazing can indirectly affect water balance through changes in vegetation structure (i.e. basal cover and botanical composition) and/or top soil attributes. For example, Whitford *et al.* (1997) documented the interception of rainfall by the canopies of encroached shrubs and its redistribution, via stemflow, to deep soil layers along root channels. Similarly, Aguiar *et al.* (1996) showed that shrub invasions triggered by grazing increased evaporation and deep percolation and reduced transpiration. Likewise, Snyman (1998) found that the contribution of evaporation to water losses increases with degradation. Another common effect of land use for animal production is trampling, which causes soil compaction, reducing infiltration and favouring run-off (Pietola *et al.* 2004). Finally, overgrazing changes surface albedo affecting the energy balance and, consequently, the water balance (Nicholson *et al.* 1998).

The study of soil water dynamics presents several methodological difficulties that, in the case of water-limited ecosystems, are magnified by the existence of precipitation events, which are spatially and temporarily unpredictable (Loik *et al.* 2004). In addition, the effect of any precipitation event does not only depend on its inherent characteristics, such as size and duration, because both antecedent and consequent conditions have strong influences on the resulting behaviour of the soil–plant–atmosphere system (D’Odorico & Porporato 2006; Fernández 2007). For that reason, any systematic sampling protocol of soil water content gives limited information on the frequently complex interactions among soil, plant and atmospheric factors of the water balance, particularly for longer time periods (Reynolds *et al.* 2000). One alternative approach is the development and employment of soil water balance models, which allows long-term continuous simulation of soil water and the evaluation of the effect of contrasting conditions. In that sense, some soil water balance models were recently developed (e.g. Paruelo & Sala 1995; Flerchinger & Pierson 1997; Rodríguez-Iturbe *et al.* 1999; Reynolds *et al.* 2000) and employed to evaluate how atmospheric, plant and soil factors interact to control water losses (Kemp *et al.* 1997; Lauenroth & Bradford 2006).

In arid ecosystems, plant phenology is coupled to water availability (Reynolds *et al.* 1999) and strongly affected by differences in annual precipitation (Ghazanfar 1997) and/or topography that cause microhabitat differences in water availability (Olivares & Squeo 1999). Although phenology and water availability are

linked, this relationship is intricate and changes in rainfall and water availability can cause complex phenological changes (Peñuelas *et al.* 2004). For example, the occurrence (Olivares & Squeo 1999), onset (Ghazanfar 1997; Myers *et al.* 1998) and duration (Olivares & Squeo 1999) of phenological phases are affected by changes in total water availability and/or in their distribution along the year. Thus, beyond direct effects of grazing on plant phenology (mediated by the removal of tissues), grazing could also have indirect effects on plant phenology as consequence of changes in the availability of soil water.

The evidence reviewed above shows that grazing can potentially affect soil water balance through its effects on vegetation and soil, and suggests that the resulting changes in water availability could affect the phenology of plant species. Consequently, our aim was to assess the alterations in the soil water balance caused by changes in plant cover induced by grazing and their consequences for vegetation function in the Patagonian Monte. In this paper, we present the results of field observations of plant phenology and soil water content carried out during two successive years at four sites along a degradation gradient caused by grazing. We also developed a simplified soil water balance model to evaluate how changes in plant cover could affect the different components of the water balance.

METHODS

Study area

The study area is representative of the Patagonian Monte (León *et al.* 1998) located in north-eastern Chubut Province, Argentina (42°39’S, 65°23’W, 115 m a.s.l.). Mean annual temperature is 13.4°C and the average precipitation is 235.9 mm with high mean interannual variation and even seasonal distribution across the year (Anon 2007). A seasonal pattern of wet (winter) and dry (summer) periods in superficial soil was observed (Coronato & Bertiller 1997). Soils are a complex of Typic Petrocalcids–Typic Haplocalcids (Soil Survey Staff 1999). Soil mounds associated with shrub patches present higher sand, organic matter and total nitrogen contents than bare soil areas (Rostagno & Del Valle 1988; Bertiller *et al.* 2004). Organic matter and nitrogen are accumulated in top soil (0–30 cm in depth), whereas deep soil layers present low concentration of these variables (Rostagno *et al.* 1991).

Vegetation is representative of the shrubland of *Larrea divaricata* Cav. and *Stipa* spp., which cover 42 000 km² of the Patagonian Monte phytogeographical District. This vegetation displays patches of varying size and species richness surrounded by bare soil areas (Bisigato & Bertiller 1997). Grazing strongly affects

the structure of Patagonian Monte ecosystems in a way consistent with the changes commonly attributed to desertification (Bertiller & Bisigato 1998; Bertiller *et al.* 2004). Plant cover, mainly that of grasses, is strongly reduced (Bisigato & Bertiller 1997) and wind erosion is triggered as a consequence of the increase in the size of bare soil areas (Ares *et al.* 2003). However, the physiognomy of Patagonian Monte communities is not changed, because both degraded and well preserved areas are dominated by the same unpalatable species.

Evergreen shrubs dominate this community, showing vegetative activity throughout the whole year (Bertiller *et al.* 1991). Less abundant grasses and deciduous shrubs (Bisigato & Bertiller 1997) show an opportunistic behaviour according to precipitation inputs (Bertiller *et al.* 1991). As consequence of the dominance of evergreen shrubs and the even distribution of precipitation throughout the year, the Patagonian Monte shows the least seasonal pattern of primary production among Patagonian ecosystems, as inferred from satellite NDVI data (Paruelo *et al.* 1998).

In a previous work, Bisigato *et al.* (2005) reported the changes in the spatial pattern of plant patches along grazing gradients in the Patagonian Monte. The scale of heterogeneity increases when the grazing pressure rises as a consequence of a bigger size of both shrub and bare-soil patches. As previously stated, a reduction in plant cover is associated with this increase in the scale of heterogeneity, which in turns leads to lower intensity (i.e. regularity) of plant spatial patterns. Based on these patterns, the scale of heterogeneity of plant patches has been proposed as an index of degradation in the region (Bisigato *et al.* 2005).

Field sampling

Sampling was performed in four sites of about 1 Ha. Plant cover (visually estimated using cover categories with increments of 1%) varied between 15% and 40%, and grain (i.e. scale of heterogeneity, obtained from the analysis of high resolution aerial photographs) between 2.64 m and 4.19 m (Bisigato *et al.* 2005). According to Dale (1999), the grain is equivalent to the average distance between shrub patch and contiguous inter-patch area centres. The reduction in plant cover was mainly due to the almost complete removal of grasses and a concomitant reduction in shrub cover. Hereafter the sites will be called WP: well preserved (grain 2.64 m), LD: low degraded (grain 2.98 m), ID: intermediate degraded (grain 3.72 m) and HD: high degraded (grain 4.19 m). A detailed description of the sites and the method employed to measure the grain can be found in Bisigato *et al.* (2005).

Table 1. Phases describing phenological development (phenophases), based on Bertiller *et al.* (1991)

| Phenophases | Description |
|---------------------|---|
| Vegetative growth | |
| 1 | Early vegetative growth: shoots or tillers with leaves not expanded. |
| 2 | Intermediate vegetative growth: shoots or tillers with green leaves both expanded and not expanded. |
| 3 | Late vegetative growth: internode elongation in tillers. Pre-bud phase. |
| Reproductive growth | |
| 4 | Ear emergence: ear pre-formed but not visible. |
| 5 | Ears visible. Flowers. |
| Fruiting | |
| 6 | Green fruits. |
| 7 | Mature fruits and seed dispersal. |
| Dormancy | |
| 8 | Dormancy. Total vegetative inactivity, no green tissues present. |

Every 15/30 days during 2 years (2003–2004), a soil sample (4.5 cm in diameter, 25 cm in depth) was taken with a metallic tube immediately close to the basis of 30 bunches of *Stipa tenuis* (Poaceae) in each site, and their soil water content was gravimetrically evaluated. During the sampling, special care was put to avoid sampling previously sampled individuals. Coincidentally, the phenophase (Table 1) of thirty individuals of *S. tenuis* was registered. Each year, phenological observations were carried out in 30 different individuals, randomly selected and protected against grazing by individual exclosures.

Data analysis

The significance of the differences in soil water content among areas throughout the sampling period was evaluated by one-way ANOVA. To highlight differences between areas (independent from the seasonal variation), the relative soil water content at each area was computed by deducting the overall average of soil water content of each sampling date from the respective soil water content value. Similarly, the significance of the differences in soil water content among areas in each sampling date was assessed by one-way ANOVA. A sigmoid curve was applied to phenological data of each plant.

$$PP = 8 / (1 + (e^{-(t-a)/b}))$$

where PP = Phenophase, t = julian day, a = inflection point (date when the highest slope is reached), b = parameter related to the curvature of the curve.

Each year, the significance of the differences in a and b parameters among sites was inspected by one-way ANOVA. The level of significance throughout this study was $\alpha = 0.05$.

Model description

A simple one-dimensional soil water balance model was developed for Patagonian Monte soils with the objective of evaluating the effects of plant cover changes on the soil water balance. Model inputs consist of soil parameters, plant variables and daily weather inputs. The soil inputs to the model, which were taken from the literature relative to the study area, include soil layer thickness, texture, volumetric gravel content and bulk density for each layer (taken from Rostagno & Del Valle 1988; and Rostagno *et al.* 1991). Plant variables are total plant cover (taken from Bisigato *et al.* 2005) and the proportion of roots in each layer (taken from Rodríguez *et al.* 2007a). The weather inputs are daily values of mean air temperature, radiation and precipitation, which were measured with an automatic data-logger (21X Micrologger, Campbell Scientific). Model output includes daily estimations of soil moisture in each layer, evaporation, transpiration and deep drainage. The model is available on internet at <http://www.cenpat.edu.ar/wbm/>

Structure and general assumptions

The water storage (expressed as water depth in units of millimetres, W_l) is modelled in four soil layers (l) (0–10, 10–20, 20–40, 40–100 cm). The model, which represents soil water at scales where rainfall and land cover are relatively uniform, calculates the amount of water evaporated from the soil, transpired by the canopy and lost by deep drainage on a daily basis. Losses by evaporation are only computed from the upper layer (0–10 cm), as direct water losses from sandy soils, such as those of the Patagonian Monte, hardly ever occur from deeper layers (Paruelo *et al.* 1991). Water lost by transpiration was a function of the potential evapotranspiration and the effective available water, which is the sum of the available water of each soil layer weighted by the root proportion in each soil layer. Soil water is refilled through precipitation in a cascading way. If water content in one layer exceeds field capacity, the excess is transferred to the next lower layer. Flow from the last soil layer downward corresponds to deep drainage. Only saturated fluxes are considered. As Patagonian Monte ecosystems are characterized by flat landscapes (León *et al.* 1998) and soils are coarse textured (Rostagno *et al.* 1991), we do not take in account surface run-off. As several soil water balance models developed in dry land ecosys-

tems (e.g. Paruelo & Sala 1995; Kemp *et al.* 1997), we did not include plant interception because low plant cover (Bisigato *et al.* 2005) and low leaf area index (LAI) values of Patagonian Monte species (Campanella & Bertiller 2008). Upward movement in the soil matrix is not considered, because it is not important in sandy soils (Gaiser *et al.* 2004). In its current version, the model does not incorporate horizontal heterogeneity in plant and/or soil attributes, which represent mean community values.

Estimation of soil parameters

Saturated (θ_s) and residual (θ_r) volumetric water contents were calculated for each layer using pedotransference functions (Schaap *et al.* 2001). These functions estimate Van Genuchten (1980) water retention parameters based on Mualem's (1976) pore-size model. We used the third model of Schaap *et al.* (2001), which includes commonly measured soil attributes: bulk density and sand, silt, and clay contents. Volumetric water content in each layer (θ) was transformed in water storage (W_l) (mm) through:

$$W_l = \theta_l z_l (1 - g_{c_l})$$

where z_l = thickness of layer l (mm), g_{c_l} = volumetric gravel content of layer l .

Evapotranspiration

Potential evapotranspiration PET (mm) was calculated using the Hargreaves and Samani (1985) equation.

$$PET = 0.0023 \frac{R_s}{\lambda} (T + 17.8) \sqrt{TR}$$

where R_s = solar radiation ($\text{MJ m}^{-2} \text{d}^{-1}$), λ = latent heat of vaporization (2.45 MJ kg^{-1}), T = mean temperature ($^{\circ}\text{C}$), TR = temperature range.

Soil evaporation was estimated following Allen *et al.* (2005). This approach considered two stages. During the first stage, soil evaporation is a function of the energy reaching the soil and equals potential evapotranspiration. During the second stage, called 'soil limited' stage, soil dryness reduces soil evaporation. The reduction in evaporation during the second stage is expressed as a simple linear function of the total water that has evaporated from the surface soil layer. Soil evaporation is proportional to $1 - PC$, where PC is Plant Cover expressed as proportion.

Transpiration is a function of potential evapotranspiration and water availability. We assigned a proportion of potential evapotranspiration to each layer according to the proportion of fine roots found in that layer (Rodríguez *et al.* 2007a). If the water required to match potential evapotranspiration in one layer is

Table 2. Mean (\pm SE) relative soil water content in each study area

| | Site | | | |
|----------------------------------|-------------------------------|-------------------------------|-------------------------------|------------------------------|
| | Well preserved | Low degradation | Intermediate degradation | High degradation |
| Relative soil water content (mm) | -0.31 \pm 0.11 ^a | -0.08 \pm 0.13 ^a | -0.38 \pm 0.22 ^a | 0.77 \pm 0.22 ^b |

Different superscript letters indicate significant differences among sites evaluated by one-way ANOVA ($P < 0.05$).

greater than the available water in that layer, only the available water is subtracted from this layer. Transpiration is proportional to PC.

Model validation

The model was validated by comparing model estimations for two strata: 0–20 and 20–40 cm with field observations reported by Mazzarino *et al.* (1998) and Bisigato (2000) in an area with a plant cover of 27%. To compare these observations with model predictions, the modelled water depth in the 0-to-10 and 10-to-20-cm layers were added. The agreement between predicted and observed values was inspected by linear regression, evaluating if the slope of the curve was statistically different from 1 and its intersection with the y-axis statistically different from 0.

Effects of changes in plant cover on soil water content

We ran the model with two levels of plant cover, corresponding to preserved (40%) and degraded areas (15%) (Bisigato *et al.* 2005). Model runs involved the period 1994–2001, the longest period with daily climatic data in the study area, including years varying in precipitation from 87 to 410 mm (37% and 174% long-term average, respectively).

RESULTS

Field measurements

Mean relative soil water content (0–25 cm depth) was higher ($F_{3,67} = 7.015$; $P < 0.001$) in the site under high degradation than in the remainder sites ($HD > ID = LD = WP$) (Table 2). The highest values of soil water content were found during the winter (Fig. 1a). After that, soil slowly dried reaching the lowest soil water content by the end of January. During the drying phase, the occurrence of precipitation (Fig. 1b) caused temporary increases in soil water content.

In both years, phenology of *S. tenuis* differed among sites subject to different grazing disturbance (Fig. 2). The succession of phenophases (*b* parameter) was

slower in high-degraded and intermediate-degraded sites (cycle 1: $WP = LD < ID = HD$, $F_{3,116} = 3.812$, $P = 0.012$; cycle 2: $LD < WP = ID = HD$, $F_{3,115} = 3.372$, $P = 0.021$) than in sites under lower grazing disturbance, which results in longer growing cycles. Similarly, the inflection point (*a* parameter, date when the highest slope is reached) was delayed in degraded areas (cycle 1: $WP < LD = ID = HD$, $F_{3,116} = 2.862$, $P = 0.040$; cycle 2: $LD < WP = HD < ID$, $F_{3,115} = 4.366$, $P = 0.006$). The second growing season was suddenly interrupted by the occurrence of an extraordinarily large precipitation event in December 2005 (see Fig. 1b), which triggered a third growing cycle (data not shown).

Model predictions

Model validation

The predictions of the model for both strata matched reasonably well with field observations reported by Mazzarino *et al.* (1998) and Bisigato (2000) ($n = 38$, $F = 161.764$, $P < 0.001$, $r^2 = 0.79$ and $n = 24$, $F = 64.967$, $P < 0.001$, $r^2 = 0.76$, for the 0-to-20-cm layer and 20-to-40-cm layer, respectively; Fig. 3). Both the slope and the interception with the y-axis of the regression curves did not differ significantly from 1 and 0, respectively.

Effects of changes in plant cover on soil water

Plant cover reduction strongly affected the water balance. Simulation suggested a switch from transpiration to a direct evaporation dominance of water losses with degradation. According to the model, the partition of precipitation inputs among transpiration, evaporation and deep drainage fluxes was 54-44-2% in the preserved situation and 38-52-10% in the degraded situation. Mean water storage in the profile was, overall, 35 mm higher in the degraded area than in the preserved area. However, this difference decreased in above-average precipitation years (Fig. 4a). In contrast, annual evaporation was directly related to annual precipitation (Fig. 4b). Transpiration losses were higher in the conserved area and in wet

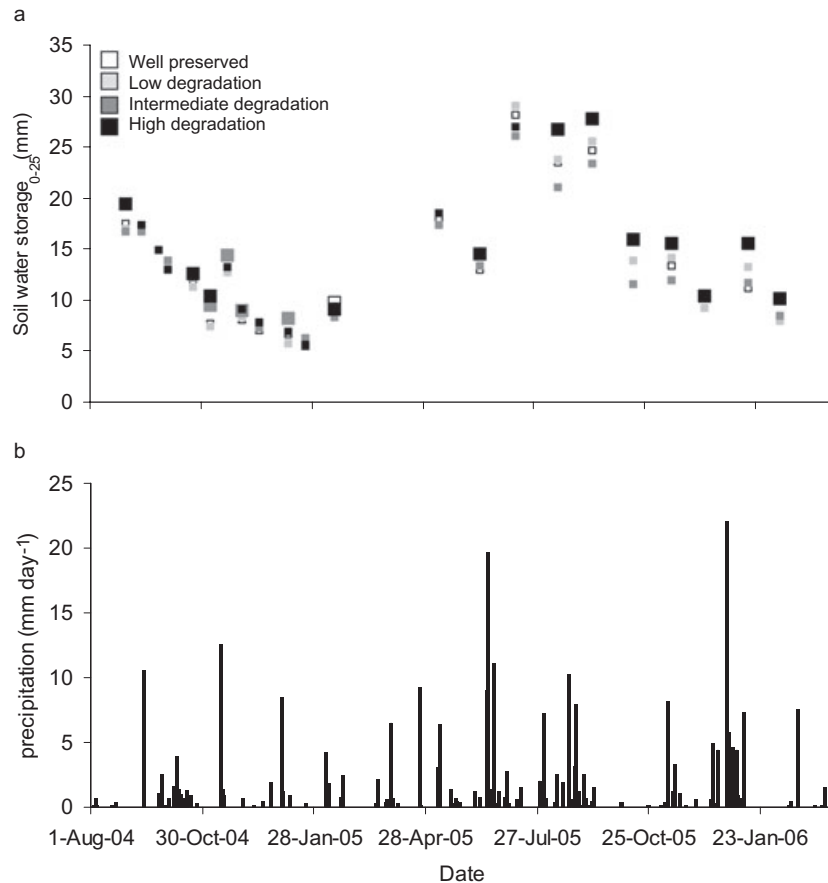


Fig. 1. Time course of soil water storage (mm) to a depth of 25 cm in the four sites included in field measurements (a). Every date, the areas with significant higher soil water storage are shown with bigger symbols. Daily precipitation depths (b).

years (Fig. 4c). Whereas annual transpiration in the degraded area was relatively stable among years with contrasting precipitation, annual transpiration in the preserved area increased with annual precipitation. As a result, in dry years degraded areas lost more water through transpiration than preserved areas, whereas the opposite happened in humid years. The relationship between deep drainage and annual precipitation was complex (Fig. 4d). Deep drainage was absent in years with precipitation lower than long-term average (235.9 mm), but it approximately account for 20% of the water losses in the degraded area during the wettest year. However, the relationship among deep drainage and precipitation was highly variable depending on the size and date of precipitation events.

Beyond these differences in annual averages, we also found temporal differences along the year in the components of the water balance between areas (Fig. 5). For example, the highest soil water storage was during winter and the lowest during summer (Fig. 5a). Likewise, the highest differences in soil water storage between areas with contrasting cover were in spring, during soil drying. In this period, differences as high as

54 mm in water storage in the whole profile were common. Losses due to evaporation showed two maximum peaks, in late summer and mid-spring (Fig. 5b). In contrast, losses by transpiration were highest in late spring/early summer (Fig. 5c). However, transpiration losses in the preserved area strongly decrease after reaching the peak. Thus, although annual water losses by transpiration were lower in more degraded areas, at the end of the growing season (austral summer: weeks 52 to 11) they were higher in degraded than in preserved areas (Fig. 5c). Finally, losses due to deep drainage were highly variable in time, according to the unpredictable occurrence of large precipitation events (Fig. 5d). However, they never occurred in summer.

Soil layers showed differences in the seasonal evolution of simulated soil water storage (Fig. 6). The water storage in the superficial layer (0–10 cm depth) showed a clear seasonal pattern, both in preserved and degraded areas, reaching the highest values in early winter (week 26) and the lowest in early summer (week 2) (Fig. 6a). This seasonal pattern was associated to the highest change in soil water storage among layers

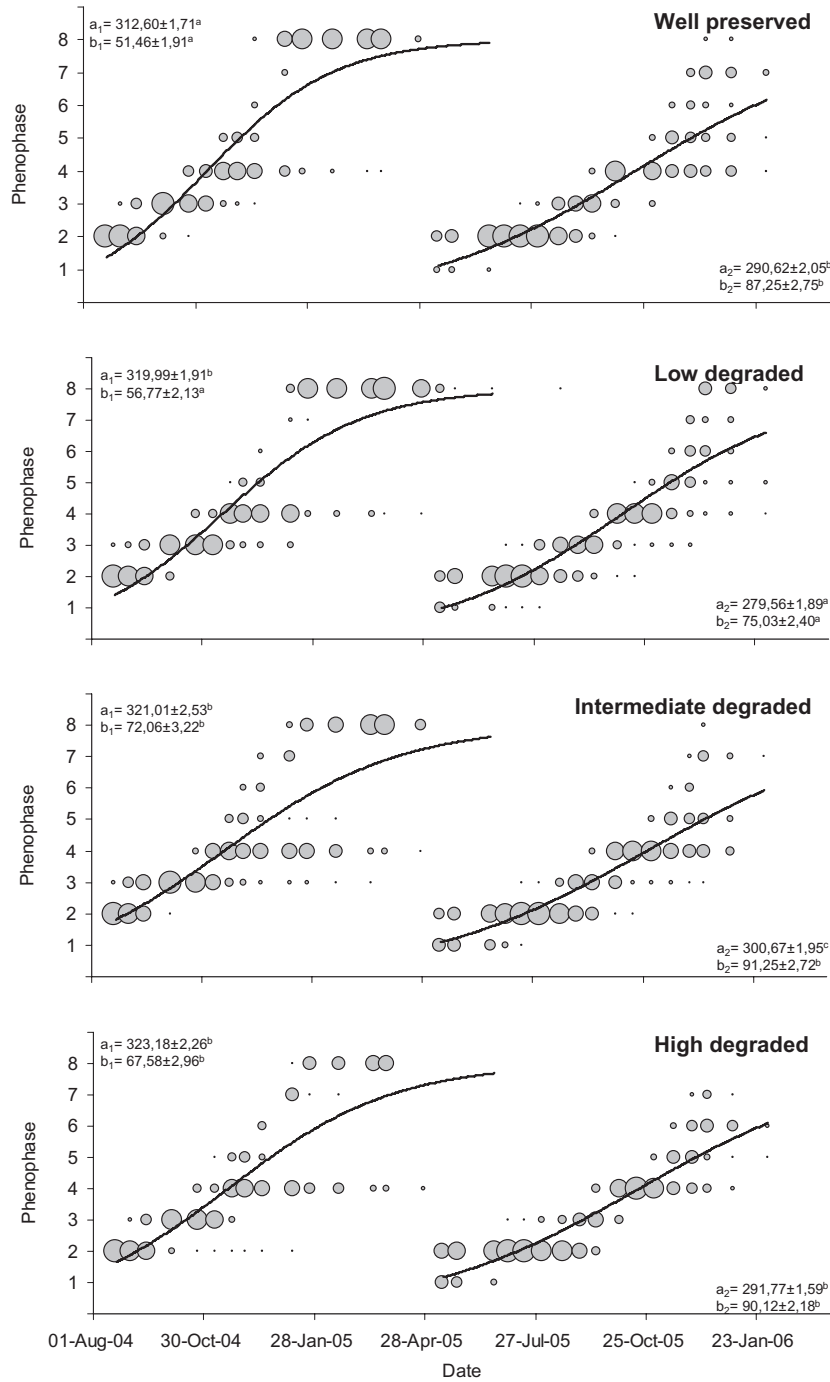


Fig. 2. Phenological patterns of *Stipa tenuis* in each site and year. Circle size indicates the number of individuals in that phenophase. Phenophases are indicated according to Table 2. The continuous line corresponds to the fitted logistic model. *a* and *b* indicate the parameters of the logistic model. Subscripts indicate the year, and different superscript letters indicate significant differences among sites in the parameters.

(winter maximum contains six times more water than the summer minimum). In comparison with the superficial layer, the remaining layers showed delayed maximum water storage and limited ranges of variation, a trend that increased with depth (Fig. 6b–d). Finally, plant cover reduction causes a slight decrease

in water storage in the superficial layer and strong increases in soil water at deeper layers.

In general, these seasonal patterns were subject to interannual variation according to differences in the amount and timing of precipitation (Fig. 7). Whereas the superficial layer showed low interannual variation,

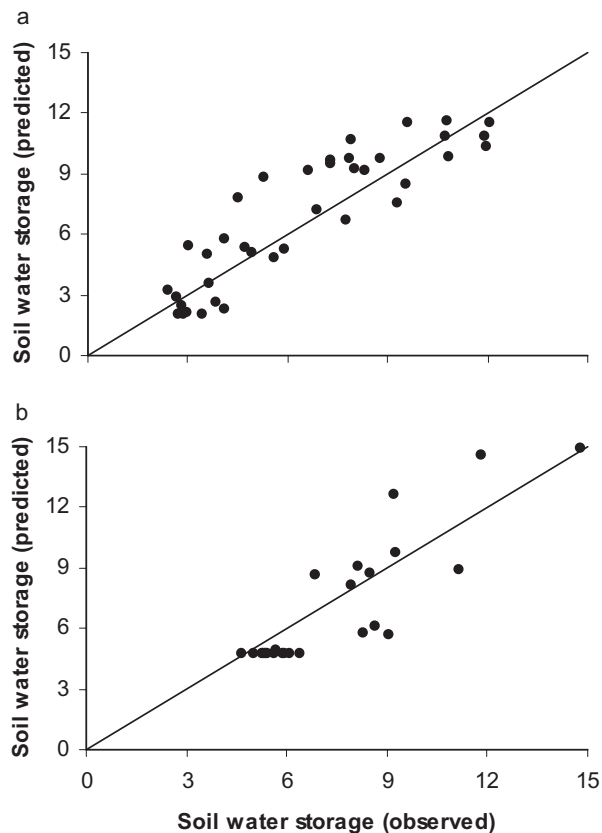


Fig. 3. Adjustment between observed and predicted values (mm) of soil water storage in 0-to-20-cm layer (a) and 20-to-40-cm layer (b). Lines along the diagonal indicate the 1:1 relationship.

deeper layers showed strong differences between years because only during the moistest years the precipitation refilled the complete soil profile. In the same way, whereas the superficial layer is slowly refilled after many small precipitation events, deeper layers are commonly refilled after the biggest precipitation events and slowly dried.

DISCUSSION

Both field results and our modelling approach showed ecohydrological consequences of grazing-induced reductions in cover in the Patagonian Monte. Soil water content was higher in degraded areas than in more conserved areas throughout the year. This result is against to the expected reduction that might be associated with desertification as it is usually taken to reflect decreased water availability. Indeed, most previous studies in water-limited ecosystems found a reduction in soil water content as consequence of grazing (e.g. Naeth *et al.* 1990, 1991; Snyman & Fouché 1991; Snyman 2000). Grazing can have a pro-

found impact on soil water through its influence on infiltration via trampling and on transpiration through defoliation (Buckhouse & Coltharp 1976). The difference between our results and those of Naeth *et al.* (1990, 1991), Snyman (2000) and Snyman and Fouché (1991) might be caused by coarser soil texture in Patagonian Monte, which prevents soil compaction by trampling and allows the expression of the effects of plant cover reduction on transpiration.

Although soil water content in the whole profile is increased in degraded areas, our modelling approach showed that the uppermost layer (0–10 cm) was drier there than in more preserved areas. Whereas evaporation only influences the soil water content in the shallow layer, transpiration extracts water from the whole profile (Gebauer *et al.* 2002). So, because of the low plant cover, the shallow layer is more quickly dried in degraded areas than in more preserved areas. However, the opposite occurs deeper than 10 cm, where water is stored until it is transpired and/or lost by deep drainage. Similar changes in the fractioning of evapotranspiration in evaporation and transpiration as consequence of cover reduction were reported by Aguiar *et al.* (1996) for the Patagonian steppe, by Kemp *et al.* (1997) for North American deserts, by Snyman (1998, 2005) for South African grasslands, and by Lauenroth and Bradford (2006) for the short grass steppe.

Partitioning of evaporation and transpiration is a scientific challenge deemed central to a better understanding of the ecohydrology of water-limited environments (Lauenroth & Bradford 2006; Newman *et al.* 2006). Our model predicts that, on average, transpiration contributed 38 and 54% to total soil water loss in degraded and preserved areas, respectively. These values are within the reported range of contribution of transpiration to water losses in deserts, 7–72% (Kemp *et al.* 1997). However, there was substantial variation among years in the contribution of transpiration to soil water loss (24–55%). This variability was also found in North American deserts (Reynolds *et al.* 2000) and in the short grass steppe (Lauenroth & Bradford 2006), where the relative importance of transpiration increased with total precipitation, the proportion of precipitation during the cold season and increasing plant cover.

Deep drainage losses were rare. These losses account for approximately 20% of total precipitation during the most humid year in the degraded area, whereas they were negligible in the years with below-average precipitation. These results show that the complete profile (0–100 cm depth) is only recharged during above-average precipitation years. Accordingly, a previous study found that the recharge of the 45-to-60-cm layer was incomplete most of the years, and it was only totally refilled during a year with twofold higher precipitation than the mean (Coronato & Bertiller 1997).

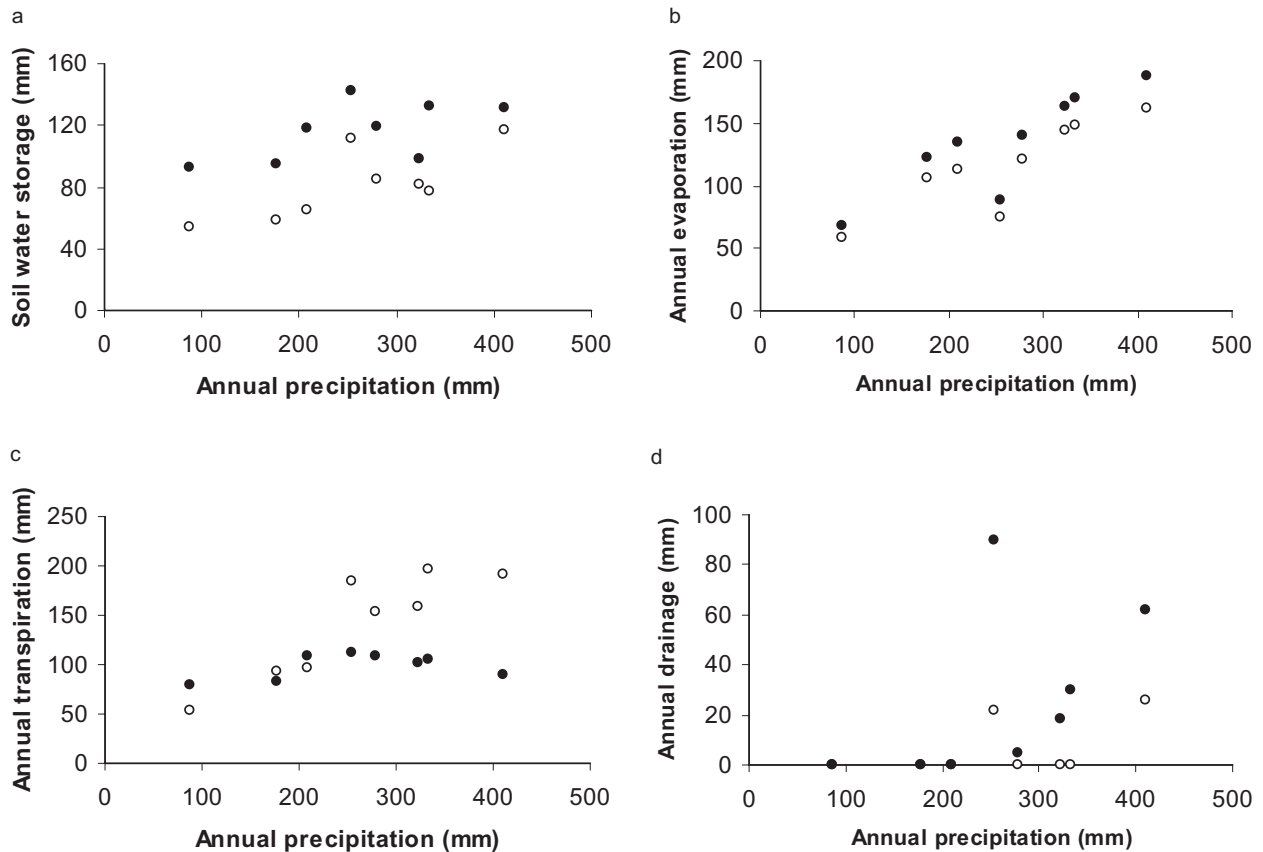


Fig. 4. Relationship between annual precipitation and modelled mean annual water storage (0–100 cm) (a), evaporation (0–10 cm) (b), transpiration (0–100 cm) (c) and deep drainage beyond 100 cm (d). ○ = preserved area (plant cover 40%), ● = degraded area (plant cover 15%).

Likewise, Snyman (1998) found that in South Africa rangelands deep percolation below the root zone only occurs under extremely high rainfall conditions; Reynolds *et al.* (2004) found that in North America deserts the majority of soil water is retained within the top 20 cm of soil and it is generally quickly removed by soil evaporation or transpiration; and Paruelo and Sala (1995) found that in the Patagonian desert deepest layers are not recharged during dry years. Finally, deep drainage was increased in degraded areas as a consequence of a reduction in plant cover, as previously reported by Paruelo and Sala (1995) in the Patagonian steppe. Field studies reporting the development of petrocalcic layers (i.e. illuvial horizons in which secondary calcium carbonate or other carbonates have accumulated to the extent that the horizon is cemented or indurated, Soil Survey Staff 1999) at depth of 40–100 cm (Rostagno & Del Valle 1988) also suggest the extraordinariness of deep drainage in Patagonian Monte. The absence of deep drainage and the shallow distribution of soil water suggest that, in accordance with findings of Rodríguez *et al.* (2007b), there is limited opportunity for vertical partitioning of the soil

water by different functional types or species in the Patagonian Monte. Reynolds *et al.* (2000) suggested that there is a lower threshold of precipitation below which there would be insufficient deep water percolation to maintain a subsurface reservoir. It seems the case for Patagonian Monte, where annual potential evapotranspiration exceeds precipitation by a factor of 4.

In arid and semiarid ecosystems, plant phenology is strongly coupled with water availability. Both an increase in annual precipitation (Ghazanfar 1997; Myers *et al.* 1998) and the accumulation of water in specific areas within the landscape (Seghieri *et al.* 1995; Olivares & Squeo 1999) can cause longer growing cycles as consequence of earlier vegetative growth and retarded senescence. Generally, these effects are stronger in herbaceous species, whereas the growing cycle of deciduous shrubs and perennial shrubs are less affected because these deep-rooted species consume deep water, which is less variable than shallow water (Seghieri *et al.* 1995; Ghazanfar 1997). Similarly, Myers *et al.* (1998) found that in northern Australia irrigation affects the phenology of

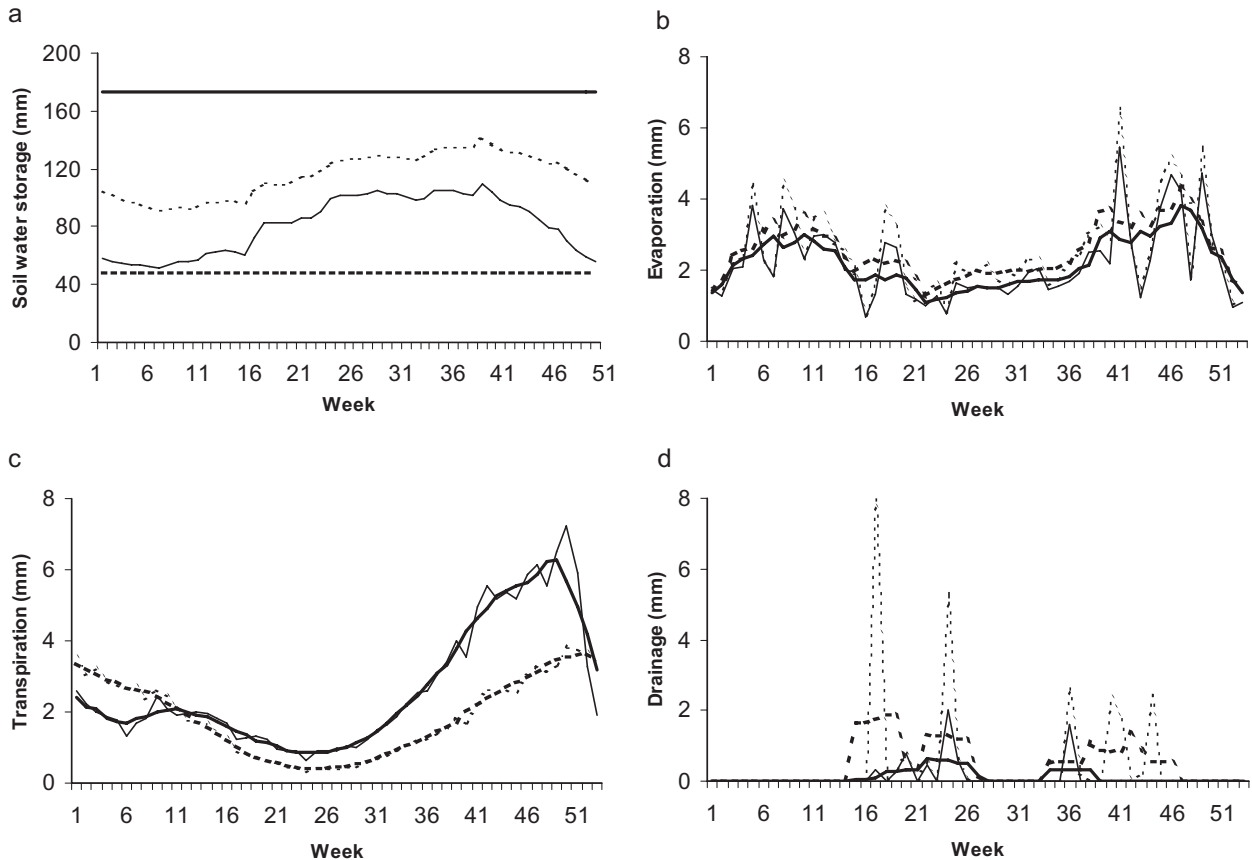


Fig. 5. Mean modelled weekly changes (mm of water) in soil water storage (0–100 cm) (a), soil evaporation (from 0–10 cm depth) (b), plant transpiration (from 0–100 cm depth) (c), and drainage (beyond 100 cm) (d) at preserved (continuous line) and degraded (broken line) areas. Thin lines are means across 8 years (1994–2001). In (a), thick lines indicate water storage at field capacity (continuous line) and at wilting point (broken thick line). In (b–d) thick lines are 4-week moving averages.

some deciduous trees whereas evergreen trees remain unaffected. Accordingly, we found a longer growing cycles (i.e. greater b coefficients) in *S. tenuis* growing at degraded sites (Fig. 2), where water availability was greater (Fig. 1), and in the second growing season, when total rainfall was higher (205 mm *vs.* 185 mm). Consequently, our modelling approach indicated that plant transpiration during summer is higher in degraded than in preserved areas.

Other results of our simple soil water balance model also agreed with the observations carried out in other arid ecosystems by other authors. For instance, the importance of pulse depth for partitioning of precipitation among transpiration, evaporation and drainage is highlighted by the results of our modelling approach because the year with approx. 250 mm of precipitation showed lower evaporation and higher deep drainage than expected. It was due to the occurrence of an extraordinary precipitation event during autumn, which added 127 mm that mostly percolated beyond 100 cm. Similar effects of high precipitation events and distribution of precipitation within the year were

reported by Sala and Lauenroth (1982) and Loik *et al.* (2004).

Our results have several conservation and management consequences. For example, restoration of degraded areas could be facilitated by greater soil water. However, soil seed bank of forage species is strongly reduced by grazing (Bisigato 2000), which also deeply limits seedling emergence and establishment (Bisigato & Bertiller 2004a). Managerial practices, such as grazing exclusion during the reproductive period, were proposed to promote seed rain and, then, the reestablishment of plant cover (Bisigato & Bertiller 2004b). On the other hand, ranch owners frequently ignore expert advice concerning incipient signs of degradation on the basis of the relative greenness of their paddocks during summer. According to our results, this greenness, which is a consequence of greater soil water content due to lower transpiration losses during winter and spring, represents a delayed productivity that does not compensate the lower productivity during the rest of the year.

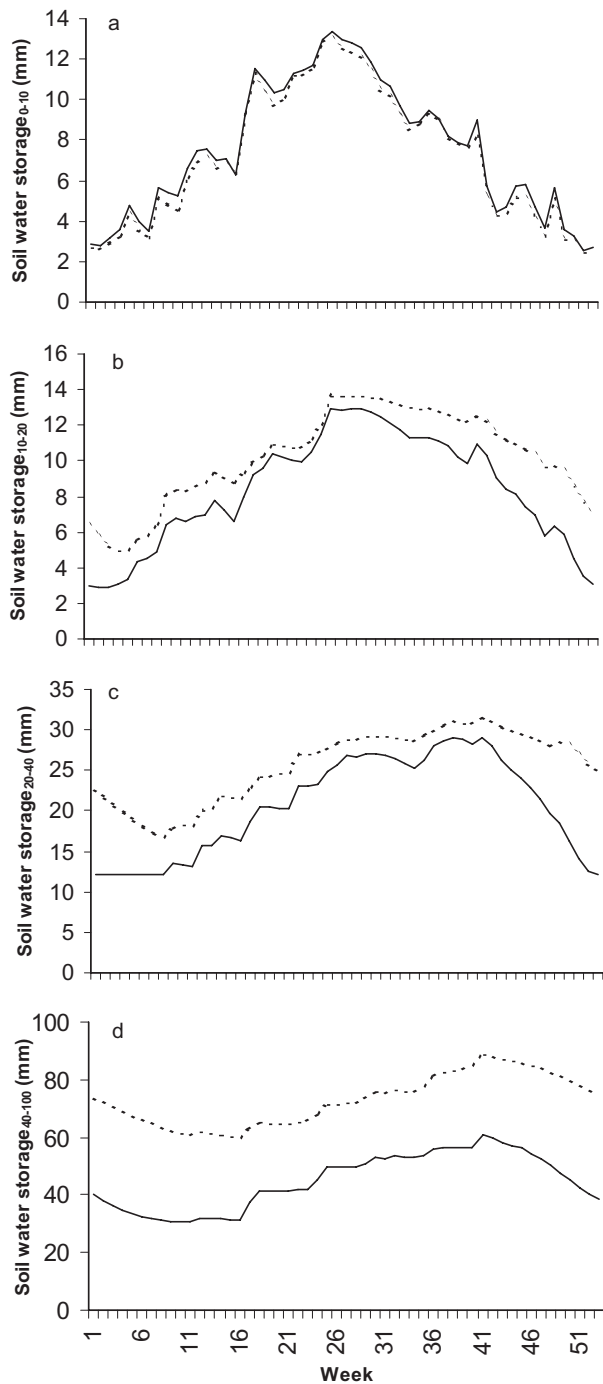


Fig. 6. Modelled mean weekly soil water storage at 0–10 cm (a), 10–20 cm (b), 20–40 cm(c), and 40–100 cm depth (d) at preserved (continuous line) and degraded (broken line) areas.

Despite its simplicity, our modelling approach fitted reasonably well field data and allowed us to build a complete picture of soil water dynamics. However, our model could be improved, for example, including lags for plant response, horizontal heterogeneity in soil and/or plant variables and explicitly separating life

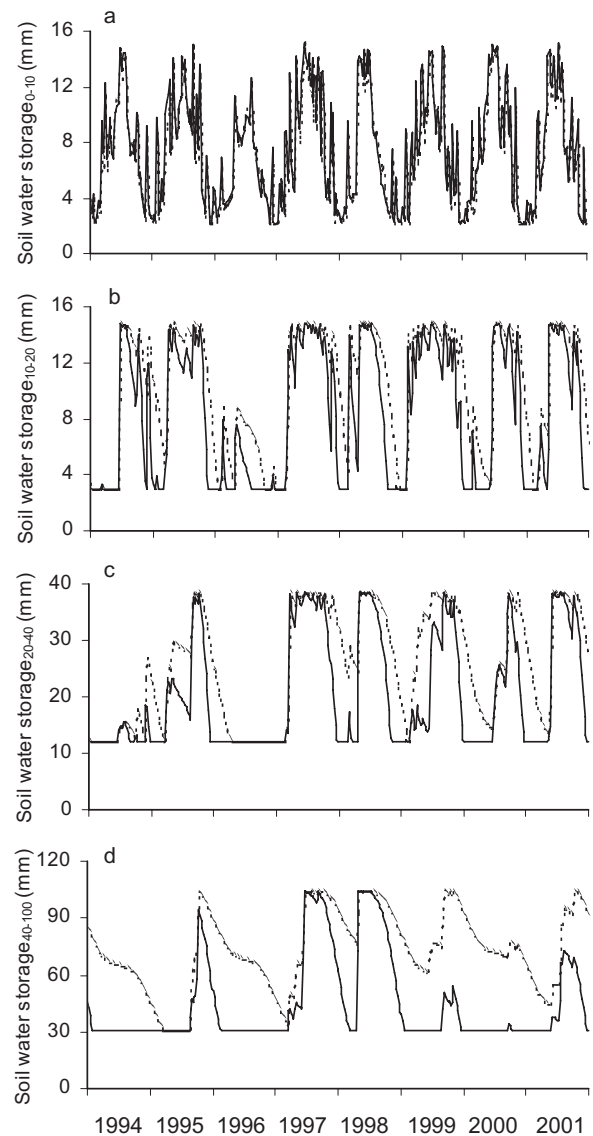


Fig. 7. Modelled weekly evolution of soil water storage 0–10 cm depth (a), 10–20 cm depth (b), 20–40 cm depth (c), and 40–100 cm depth (d) at preserved (continuous line) and degraded (broken line) areas.

forms and/or palatable/non-palatable plants. The development of one more mechanistic model to obtain a better understanding of the complex relationships between vegetation, grazing and soil water is the focus of our ongoing research.

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