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Water relations only partly explain the distributions of three perennial plant species in a semi-arid environment

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Abstract

The water relations and stomatal conductances of three perennial plant species, *Stipa tenacissima* L., *Anthyllis cytisoides* L., and *Retama sphaerocarpa* (L.) Boiss., dominant on the upper slopes, mid-slopes and floor of a valley, respectively, in semi-arid south-east Spain, were investigated to test the hypothesis that differences in plant-soil water relations could account for the different distributions of each species in the catena. Diurnal measurements of water potential (ψ_w), relative water content (RWC) and stomatal conductance (g_s) of leaves were made over one year. Leaf temperature, air humidity, wind-speed and incident quantum flux density were measured concurrently. Soil water content was determined gravimetrically at 0 - 5 cm and 15 - 20 cm depths. Measurements of ψ_w, RWC and g_s were analysed according to meteorological conditions, based on the maxima for daily air temperature and atmospheric saturation water vapour deficit and on soil moisture content. The hypothesis that plant-soil water relations can explain the distribution of the three species along the catena from valley side to valley floor was rejected for *Anthyllis* and *Stipa* but confirmed for *Retama*.

Additional key words: *Anthyllis cytisoides*, relative water content, *Retama sphaerocarpa*, *Stipa tenacissima*, stomatal conductance, water potential.

Introduction

Drought, low rainfall, high temperatures and unpredictability of the rainfall are the overriding features of warm arid and semi-arid environments throughout the world. Given the restrictions to plant function imposed by such environments, strong directional selection for common adaptive features has resulted in convergence across unrelated taxa, leading to uniformity in many features of the vegetation, as exemplified by the sclerophyllous shrublands of mediterranean climates (Cody and Mooney 1978). However, there is also wide variation in morphological and physiological traits in communities of semi-arid environments (McKitrick 1993, Miles and Dunham 1993). This variation was investigated in three main species in the Rambla Honda, a dry valley in south-east Spain, *Stipa tenacissima* L., *Anthyllis cytisoides* L., and *Retama sphaerocarpa* (L.) Boiss. *Stipa*

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Abbreviations: ψ_w - water potential; RWC - relative water content; g_s - stomatal conductance; g_s^{Qmax} - light-saturated conductance of a leaf; g_s^{max} - maximum leaf conductance; θ - soil water content; VPD - atmospheric water vapour pressure deficit; Q - incident quantum flux density.

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tenacissima is a perennial tussock grass with narrow leaves that can fold concealing a grooved abaxial surface which contains stomata, *Anthyllis cytisoides* is a small leguminous shrub with drought deciduous leaves and *Retama sphaerocarpa* is a tall evergreen leguminous shrub in which cladodes are the photosynthesising organs.

The climate of the Rambla Honda is typically semi-arid with dry summer (temperature reaching 45 °C, saturation deficit of 3 - 4 kPa). On average most of the rain falls between autumn and spring, with an almost rainless summer. However, the amount and timing of the rainfall varies within and between years, as do the duration and timing of drought conditions (Lázaro *et al.* 2001). This investigation tested the hypothesis that differences in plant-soil water relations account for the different distributions of each species in the Rambla Honda.

Materials and methods

Plants: The Rambla Honda (37°08' N, 2°22' W) is a north-south oriented valley at an altitude of 630 m a.s.l. in the valley bottom, rising to 800 m a.s.l. on the crests of the slopes on either side (see Puigdefábregas *et al.* 1996 for detailed information on the field site). Geomorphologically it consists of steep denuded upper slopes, with relatively shallow (< 1 m deep), fine textured soil with much exposed rock, less steeply inclined lower slopes consisting of alluvial fans of varying depth (< 10 m) formed of coarser textured material and a flat basal flood plain of colluvium (> 30 m deep) of different textures ranging from silts to coarse shaley gravels. *Stipa* occupies the upper slopes, *Anthyllis* the mid to lower slopes and *Retama* the flood plain. The availability of the species of deep-seated water, *i.e.*, that which is not directly dependent on current rain storms, changes markedly down slope. In the uppermost zone, the soil is shallow for long-term storage of water, except in fissures in the rock and in exceptionally deep pockets of soil (Puigdefábregas *et al.* 1998). However, the fans of the mid-slope and the deposits on the flood plain are deep enough for long term storage (Domingo *et al.* 1999). In addition on the flood plain, water is present all the year round at a depth of 30 m or more (Puigdefábregas *et al.* 1998).

Selection of plants: Three 50 × 100 m stands were selected, one dominated by *Retama*, one by *Stipa* and the third by *Anthyllis*. A sample of 100 plants of the dominant species was selected and labelled in each area. The heights, diameters and positions of these plants were determined. From these data, the frequency distributions of the size classes of the three species were obtained. Forty plants of each species from the classes containing most plants were used for this investigation.

Relative water content: For each measurement, two 10-cm cladodes of *Retama,* shoots of *Anthyllis* and leaves of *Stipa*, were cut from a plant at each cardinal position. *Anthyllis* leaves were plucked from the shoots. When *Anthyllis* shoots had lost their leaves, 8 shoots were sampled and treated in the same way as samples of *Stipa* and *Retama*. The eight *Retama* cladodes, eight *Stipa* segments and all the *Anthyllis* leaves from each plant were bulked. Each bulked sample was weighed immediately after collection to 0.01 g on a portable top pan balance (*PT120*, *Sartorius*, Göttingen, Germany) and placed in a dark humid chamber with their cut ends in or covered by saturated cotton wool and held at 4 °C until fully hydrated. After equilibration, samples were dried at 70 °C for 24 h.

Water potential: Four leaves, cladodes or shoots, one from each cardinal position, were cut from the plant and their water potentials determined with a pressure chamber (*Skye SKPM1400,* Llandrindod Wells, UK). Modifications to the sealing system enabled measurements down to -5 MPa.

Leaf conductance: Gas exchange was measured by an infra-red gas analyser (*LCA-3*, *ADC*, Hoddesdon, UK) using a narrow leaf chamber *PLC-3(N)*. Leaf area was measured by analysing images of detached leaves by image analysis software (*ACAD*, *Autodesk Inc.*, San Rafael, USA). The images had been recorded on to a laptop computer with a hand-held scanner (*Scanman 256*, *Logitek*, Los Angeles, USA). A leaf area meter (*Mk2*, *Delta-T Devices*, Burwell, UK) was also used for some samples. Leaf conductance (g_s) was a combination of cuticular and stomatal conductance. For convenience leaf conductance will also be called stomatal conductance. Measurements of leaf conductance were analysed to separate the effects of quantum flux density (Q) and vapour pressure deficit (VPD) on g_s (Brenner and Incoll 1997). The following relationships were used:

a) for the response to Q

$$g_s = g_s^{Qmax} \times [Q/(Q + b_Q)]$$

where g_s^{Qmax} is light-saturated conductance of a leaf and b_Q is an empirical constant (Baldocchi *et al.* 1991, Saugier and Katerji 1991).

b) for the response to VPD

$$g_s = g_s^{max} + (b_{VPD} \times VPD)$$

where g_s^{max} is maximum leaf conductance on a particular day, b_{VPD} is an empirical constant representing sensitivity of stomata to VPD (Aphalo and Jarvis 1991, Turner 1991).

These equations have been used in recent works on evapotranspiration modelling (Brenner and Incoll 1997, Domingo *et al.* 1999, 2001, Villagarcía 2000), predicting successfully the transpiration rate the species studied here.

Soil water content and meteorological data: Gravimetric soil water content (θ) was determined from cores obtained at 0 - 5 cm and 15 - 20 cm depth and subsequently dried to constant mass at 105 °C. Samples were collected within one day of a rainfall event, one week later and at two-week intervals thereafter.

Meteorological data were collected at hourly intervals at a weather station approximately 0.5 km from the site.

Results

The results presented here are separated in two types of measurement days, when conditions were most and least favourable. For the favourable days, average maximum air temperature was 17.2 °C, maximum VPD was 1.1 kPa and soil moisture content was 0.15 % and for the unfavourable days, 27.4 °C, 2.7 kPa and 0.04 %, respectively.

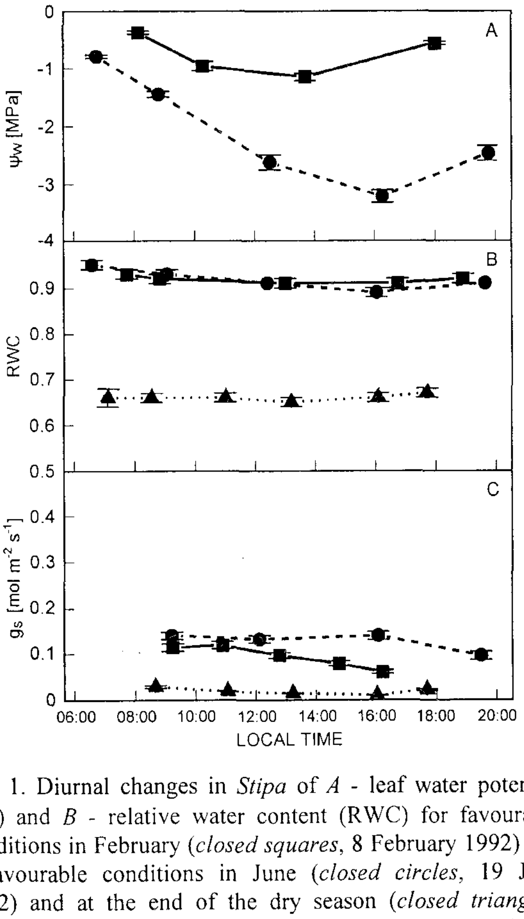

Fig. 1. Diurnal changes in *Stipa* of *A* - leaf water potential (ψ_w) and *B* - relative water content (RWC) for favourable conditions in February (*closed squares*, 8 February 1992) and unfavourable conditions in June (*closed circles*, 19 June 1992) and at the end of the dry season (*closed triangles*, 1 October 1992), and *C* - for leaf conductance (g_s) for favourable conditions in January (*closed squares*, 21 January 1993) and unfavourable conditions in June (*closed circles*, 19 June 1992) and at the end of the dry season (*closed triangles*, 1 October 1992). Water potential could not be determined on 1 October 1992 because it was < -5 MPa. Means ± SE, $n = 24$.

Over the measurement period, soil water content varied in response to rainfall. Although maximum and minimum temperatures changed over the period, diurnal variation remained approximately the same. Diurnal change inVPD was maximal in summer and minimal in winter.

Diurnal changes in ψ_w and RWC were similar for all three species when the soil moisture content was relatively high, VPD was minimal and temperature was below the summer maximum (Figs. 1, 2, 3). However, the

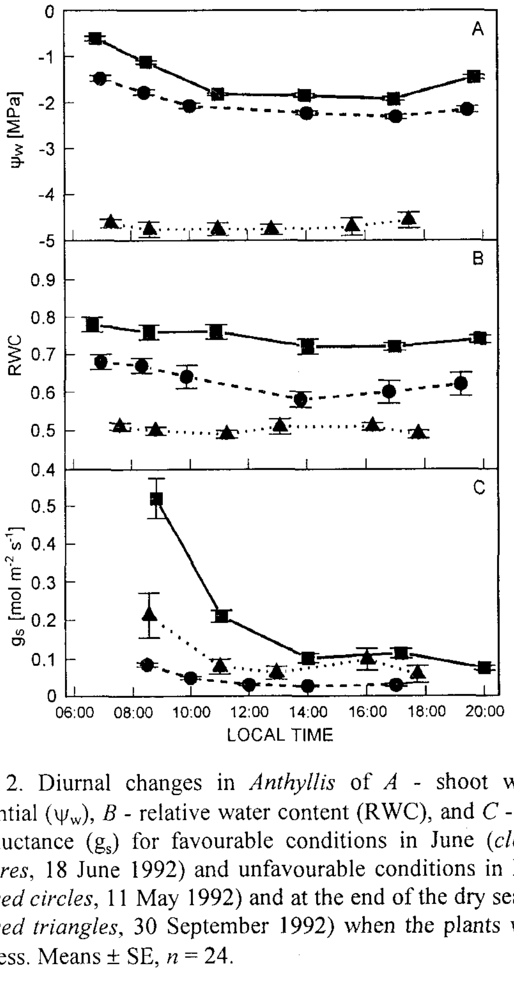

Fig. 2. Diurnal changes in *Anthyllis* of *A* - shoot water potential (ψ_w), *B* - relative water content (RWC), and *C* - leaf conductance (g_s) for favourable conditions in June (*closed squares*, 18 June 1992) and unfavourable conditions in May (*closed circles*, 11 May 1992) and at the end of the dry season (*closed triangles*, 30 September 1992) when the plants were leafless. Means ± SE, $n = 24$.

values for ψ_w diverged when soil moisture content decreased, and temperature and VPD was high, indicating different susceptibilities of the species and/or their habitats to drought. Maximum g_S occurred in the early morning, when VPD was minimum (Figs. 1*B*, 2*B*, 3*B*). Changes in g_S were related to those in ψ_w and RWC in the early morning but not at other times. This is a widely reported response to climate, in particular to VPD (Fischer and Turner 1978) (see also Domingo *et al.* 2002).

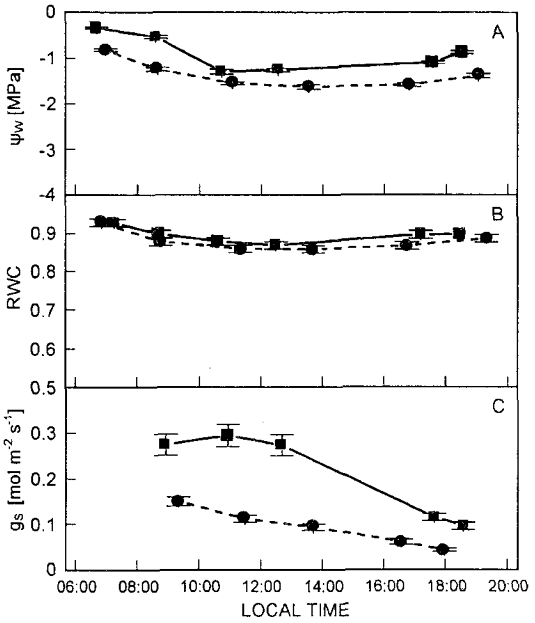

Fig. 3. Diurnal changes in *Retama* of *A* - cladode water potential (ψ_w) and *B* - relative water content (RWC) for favourable conditions in June (*closed squares*, 17 June 1992) and unfavourable conditions in August (*closed circles*, 7 August 1992), and *C* - for cladode conductance (g_s) for favourable (*closed squares*, 17 June 1992) and unfavourable (*closed circles*, 29 September 1992) conditions. Means ± SE, $n = 24$.

Water potential was higher in leaves of *Stipa* and leafless shoots of *Anthyllis* but not in cladodes of *Retama*, in favourable compared with unfavourable conditions, and there were no consistent differences in RWC. There were marked differences in the relationship between ψ_w and RWC of the three species over the year, with RWC in *Stipa* changing the least and in *Anthyllis* the most, in relation to change in ψ_w (Fig. 4). The slopes of the relationship (ψ_w/RWC) were 35.7 for *Stipa*, 12.9 for *Anthyllis* and 14.9 for *Retama*.

The response of light saturated leaf conductance to VPD (Fig. 5) suggest that *Stipa*, compared with *Retama* and *Anthyllis*, was unresponsive to changes in VPD (Table 1). Sensitivity increased in *Stipa* and *Anthyllis* with increase in plant RWC after rain. *Retama* was highly responsive to VPD except in winter and conductance was differently sensitive to increasing VPD in old and young cladodes (5 June, Fig. 5*C*).

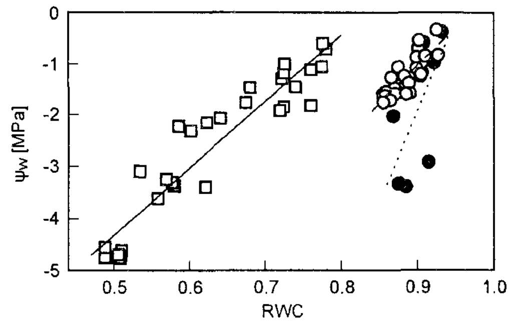

Fig. 4. The relationship between water potential and relative water content for *Stipa* (*closed circles*) ($r^2 = 0.44$, $n = 7$, $P < 0.05$), *Anthyllis* (*squares*) ($r^2 = 0.89$, $n = 28$, $P < 0.05$), and *Retama* (*open circles*) ($r^2 = 0.67$, $n = 23$, $P < 0.05$) between 1 February 1992 and 1 February 1993.

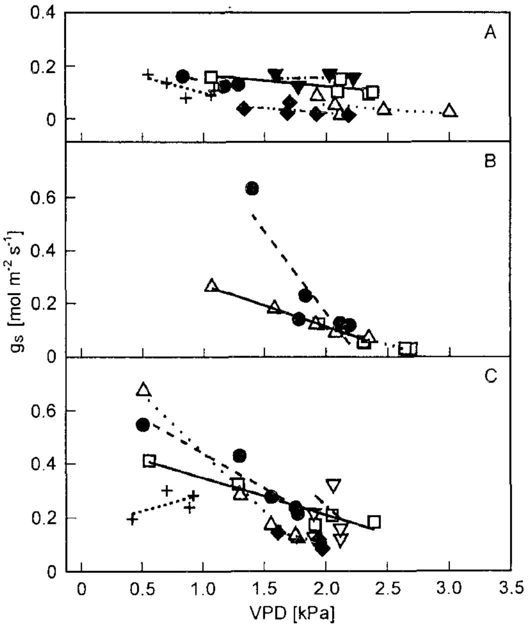

Fig. 5. The relationship between leaf conductance (g_s) and VPD in *A* - *Stipa* for 24 April (*open squares*), 2 May (*closed circles*), 28 May (*open triangles*), 19 June (*closed triangles*), 1 October 1992 (*rhombs*) and 21 January 1993 (*crosses*), *B* - *Anthyllis* for 11 May (*open squares*), 18 June (*closed circles*) and 30 October (*open triangles*), and *C* - *Retama* for 15 April (*open squares*) and 5 June (*closed circles*) for young cladodes and 5 June (*open triangles*), 17 June (*open reverse triangles*), 29 September 1992 (*rhombs*) and 14 January 1993 (*crosses*) for old cladodes.

There were overall differences between the species in that *Stipa* had significantly lower g_s and *Anthyllis* had lower RWCs than the other two species in both favourable and unfavourable conditions.

Table 1. Parameters of the response of leaf conductance [mol m^{-2} s^{-1}] to VPD (derived from equation 2). For *Retama* b_Q = 200 mmol m^{-2} s^{-1}, for *Anthyllis* and *Stipa* b_Q = 100 μmol m^{-2} s^{-1}. NS - not significant, * - significant at $P < 0.05$, ** - significant at $P < 0.01$, *** - significant at $P < 0.001$.

Species	Date	Age	g_s^{max}	b_{VPD} [kPa^{-1}]		r^2	*n*
Retama	15 April 92	old	0.485	−0.136	*	0.92	5
	5 June 92	old	0.703	−0.262	**	0.93	5
	5 June 92	young	0.880	−0.436	***	0.99	5
	17 June 92	old + young	1.071	−0.411	*	0.57	10
	29 September 92	old + young	0.340	−0.118	**	0.63	10
	14 January 93	old	0.162	+0.127	NS	0.36	4
Stipa	24 April 92		0.207	−0.042	NS	0.59	5
	2 May 92		0.222	−0.077	NS	0.84	3
	28 May 92		0.126	−0.036	NS	0.30	5
	19 June 92		0.141	+0.007	NS	0.01	4
	29 September 92		0.091	−0.034	NS	0.30	5
	21 January 93		0.220	−0.122	NS	0.63	5
Anthyllis	11 May 92		0.338	−0.116	*	0.90	5
	18 June 92		1.398	−0.616	*	0.78	5
	30 September 92		0.426	−0.156	***	0.99	5

Discussion

Results indicate that inherent properties of the species, rather than differences in the measured external variables, could account for the observed differences between the species. There were significant differences in ψ_w between *Stipa* and *Anthyllis* (Figs. 1, 2) despite similar soil moisture regimes and over the whole period of the measurements in favourable and unfavourable conditions, *Stipa* had significantly lower g_S and *Anthyllis* lower RWC than had *Retama*. These differences were not related to soil moisture. Also the relationship between ψ_w and RWC (Fig. 4) differed markedly between the three species in both favourable and unfavourable conditions. Similarly, the large differences between the relationships of ψ_w to RWC of the three species cannot be explained by the soil moisture regime as the data for *Retama* in the non-droughted habitat lies between those of *Anthyllis* and *Stipa*. These differences between the species were most marked in the early morning, suggesting that each responded differently to external factors as the day progressed.

One inherent property of the species that could explain some of their differential responses, is the localization of the stomata (Meidner and Mansfield 1968) (Fig. 5). In *Stipa*, with minimum change in sensitivity to VPD from spring to summer, the stomata are at the base of deep grooves and additionally, in summer, most leaves are folded (Pugnaire *et al.* 1996). In *Anthyllis* and *Retama*, the stomata are at the leaf/cladode surface and so are more exposed to free air. Hall *et al.* (1976) have shown that vegetation can differ in their response to changes in g_S in relation to changes in VPD and that these differences are not related to habitat. Our results support these findings.

In all three species, g_s was correlated positively with ψ_w and RWC and negatively with VPD during the 2 to 4 h after dawn but not later in the day. The failure of g_s to increase with increase in ψ_w and RWC and with the decrease in VPD from late afternoon onwards (Figs. 1*C*, 2*C*, 3*C*), was due to the fact that ψ_w and RWC had not regained their early morning values in this period.

Our hypothesis that plant-soil water relations can explain the distributions of *Stipa*, *Anthyllis* and *Retama* was supported for *Retama* but not for *Stipa* and *Anthyllis*. Thus *Stipa* water relations could not explain its absence from the fan or flood plain habitats. Scattered plants of normal vigour, propagated by seed, are present in the fan habitat. *Stipa*'s clonal habit of growth, with little dispersal by seed, can be a factor in confining it to its present habitat (Haase *et al.* 1995). Its slow growth in the juvenile stage may be a factor barring it from the flood plain where there are sporadic flash floods, on average once every 2 - 3 years (Domingo *et al.* 2001). Factors other than plant-soil water relations must therefore explain its present distribution.

Similarly, plant-soil water relations cannot explain the fact that *Anthyllis* is largely confined to the fan habitat because there are mixed stands of *Anthyllis* and *Stipa* on the upper slopes and scattered plants of *Anthyllis* on the flood plain. The cessation of occasional cultivation of the fans could enable *Anthyllis* to colonise and become established in this habitat. *Anthyllis*'s almost complete absence from the flood plain, as with *Stipa*, probably concerns the establishment phase.

Retama by contrast, requires more water in the growing season than can be supplied by either the fan or the upper slope habitats (Domingo *et al.* 2001).

In conclusion, results suggest that in terms of water relations, *Anthyllis* and *Stipa* would be successful in a wider range of habitats than at present occupied in the Rambla Honda, hence other factors must be involved in determining their distribution. However, *Retama* is confined to the flood plain in the Rambla Honda because it is the only one of the three habitats where sufficient water is available all the year round because of the presence of deep-seated stored water that it can utilise (Haase *et al.* 1996, 1999, Domingo *et al.* 1999, 2001).

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