

Soil water regime through contrasting pasture communities in a Submediterranean landscape

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KEYWORDS Drought; Grassland; Phenology; Soil water; Soil-vegetation relationships **Summary** Submediterranean landscape around Vic includes, scattered over intensively farmed ground, a number of hills holding diverse mosaics of natural and seminatural communities. We chose two contrasting communities of pastures to investigate the soil water regime, assumed to be the cause of noticeable shifts in the landscape mosaics. *Brachypodio-Aphyllanthetum* is a Mediterranean, xerophilous, open pasture dominated by the chamaephytic grass *Brachypodium retusum*, whereas *Plantagini-Aphyllanthetum* is a dense grassland of *Brachypodium phoenicoides*, similar to Medioeuropean mesoxerophilous grasslands.

We recorded the soil water content in three plots for each community in different hills, during two and a half years. From gravimetric water percentages and soil water retention curves in each plot, we evaluated the soil water potential and the available water during the study period at different depths.

Both communities showed roughly similar seasonal soil water dynamics, which included three clearly differentiated hydric periods: (i) humid (October–April), with soils not far from field capacity; (ii) dry (July–August), when soils were drier than wilting point; and (iii) transitional (May–June), defined by a dramatic water loss. The summer values of water content and hydric potential were similar in the two analysed communities, thus rejecting the hypothesised better summer conditions in the mesoxerophilous grassland. The only clear difference was in the way in which the spring transition occurred, namely it was faster and showed sharper ups and downs in the xerophilous Mediterranean pasture. The inverse seasonal transition, from dry to humid, was clearly a sudden event, strongly depending on the timing of late summer rainfall, and it seems not to be a key factor in

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shaping the functioning of the communities. The lower moisture values at deep soil layers during the humid periods suggest a deficient hydrological functioning, perhaps connected with the pasture-type vegetation.

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Introduction

The key ecological factor in Mediterranean landscapes is their particular seasonality, in which the warmest months coincide with a low rainfall period. Summer conditions of high potential evapotranspiration enhance water shortage in plant communities, which show adaptive responses at individual and community levels (Walter, 1998; Archibold, 1995; Porporato et al., 2001; Mamolos et al., 2001; Pereira et al., 2004). In sclerophyllous forests and maguis the dominant species are good stress avoiders, since through strong control of stomatal flux and water pumping from deep soil lavers they maintain most of their aerial structures, at the cost of cutting growth and lowering metabolism (Savé et al., 1999; Ferrio et al., 2003). In contrast, open scrubs and pastures are much more sensitive to summer stress, and show a wide scope of strategies, from escapism in therophytes to various degrees of endurance in perennial herbs and grasses or in dwarf shrubs (Figueroa and Davy, 1991; Espigares and Peco, 1993; Guàrdia et al., 1998; Llorens et al., 2004).

The transition from Mediterranean to Medioeuropean landscapes, i.e. the gradient of decreasing summer drought, is well expressed in Submediterranean landscapes, which are well characterized and extended in the southern Pyrenees and the northern Catalanidic mountains (Bolòs, 1985). The vegetation expressing this transition is actually formed by landscape mosaics in which both vegetation types, Medioeuropean and Mediterranean, settle on particular ecologic locations, respectively mild or dry slopes, whereas vegetation types intermediate in character occupy most of the surface (Bolòs, 1959, 1985). Taking into account one main vegetation type, i.e. seminatural pastures, the transition is expressed through gradual changes in the proportions of life forms and of biogeographic elements (Casas and Ninot, 1995, 1996).

Water use by plants in Medioeuropean forests and pastures is well known from a good deal of papers and reviews. Referring to Mediterranean communities, some case studies have been aimed at water regime in sclerophyllous forests and the plant response to normal seasonality, to betweenyear irregularities and to extreme drought events (Ogaya et al., 2003; Rodà et al., 1999). But dry pastures and scrubs have attracted much less attention, since no case studies have been published similar to that of forests. Still, well documented analyses of soil water regime in the non-forest Mediterranean landscapes become very interesting, since water flows may become strong drivers in the evolution of large Mediterranean landscapes under changes in land use and in climate change.

Moreover, the transitional aspect of water shortening and plant responses through the Submediterranean area has not been analysed, although soil water regime and water use by plants have been assumed to be the main causes for vegetation shifts (Izco et al., 1985; Moreno et al., 1990; Porporato et al., 2001). Also differences in soil moisture dynamics are among the principal reasons for the existence of particular vegetation types (Rodriguez-Iturbe et al., 2001).

Climate change is expected to play a stronger influence in the transition areas, through replacement between plant species and communities, which shall result into landscape shifts (Sanz-Elorza et al., 2003; Peñuelas and Boada, 2003; Peñuelas et al., 2005). Increasing between-year irregularities and drought events would produce a northwards displacement of the Mediterranean—Submediterranean— Medioeuropean transition, but in this area the precise links between rainfall regime, soil water balance, and plant responses are still poorly known.

The objectives of this study are: (a) to characterize and compare the temporal and vertical distribution of soil water regime in the two contrasted Submediterranean pastures, (b) to analyse how the soil water regime is coupled with the shift from mesoxerophilous, hemicryptophytic grasslands, to xerophilous, chamaephytic pastures, as the dominant plant functional types and vegetation patterns reflect the main environment conditions (Box, 1996; Shmida and Burgess, 1988). It is generally assumed that a key factor would be the degree of soil drought during summer, as mesoxerophilous species would need at least some available water at deep soil level.

Material and methods

The study area

The study was conducted in the small hills located around Vic (Catalonia, Spain; Fig. 1). The area is a small depression (Plana de Vic) located in the northern half of Catalonia, limited to the south and east by the Mediterranean, Catalanidic mountains, and to the north by the pre-Pyrenean ranges. It comprises flat, lime rich, tertiary rocks, which are in the main Eocene marls. The vertical alternation of soft marl and harder outcrops (conglomerate, limestone) is particularly evident in the hills where this study was centred. The macroclimate of the area is Submediterranean axeromeric (Bolòs and Vigo, 1984), a transition type between Mediterranean and Montane (Pyrenean). The mean annual temperature over Vic runs between 12 and 13 °C and the annual rainfall normally ranges from 650 to 750 mm (Fig. 1). There is usually no arid season in this area and so the vegetation is mainly mesoxerophilous, with xerophilous Mediterranean communities being restricted to drier habitats, such as south facing slopes and rocky shelves. The hills and the peripheral relieves of Plana de Vic stand out from the intensively farmed surrounding plains, being the main location of varied mosaics of semi-natural communities (Casas, 2001). The climax vegetation is a deciduous, mesoxerophilous oak forest (Buxo sempervirentis-Quercetum pubescentis),



Figure 1 Location of the area studied (a), and climatic diagram of Vic, corresponding to Submediterranean climate with continental tendency (b).

which remains in a few gently sloping sites. Deforested slopes, on various exposures and with soils ranging from well preserved to highly eroded, are the location for a wide variety of pasture communities, used as extensive rangeland from centuries ago.

Most of the pastures correspond to perennial communities, from xerophilous to mesophilous (Casas and Ninot, 1995, 1996). Excluding both extremes of this transition, all the communities are included in *Aphyllanthion*, a well characterized alliance of Submediterranean to mild Mediterranean range. Within this alliance, two pasture types were chosen as the most extended communities in the area, and as strongly contrasted both in composition and in environment conditions (Table 1). *Plantagini-Aphyllanthetum*, the most general association in the area, is a dense grassland type covering north facing and intermediate gentle

	Plantagini-Aphyllanthetum	Brachypodio-Aphyllanthetum brachypodietosum retusi Brachypodium retusum (68) Thymus vulgaris(30) Koeleria vallesiana(17) Teucrium polium (13) Aphyllanthes monspeliensis (12)					
Dominant species, with cover percentages	Brachypodium phoenicoides (64) Avenula pratensis iberica (35) Aphyllanthes monspeliensis (32) Carex caryophyllea (11) Plantago media (11)						
Plant types (%)							
Hemicryptophytes	78	50					
Chamaephytes	20	47					
Geophytes	2	0					
Therophytes	0	3					
Aspect; slope (°)	N (any); 4	S (SW-SE); 17					
Total plant cover (%)	99	89					
Phytogeographic groups (%)							
Mediterranean	53	78					
Medio-European	34	16					
Pluriregional	13	6					
Rooting density (mg cm^{-3})							
0–5 cm	20.9	14.7					
5–10 cm	11.7	9.1					
10–20 cm	6.1	5.6					
20–30 cm	3.6	3.3					
30—40 cm	2.8	2.4					

Percentages summarise mean covers in both communities (synthesised from 19 and 15 relevés, respectively, from Casas and Ninot, 1995); and rooting density is expressed as dry weight of rhizomes and roots per soil volume (means in the plots studied, unpubl. data).

slopes. Its species composition combines a bulk of plants typical of *Aphyllanthion*, with some *Bromion* differentials, the dominant species being mesoxerophilous grasses, chiefly *Brachypodium phoenicoides*. On steep, eroded, south facing slopes, *Brachypodio-Aphyllanthetum brachypodietosum retusi* settles, a clearly Mediterranean community, dominated by the xerophilous, chamaephytic grass *Brachypodium retusum*, and including a number of sub-shrubs and therophytes. In both communities most of the rooting system (from fine roots to rhizomes) is concentred in the shallow levels of the soil (up to 10 cm deep) and decrease at deeper levels.

All the soils studied are carbonated and basic (pH: 7.8-8.2). The most important soil differences between the two communities are found in the upper soil level properties (texture, organic matter and nutrients content), and in the total depth, which is higher in the mesoxerophilous community. The soil of the mesoxerophilus community at the level of maximum root density (0-10 cm) is fine-textured (loam, clay loam, silt loam), and the organic matter content (6% mean) and nutrients (N, P, K) content are higher. Instead, in the xerophilous pasture the soil is stonier, coarse textured, with more sand content (sandy loam) and poorer in silt, organic matter (4.8% mean) and nutrients. Generally the soil of the mesoxerophilus community bears higher fertility levels and cation exchange capacity than that of the xerophilous community. At the lower levels, the soil properties are similar in both communities (Casas, 2001).

Soil sampling and analyses

Soil water content

We recorded the soil moisture in the two pasture communities mentioned above, situated in contrasted environmental conditions. We installed three pairs of plots in different hills, each pair including one steep, south facing plot, and one gentle, north facing plot, showing typical aspects of these communities. The study period lasted 953 days, from May 1993 to December 1995. Soil samples for determination of gravimetric water content were obtained monthly from October through April and fortnightly from May to September. In each plot three soil cores, 50 cm long, were taken by means of a steel drill. In 6 representative recording dates we obtained 100 cm long cores, to obtain data from deeper layers. Each core was sectioned into 10 cm deep segments, weighted and then dried at 105 °C until constant weight, to determine gravimetric soil water content recorded as mass percentage.

Soil water retention curves

Several methods have been proposed to estimate the soil water retention function from easily measured soil properties, such as soil texture (percentage of sand, silt and clay), organic matter content, and bulk density (Ahuja et al., 1985; Rajkai and Varallyay, 1989; Williams et al., 1992). Rawls et al. (1989) developed three levels of linear regressions relating the soil water content to each of 12 matrix potentials. The first level includes only the basic soil properties mentioned above; the second level adds the water content at -1500 kPa and the third level incorporates the water content at -33 kPa.

We calculated the soil water retention curves for each plot at several soil depths from the water retained at different matrix potentials: -33, -60, -100, -500 and -1500 kPa. From soil samples yielded in several sampling data we obtained mixed samples for each plot and depth (from -10 to -100 cm). Then, we analysed the soil texture and the organic matter content. We selected 64 samples (of a total of 90) corresponding to representative soil textural classes of plots and with different organic matter content. For these samples the soil water content at different water potentials was determined by means of the pressure plate method in the desorption phase from saturated soil samples. Step-wise multiple linear regression was applied to the obtained data in order to relate the water content at each water potential with the soil texture and organic matter content. The equations of these regressions were used to estimate the relationship between soil water content and soil water potential for the remaining samples, from their soil properties.

According to Saxton et al. (1986) the soil water retention curves, from -10 to -1500 kPa may be described by a potential function like $\Psi = A\theta^{B}$, where Ψ is a soil water potential (kPa) and θ is a soil water content (cm³/cm³). Following this model, all the soil water retention curves obtained fitted this equation, and the coefficients (A and B) were calculated using the statistics SPSS, vs. 9.0 (Norusis, 1999).

Soil water potential and available water

Soil water potential at each recording date and depth was estimated from the soil water content by the equation of soil water retention curves.

Total available soil water for plant growth has been theoretically evaluated as the difference between the amount of water retained at field capacity (-10 to -33 kPa, depending)on texture) minus that retained at the wilting point (-1500 kPa; Kramer, 1983). However, it is clear that in soils with low permeability plants may use water above the field capacity, before being drained. And on the contrary, water retained at low potentials (e.g. near the wilting point) becomes very difficult to be used. But, given the complexity to approximate the actual available water in heterogeneous soils (Ritchie, 1981) we assumed for sake of simplicity that the total water available for plant growth was the difference between the field capacity and the wilting point. This amount remains as a reference value reasonably useful, especially for comparative purposes. The total available water in each soil layer and for the two communities considered was estimated from the difference between the volumetric water content (θ_{mm}) measured on a given day and the water content at the wilting point ($\theta_{\rm mm-~1500\,kPa}).$ The volumetric water content $(\theta_{\rm mm})$ at each soil layer was calculated by multiplying the mass water (g water per g soil) by the bulk density (g/m^3) and by the thickness of the layer. We calculated the available water in the two upper layers (0-10 cm and 10-20) and values of the lower layers were integrated in two levels: 20-50 cm and 50-100 cm.

Data analyses

To analyse the differences in soil water content, the water potential, and the available water between communities, depths, and sampling data, we used the analysis of variance ANOVA, and the differences between groups were evaluated by means of the Tukey-HSD test. The analyses were performed on arcsin (percentage of water content) and logarithmic (water potential) transformed data, and on nontransformed data for the available water. All statistical analyses were performed by SPSS software, vs. 9.0 (Norusis, 1999).

Results

Soil water retention curves

The coefficients for the equation of step-wise multiple linear regression obtained from the relationship between soil water content at each water potential and basic soil properties (texture and organic matter content) are summarised in Table 2 (more detailed data are in Casas, 2001). These values were used to calculate the water content at different selected matrix potentials for the samples not analysed via the pressure plates. The results showed the main influence of the organic matter in the soil water retention, since this feature was selected in all regression models, for all the potentials.

The soil water retention curves fitted well with an exponential function (Fig. 2), with a highly significant correlation coefficient (0.98 < r < 1; p < 0.05). The differences in soil water retention curves between different depths in each plot are related to the variations in organic matter, sand, silt and clay contents. Among the soils investigated, those of the xerophilous pasture had, on the whole, lower water potentials at any water content and depth, since their clay and organic matter contents were lower. As for the meso-xerophilous grassland, the higher organic matter content in the shallow level (0-10 cm) was responsible for neatly higher potentials in this level than in deep levels (>10 cm) of the same grassland. This trend was scarcely observed in the xerophilous pasture.

Seasonal soil water dynamics

In all plots the water content and the water potential at any depth followed a roughly parallel evolution throughout the studied period (Fig. 3), and varied significantly among sampling dates (p < 0.01), according to the timing of rainfall and potential evapotranspiration. Three hydric periods were clearly detected in all cases, such as is general under Mediterranean and Submediterranean conditions:

- Humid (October-April), when the water content was higher than 15%, the soil water potential remained around or even above the field capacity (-33 kPa), and thus there was available water for plants in the soil.
- Dry (July-August), when the water content was lower than 10%, and the soil water potential was clearly lower than at the wilting point (-1500 kPa). The soil remained extremely dry and there was no available water for plants.
- Transitional from humid to dry (May-June), when temperature and potential evapotranspiration increased, and caused a dramatic water loss. The available water decreasing during this period coincided with the main growing season in these pastures (Guàrdia et al., 1998).

The inverse seasonal transition, from dry to humid, was clearly a sudden event, which peaked from October to January, depending on the time distribution and amount of late summer and autumn rainfall.

Interannual variations were drawn mainly during the transitional period and in summer. The drought period was intense and long in 1994, and a little softer in 1993, due to rainfall events that brought some soil moisture irregularities. In 1995 spring was fairly rainy, and even in summer some precipitation occurred, which resulted in a very irregular drought period, with sharper ups and downs of water potential in the xerophilous pasture (Fig. 4).

Depth soil water profile

During the year cycle, the soil water percentages were higher at the top levels, and decreased at deeper levels, though these differences were small and not significant in summer. These depth water decrease showed small differences between communities and plots, but in general the differences were higher in the mesoxerophilous grassland, where the water percentage at -10 cm was significantly higher (p < 0.001) than that held at deeper layers. The difference between levels was smaller for water potentials. Moreover, they showed inverse values between humid and dry periods. Thus, in both communities the water potential at the top level ran next to field capacity (mainly between -33 and -100 kPa) during the humid period, and were significantly (p < 0.05) stronger at the lower levels, ranging mainly from -100 to -1000 kPa. During the summer drought, water potentials remained lower than the wilting point across the whole soil profile, showing a tendency to be stronger near the soil surface than at deep levels, though these

Table 2Constants and coefficients of the step-wise multiple linear regression equations for each matrix potential, obtainedfrom the 64 soil samples analysed

Potential (kPa)	Constant (intercept)	Coefficients				r	r ²	n
		% sand	% silt	% clay	% org. mat.			
-33	24.339351	-0.2129			1.977223	0.81	0.66	62
-60	5.153694		0.254873		1.362655	0.85	0.73	40
-100	20.767303	-0.17913			1.07347	0.89	0.79	20
-500	13.946855	-0.14499			1.074218	0.83	0.68	20
-1500	7.397018	-0.07765			1.136655	0.86	0.75	62

water potential I-kPal

water potential I-kPal

water potential I-kPal



Water percentage Water percentage

Figure 2 Soil water retention curves at different depths in the plots of the mesoxerophilous grassland (three plots, left column) and xerophilous pasture (right column).

depth differences were not significant. The water loss via evapotranspiration caused a strong depletion of soil water in the shallow layers.

Differences between communities

The soil water content was significantly higher (p < 0.001) in the mesoxerophilous community across the whole depth profile and through all the seasons, including summer, when at least in their deep soil layers a little more water was kept (Fig. 3). However, these differences were noticeable only during the humid and transitional periods (5-10% more water content), and very small during the summer drought (2-4%). The differences were in general smaller if expressed as water potentials, and were significant (p < 0.05) only during the spring transition.



Figure 3 Soil water dynamics in the two communities studied at different soil depths, expressed as water percentage (left) and water potential (SWP, right). The curves express mean values and the vertical bars give the range of values from the three plots.

As main differences between communities, the transition period in the xerophilous pasture stands out as faster in the whole, occurring a bit earlier, and showing secondary ups and downs, which corresponded to small rainfall events and to sudden drying periods. Also, the xerophilous pasture showed short occasional drought episodes after and before the main summer drying period, which in spring and autumn of 1995 produced water potentials lower than the wilting point.

Available water and hydric balance

Fig. 4 shows the evaluated dynamics of available water (AW) in the two communities at different soil depths. The main dynamics corresponded to the above mentioned seasonality, namely a period of good water supply, extending from the noticeable autumn rainfall onwards, which gives way to the summer drought period through a variable transition. The amounts of available water were significantly lower



Figure 4 Available water (AW) dynamics in the two communities at different soil depths, compared with potential evapotranspiration (PET), mean temperature (*T*) and rainfall (*P*).

(p < 0.001) at the deeper soil levels (20-50 cm) of the xerophilous pasture than at the same depth of the mesoxerophilous community, during all the seasons. However, in the upper soil levels (0-20 cm) it was similar in both communities, except during spring, when it was significantly higher in the mesoxerophilous community. As for the timing of these periods, it is interesting to point out that small amount differences between communities resulted in earlier starting of the drought period in the xerophilous pasture, and even in short secondary drought periods out of summer.

Discussion

In the area studied, the soil ability to retain water varies from place to place depending on their texture and organic matter content. This is clearly reflected through noticeable vegetation variations (Casas and Ninot, 2003), as has been shown for other areas (Singh et al., 1998). The differences in the water dynamics at different soil depths are partly related to profile variations, chiefly in organic matter content. These variables are closely related to topography, i.e. exposition, inclination and situation along the slope (Casas, 2001), thus the correlation between topographic location and plant composition of the communities occurs as the result of edaphogenic and hydrologic processes.

The most striking factor in Mediterranean and Submediterranean communities is the summer drought, which in the communities studied brought the soils to lower water potentials than the wilting point, even at deep levels. Moreover, it has to be pointed out that plants experience noticeable water stress even before reaching the theoretical wilting point, due to the low permeability of the soils studied (Ritchie, 1981). On the other hand, the main species of both communities, i.e. perennial grasses and subshrubs, remain active through summer, and even maintain high covers due to green leaves, mainly in the mesoxerophilous grassland (Guàrdia et al., 1998). Several studies done under controlled conditions show that the actual wilting point for a number of species is clearly lower than -1500 kPa (Gardner and Nieman, 1964; Rawlins et al., 1968; Savage et al., 1996; Shein and Pachepsky, 1995). Moreover, Joffre et al. (1999) and Ritcher (1976) measured water potentials also clearly lower than -1500 in the cell sap of diverse Mediterranean and Submediterranean plants. And Herbès (1979) showed that B. retusum can even grow and produce new leaves while water potentials remain above -4000 kPa. This xerophilous grass is very efficient at lowering the soil moisture, and also at recovering from water depletion after small summer rains (Clary et al., 2004). According to Larcher (2003) most plants can obtain water from the rhizosphere at lower potentials than the wilting point via lowering the potential in their roots. In this way, mesoxerophilous plants would be able to reach -4000 kPa, whereas xerophilous species could exceed -6000 kPa. This has been corroborated by Singh et al. (1998), who measured water potentials as low as -9000 to -10,000 kPa in the soil of the American short grass prairie, while the leaves of the xerophytic grass *Bouteloua gracilis* remained at -5000 kPa.

The data obtained do not support the hypothesis that in the mesoxerophilous grassland the summer water stress acquieres lower intensity than in the xerophilous pasture, since the soil hydric potentials achieved in both communities do not differed significantly. Even the length of the drought period was roughly the same (over three months), at least in the shallow soil levels. The main mesoxerophilous species of the grassland have to thrive across the summer drought in a similar way than the components of the xerophilous pasture do. But a key factor in the Mediterranean seasonality is the spring dynamics, when the main plant development takes place during the soil drying out (Orshan, 1989; Rambal, 2001). In our case study, late spring resulted into a direct stress factor on plant communities, since it took place during the most active growing period (Guàrdia et al., 1998). Henkin et al. (1998) and Bertiller et al. (1996) showed that soil drying out during spring is a very determinant factor in the mortality of juvenile shrubs and xerophytic grasses, respectively. Also, dry events during spring reduce growing and production, which is tolerated less by mesoxerophilous grasslands than by xerophilous communities, where most species are sub-shrubs or stress tolerant perennial herbs, able to grow and thrive also during other seasons (Orshan, 1989; Shmida and Burgess, 1988). Thus, the most influencing water factors in the ecological location of the two contrasted communities analysed must be related with the way in which the spring transition occurs, namely it is faster and shows sharper ups and downs in the xerophilous Mediterranean pasture.

The combination of high rainfall occurring from late summer to early winter, with a progressive decrease of temperatures and PET, produced a good water supply in both communities at any depth. This humid period involved no substantial differences between pasture communities, since it occurred in the main during a low activity period, when the water demand remains much lower than the soil content. The seasonal transition from dry to humid soil could not have been a key factor in the evolution of phenological patterns in the communities treated, since it did not produce differences in the soil water dynamics between pasture types, and shows a great interannual timing variation (Casas, 2001).

As for the depth differences in water contents and potentials, these are greater over the year in the xerophilous pasture, which is partly due to its open structure enabling higher drying out at the ground level (Singh et al., 1998). The mesoxerophilous grassland exhibited higher control of the soil water dynamics, due to higher and more regular plant cover, and also to milder conditions in the north facing slopes (Casas and Ninot, 1999). But it has to be also pointed out that the high ability of *B. retusum* in lowering soil moisture may play a noticeable role in the worse water balance of the xerophilous pasture. This would be enhanced through differences in water infiltration and runoff between the two communities, due to their contrasting structure. The irregular, gap pattern of the xerophilous pasture together with its ground heterogeneity suggest irregular water infiltration, i.e. runoff from bare spots to localized infiltration through vegetated surfaces (Meron et al., 2004) and slope loses evidenced by erosion traces. In contrast, the dense, uniform structure of the meso-xerophilous grassland (both aboveand below-ground) and the gentle ground surface ensure a more uniform water dynamics in this community. A similar trait was found by Scanlon et al. (2005) in the savanna ecosystem, where the space gradient from lighter to denser grass cover is coupled both with higher rainfall and with better water use by the grass cover. Therefore, plant communities partly condition the soil water dynamics, and thus positive feedback processes would play a role in maintaining coupled each pasture type with the corresponding soil water dynamics (Wilson and Agnew, 1992).

A rather surprising general trend consisted in the relative dryness of the deep soil layers during the rainy period, in contrast with the moister conditions kept for several months in the upper levels, which even showed temporal waterlogging. This is evidence for low rainfall infiltration across the pasture soils, which are fine-textured and poorly structured at medium and lower levels due to strong root concentration at the superficial layer (Casas, 2001). Therefore, the pasture soils studied have lower water storage capacity that previewed if saturation were achieved at lower levels during the humid period. In Spanish Mediterranean woodlands it has been demonstrated that the water balance can differ as much as 50% between analogous grass and treegrass communities (Joffre and Rambal, 1993). Similarly, the tree-grass savanna ecosystem achieves more efficient equilibrium than the treeless savanna with respect to the water use, even over interannual rainfall variability (Scanlon et al., 2005). Thus, water fluxes are more balanced in forest soils, since the amount and profile distribution of organic matter in these woody communities enhance better water storage and infiltration.

References

- Ahuja, L.R., Naney, J.W., Williams, R.D., 1985. Estimating soil water characteristics from simpler properties or limited data. Soil Sci. Soc. Am. J. 49, 1100–1105.
- Archibold, O.W., 1995. Ecology of World Vegetation. Chapman and Hall, London.
- Bertiller, M.B., Zaixso, P., Irisarri, M.P., Brevedant, R., 1996. The establishment of Festuca pallescens in arid grasslands in Patagonia (Argentina): the effect of soil water stress. J. Arid Env. 32, 161–171.
- de Bolòs, O., 1959. El paisatge vegetal de dues comarques naturals: la Selva i la Plana de Vic. Arx. Sec. Ciènc. 26, 1–175.
- de Bolòs, O., 1985. Le territoire subméditerranéen et le territoire carpetano-atlantique dans la Péninsule Ibérique. Bot. Helvetica 95 (1), 13–17.
- Bolòs, O. de, J. Vigo, 1984. Flora dels Països Catalans, I. Barcino, Barcelona.
- Box, E.O., 1996. Plant functional types and climate at the global scale. J. Veg. Sci. 7 (3), 309–320.

- Casas, C., 2001. Estudi tipològic, ecològic i funcional de les pastures de la Plana de Vic. Ph. D. Thesis, Univ. Barcelona, Spain.
- Casas, C., Ninot, J.M., 1995. Estudi fitocenològic de les pastures de la Plana de Vic I: comunitats vivaces (Mesobromion i Aphyllanthion).. Butll. Inst. Cat. Hist. Nat. 62, 25–52.
- Casas, C., Ninot, J.M., 1996. Estudi fitocenològic de les pastures de la Plana de Vic II: comunitats terofítiques (Thero-Brachypodietea) i síntesi.. Butll. Inst. Cat. Hist. Nat. 63, 27–50.
- Casas, C., Ninot, J.M., 1999. Relación entre microclima y vegetación pratense en ''la Plana de Vic'' (Cataluña). Ecologia Mediterranea 25 (1), 41–56.
- Casas, C., Ninot, J.M., 2003. Correlation between species composition and soil properties in the pastures of Plana de Vic (Catalonia, Spain). Acta Bot. Barc., 49–291–310.
- Clary, J., Savé, R., Biel, C., de Herralde, F., 2004. Water relations in competitive interaction of Mediterranean grasses and shrubs. Ann. Appl. Biol. 144, 149–155.
- Espigares, T., Peco, B., 1993. Mediterranean pasture dynamics: the role of germination. J. Veg. Sci. 4, 189–194.
- Ferrio, J.P., Florit, A., Vega, A., Serrano, L., Voltas, J., 2003. Δ^{13} C and tree-ring width reflect different drought responses in *Quercus ilex* and *Pinus halepensis*. Oecologia 442, 512–518.
- Figueroa, M.E., Davy, A.J., 1991. Response of Mediterranean grassland species to changing rainfall. J. Ecol. 79, 925–941.
- Gardner, W.R., Nieman, R.H., 1964. Lower limit of water availability to plants. Science 143, 1460–1462.
- Guàrdia, R., Casas, C., Ninot, J.M., 1998. Phenological patterns in Mediterranean pastures and scrubs of Catalonia. Acta Bot. Barc. 45, 557–576.
- Henkin, Z., Seligman, N.G., Kafkafi, U., Prinz, D., 1998. End-ofseason soil water depletion in relation to growth of herbaceous vegetation in a sub-humid Mediterranean dwarf-shrub community on two contrasting soils. Plant Soil 202, 317–326.
- Herbès, J.M. d' 1979. Quelques bases physiologiques simples pour tenter d'interpréter la place occupée par quatre graminées dans deux communautés herbacés spontanées des garrigues du Montpellièrais. PhD Thesis, Univ. Sci. Techn. Languedoc, Montpellier.
- Izco, J., Amigo, J., Guitián, J., 1985. El papel de la topografía en la transición Eurosiberiano-Mediterránea en el extremo Noroeste Ibérico. Coll. phytosoc. 13, 343–359.
- Joffre, R., Rambal, S., 1993. How tree cover influences the water balance of Mediterranean rangelands. Ecology 74, 570–582.
- Joffre, R., Rambal, S., Damesin, C., 1999. Functional attributes in Mediterranean-type ecosystems. In: Puignaire, F.I., Valladares, F. (Eds.), Handbook of Functional Plant Ecology. Marcel Dekker Inc., New York, pp. 347–380.
- Kramer, P.J., 1983. Water Relations of Plants. Academic Press, New York.
- Larcher, W., 2003. Physiological plant ecology. In: Ecophysiology and Stress Physiology of Functional Groups, 4th ed. Springer, Berlin.
- Llorens, L., Peñuelas, J., Estiarte, M., Bruna, P., 2004. Contrasting growth changes in two dominant species of a Mediterranean shrubland submitted to experimental drought and warming. Ann. Bot. 94, 843–853.
- Mamolos, A.P., Veresoglou, D.S., Noitsakis, V., Gerakis, A., 2001. Differential drought tolerance of five coexisting plant species in Mediterranean lowland grasslands. J. Arid Env. 49, 329–341.
- Meron, E., Gilad, E., von Hardenberg, J., Shachak, M., Zarmi, Y., 2004. Vegetation patterns along a rainfall gradient. Chaos Soliton. Fract. 19, 367–376.
- Moreno, J.M., Pineda, F.D., Rivas-Martínez, S., 1990. Climate and vegetation at the Eurosiberian–Mediterranean boundary in the Iberian Peninsula. J. Veg. Sci. 1, 233–244.
- Norusis, M.J. 1999. SPSS 9.0 guide to data analysis. Prentice Hall, Upper Saddle River.

- Ogaya, R., Peñuelas, J., Martínez-Vilalta, J., Mangirón, M., 2003. Effect of drought on diameter increment of *Quercus ilex*, *Phyllirea latifolia* and *Arbutus unedo* in a holm oak forest of NE Spain. Forest Ecol. Manage. 180, 175–184.
- Orshan, G. (Ed.), 1989. Plant pheno-morphological studies in Mediterranean type ecosystems. Kluwer, Dordrecht.
- Peñuelas, J., Boada, M., 2003. A global change-induced biome shift in the Montseny mountains (NE Spain). Global Change Biol. 9, 131–140.
- Peñuelas, J., Filella, I., Sabaté, S., Gràcia, C., 2005. Sistemes naturals: ecosistemes terrestres. In: I.D E. Catalans (Ed.), Informe sobre el canvi climàtic a Catalunya. Departament de Medi Ambient de la Generalitat de Catalunya, Barcelona, pp. 517–608.
- Pereira, J.S., David, J.S., David, T.S., Caldeira, M.C., Chaves, M.M., 2004. Carbon and water fluxes in Mediterranean-type ecosystems Constraints and Adaptations. In: Esser, K., Lüttge, U., Beyschlag, W., Murata, J. (Eds.), Progress in Botany, vol. 65. Springer, Berlin, pp. 66–497.
- Porporato, A., Laio, F., Ridolfi, L., Rodriguez-Iturbe, I., 2001. Plants in water-controlled ecosystems: active role in hydrologic processes and response to water stress III. Vegetation water stress. Adv. Water Resour. 24, 725–744.
- Rajkai, K., Varallyay, G., 1989. Estimating soil water retention from simpler properties by regression techniques. In: Proceedings of the International Workshop on Indirect methods for estimating the hydraulic properties of unsaturated soils. Univ. California, Riverside, pp. 417–426.
- Rambal, S., 2001. Hierarchy and productivity of Mediterranean-type ecosystems. In: Roy, J., Saugier, B., Mooney, H.A. (Eds.), Terrestrial Global Productivity. Academic Press, New York, pp. 315–344.
- Rawlins, S.L., Gardner, W.R., Dalton, F.N., 1968. In situ measurement of soil and plant leaf water potential. Soil Sci. Soc. Amer. Proc. 32, 468–470.
- Rawls, J.W., Ahuja, L.R., Brakensiek, D.L., 1989. Estimating soil hydarulic properties from soils data. In: Proceedings of the International Workshop on Indirect methods for estimating the hydraulic properties of unsaturated soils. Univ. California, Riverside, pp. 329–340.
- Ritcher, R., 1976. The water status in the plant experimental evidence. In: Lange, O.L., Kappen, L., Shulze, E.D. (Eds.), Water and Plant Life. Springer, Berlin, pp. 43–58.
- Ritchie, J.T., 1981. Soil water availability. Plant Soil 58, 327-338.
- Rodà, F., Retana, J., Gracia, C.A., Bellot, J. (Eds.), 1999. Ecology of Mediterranean evergreen oak forests. Ecological Studies. Springer, Berlin, p. 137.
- Rodriguez-Iturbe, I., Porporato, A., Laio, F., Ridolfi, L., 2001. Plants in water-controlled ecosystems: active role in hydrologic processes and response to water stress I. Scope and general outline. Adv. Water Resour. 24, 695–705.
- Sanz-Elorza, M., Dana, E.D., González, A., Sobrino, E., 2003. Changes in the high mountain vegetation of the central Iberian Peninsula as a probable sign of global warming. Ann. Bot. 92, 273–280.
- Savage, M.J., Ritchie, J.T., Bland, W.L., Dugas, W.A., 1996. Lower limit of soil water availability. Agron. J. 88, 644– 651.
- Savé, R., Castell, C., Terradas, J., 1999. In: Rodà, F., Retana, J., Gracia, C.A., Bellot, J. (Eds.), Ecology of Mediterranean evergreen oak forests. Ecological Studies 137. Springer, Berlin, pp. 135–147.
- Saxton, K.E., Rawls, J.S., Romberger, J.S., Papendick, R.I., 1986. Estimating generalized soil-water characteristics from texture. Soil. Sci. Soc. Am. J. 50, 1031–1036.
- Scanlon, T.M., Caylor, K.K., Manfreda, S., Levin, S.A., Rodriguez-Iturbe, I., 2005. Dynamic response of grass cover to rainfall

variability: implications for the function and persistence of savanna ecosystems. Adv. Water Resour. 28 (3), 291–302.

- Shein, E.V., Pachepsky, Y.A., 1995. Influence of root density on the critical soil water potential. Plant and Soil 171, 351– 357.
- Shmida, A., Burgess, T.L., 1988. Plant growth-form strategies and vegetation types in arid environments. In: Werger, M.J.A., van der Aart, P.J.M., During, H.J., Verhoeven, J.T.A. (Eds), Plant form and vegetation structure. SPB Academic Publishing, The Hague, pp. 211–241.
- Singh, J.S., Milchunas, D.G., Lauenroth, W.K., 1998. Soil water dynamics and vegetation patterns in a semiarid grassland. Plant Ecol. 134, 77–89.
- Walter, H. 1998. Vegetació i zones climàtiques del Món. Universitat de Barcelona. Barcelona.
- Williams, R.D., Ahuja, L.R., Naney, J.W., 1992. Comparison of methods to estimate soil water characteristics from soil texture, bulk density, and limited data. Soil Sci. 153 (3), 172–184.
- Wilson, J.B., Agnew, A.D.Q., 1992. Positive feedback switches in plant communities. Adv. Ecol. Res. 23, 263–336.