

Linking population density and habitat structure to ecophysiological responses in semiarid Spanish steppes

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Abstract We have studied the underlying factors responsible for the heterogeneous ecophysiological status of a semiarid *Stipa tenacissima* L. steppe in a subcatchment of SE Spain by assessing population composition and habitat structure of *S. tenacissima* stands. To do this, we measured and estimated 18 variables (11 biotic and seven abiotic) in 15 plots randomly distributed in the subcatchment, and then zoned this area by plot affinity using PCA. This analysis produced three sectors determined mainly by *S. tenacissima* cover and soil depth variables. The linear relationship fitted between *S. tenacissima* tussock biomass and tussock density in monospecific stands (both logarithmic) indicated a curve close to -1 , suggesting that the system is close to the maximum constant yield state. Ecophysiological measurements (gas exchange, fluorescence and individual leaf area index) were taken in two periods with different water availability in a representative plot in each sector. The intraspecific competition (inferred from the density dependence of green biomass) and rock outcrops were the main factors influencing the ecophysiological status in the study area. While, in

the wet season, intraspecific competition regulated water consumption in zones where *S. tenacissima* tussocks (monospecific stands) are dominant, during the dry season, stands in zones with extensive rock outcrops and stone cover (tussocks in “soil pockets”) had no access to non-rainfall water gains because of the adjacent bare soil, and so in these stands, gas exchange was lower and photoinhibition higher. This article stresses the importance of considering the connection between tussocks and bare-ground interspace in the functional and structural analysis of semiarid steppes.

Keywords Biomass-density relationship · Intraspecific competition · Self-thinning · *Stipa tenacissima* · Soil connectivity

Introduction

Vegetation development is subject to the amount and distribution of resources, which in turn depends on the number of individuals, and their proximity to each other (Harper 1977). In monospecific stands, intraspecific competition is responsible for the growth rate of individuals within a population, and its intensity could generate a self-thinning process in which density-dependent mortality affects the smallest individuals in dense populations (Silvertown 1982). This process describes the inverse power relationship between the average biomass per individual and survival densities

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in a plant population, as mathematically formalized by Yoda et al. (1963), later known as the “Yoda law or $-3/2$ power rule” (White and Harper 1970). In high-density (N) monocultures, intraspecific competition regulates plant growth or mean biomass per plant (\hat{w}) until by the “law of constant final yield” (Kira et al. 1953), defined as $\hat{w} = KN^{-1}$ (K is a constant), the reduction in mean plant weight is proportionally compensated by increased population density. In this state, environmental resources limit plant yield, which becomes independent of density and competition becomes less prominent (Harper 1977). This condition is to be expected in poor or degraded environments where plant–plant competition depends on availability of spatio-temporal resources. For example, in arid and semiarid zones where water is the main limiting resource, vegetation attributes like cover, density, biomass, nutrient acquisition and evapotranspiration (e.g. Puigdefábregas and Sánchez 1996; Ivans et al. 2003; Kurc and Small 2004; Reynolds et al. 2004; Ramírez et al. 2007), and the type and intensity of competition are subject to water dynamics (e.g. Bertiller et al. 1996; Maestre and Cortina 2004a; Armas and Pugnaire 2005).

Arid and semiarid resources and spatial vegetation arrangements are eminently heterogeneous (Tongway et al. 2004), mainly because of the irregular rainfall events in these zones (Lázaro et al. 2001; Sher et al. 2004; Schwinning and Sala 2004). When it rains, water redistribution is not uniform due to its dependence on soil surface (Valentini et al. 1999) and vegetation patches (Puigdefábregas and Sánchez 1996). Puigdefábregas et al. (1999) believe the heterogeneity of such local factors as “soil pockets”, plant distribution patterns and infiltration do not allow large-scale flow rate synchronization or redistribution of resources in semiarid catchments. In the semiarid Mediterranean region, *Stipa tenacissima* L. is the most representative vegetation type (Le Houérou 2001). Recent studies analysing spatial heterogeneity in such grassland ecosystems in SE Spain using assessments made at the same moment in time suggest that its spatial patterns and patch attributes (spatial heterogeneity) significantly affect structural and functional ecosystem characteristics (Maestre and Cortina 2004b; Maestre 2006). On the other hand, studies analysing temporal heterogeneity in one representative stand have found that temporal water availability (water shortage periods) in such zones is counterbalanced by

species morphophysiological attributes. In-depth studies (Pugnaire and Haase 1996; Pugnaire et al. 1996; Haase et al. 1999; Valladares and Pugnaire 1999; Balaguer et al. 2002; Domingo et al. 2002) have shown that stomatal closure, leaf folding, reversible senescence, morphological photoprotection, de-epoxidation of xanthophylls and a + b chlorophyll concentration reduction are the main functional mechanisms of *S. tenacissima*. However, no work has been done relating the temporal ecophysiological patterns to population composition and habitat structure in these steppes. This approach could help determine the role of the factors responsible for the heterogeneity of *S. tenacissima*'s physiological performance.

We assessed the ecophysiological performance and population structure of *S. tenacissima* L. stands in SE Spain in two different water availability seasons. Our main goals were to analyse: (i) the density-dependent effects on biomass composition and tussock size in *S. tenacissima* stands and (ii) the influence of the main environmental factors (vegetation attributes, topographic variables and bare soil conditions) on their heterogeneous ecophysiological responses. Water competition in *S. tenacissima* stands is an important characteristic that affects tillers in the same tussock and also interspecific relationships (Puigdefábregas and Sánchez 1996; Maestre et al. 2003; Armas and Pugnaire 2005; Maestre 2006). We hypothesize that intraspecific competition is mainly responsible for the difference in the ecophysiological pattern in *S. tenacissima* stands, and that how influential this is depends on habitat quality (structural restrictions) and water seasonality (water restrictions).

Materials and methods

The study area

We assessed *S. tenacissima* L. stands in a South-facing subcatchment (19 ha, altitude and slope range from 479 to 800 m a.s.l. and 37–73%, respectively) located in the Ventós-Castelar aquifer recharge area (38°28' N, 0°37' W) in the “Ventós” catchment (Agost, Alicante, Spain) (Fig. 1). The soil is a calcareous regosol (FAO-UNESCO) silt loam developed over marls and calcareous bedrock (Chirino 2003). The vegetation is dominated by *S. tenacissima*, a perennial rhizomatous tussock grass species with vegetative and

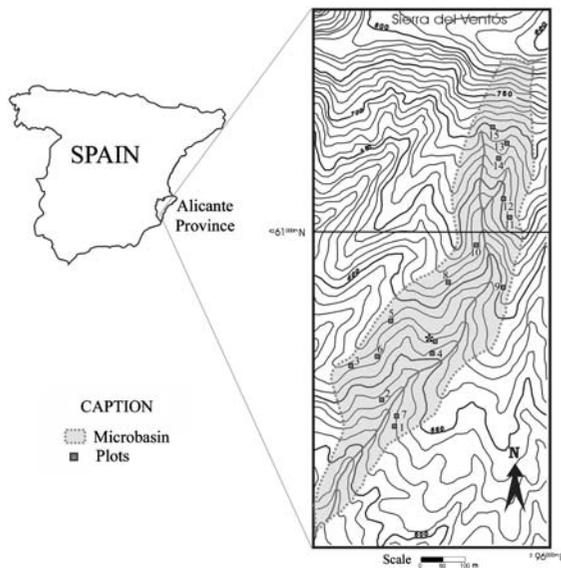


Fig. 1 Map of the study area showing the 15 plots sampled using habitat structure analysis. One plot (*) was added for the population structure analysis and the ecophysiological assessment

sexual reproduction (see Sánchez and Puigdefábregas 1994, for morphological characterization of this species).

The climate in the “Ventós” catchment is “Mediterranean” and “semiarid” according to the Köppen and Thornthwaite classification (Guijarro 1981). Rainfall events are scarce and highly variable over both time and space, with a severe water deficit in the summer (July and August). The yearly average rainfall (1998–2004, “Ventós 2” meteorological station: 38°27' N, 0°37' W) in the study area is 269.6 mm. The wettest and the driest months of the year are September–October (36.4–34.3 mm) and July–August (9.6–13.3 mm), respectively (Chirino 2003; Ramírez 2006). The average yearly temperature is 17.4°C, and the maximum and minimum monthly temperatures are 26.3°C in August and 11.7°C in January, respectively (Chirino 2003).

Plot characterization

Fifteen plots (10 × 10 m²) in the subcatchment were sampled at random, five plots for each of the three aspect ranges, south–west, south–east and south–south (Fig. 1). The following biotic and abiotic variables in the plots were measured and estimated:

- *Total plant cover*: The crown at maximum height, (Diameter 1) and a line perpendicular to it (Diameter 2) were measured for each individual plant in the plot. Each individual plant cover area was fitted to the ellipse formed by the two diameters measured.
- *Plot leaf area index*: A “fish-eye” optical sensor (“Plant Canopy Analyser” Model LAI-2000, LICOR Biosciences Inc., Nebraska, USA) was used to estimate the plot leaf area index (LAI_{plot}), and eight LAI_{plot} measurements were taken using two different optical apertures (90° and 180°) depending on the sensor position in the plot.
- *Species and vertical structure diversity*: The Shannon–Weaver species diversity index (Hs, bits/individual) was calculated using individual plant cover in each plot:

$$Hs = - \sum p_i \log_2 p_i \quad (1)$$

where p_i is the relative cover of perennial i -species (for a list of the species assessed see Appendix 1). One hundred and twenty one points per plot were systematically sampled, measuring vegetation height at each sampling point by placing a 1.8-m-long graduated stick upright next to the plant and recording the number of contacts at each of 9 heights (every 0.2 m from the ground). Vertical structure diversity (Hv) was estimated in a similar manner, using the Shannon–Weaver formula (1) where p_i was the relative number of vegetation contacts at i -height.

- *Tussock size groups (TSG)*: *S. tenacissima* tussocks were classified in five size groups according to their average diameter (\emptyset), TSG 0: $\emptyset < 0.15$ m, TSG 1: $0.15 \text{ m} \leq \emptyset < 0.30$ m, TSG 2: $0.30 \text{ m} \leq \emptyset < 0.60$ m, TSG 3: $0.60 \text{ m} \leq \emptyset \leq 1.20$ m and TSG 4: $1.20 \text{ m} < \emptyset$. The homogeneity of the number of tussocks in each TSG was found by calculating the variability coefficient (CV = standard deviation/average).
- *Relative dead foliar (litter) cover from Stipa tenacissima tussocks (RDFC)*: The amount of litter accumulated is an indicator of tussock age in this species (Sánchez and Puigdefábregas 1994). Therefore, RDFC was assessed by placing a wooden frame with a nylon grid in it over the tussocks. Four tussocks belonging to four TSGs (1, 2, 3 and 4 + 5) per plot were assessed. A

different size frame was used depending on the TSG measured, so TSG 1, 2 + 3 and 4 + 5 frame and grid areas were 0.04 m² and 4 × 10⁻⁴ m², 0.25 m² and 25 × 10⁻⁴ m², and 1 m² and 100 × 10⁻⁴ m², respectively. One hundred sampling points (vertexes of the squares in the nylon grid) were examined to find out whether the first leaf layer intercepting each point was green or dead, by inserting a thin metal rod perpendicularly at each sampling point.

- *Topographical variables*: The altitude, aspect azimuth (compass model A-10, Suunto) and slope (manual clinometer Model SLT-100, Tajima, Japan) were measured for each plot. Then the aspect (measured as compass direction) was converted into a symmetrical scale (from -90 to +90) following the procedure of Ferrer-Castán et al. (1995).
- *Rock cover*: Gravel and rock cover were systematically sampled at 121 sampling points, by dividing the plot into 1-m² squares, and assessing rock and gravel at each vertex.
- *Soil depth*: The plot was divided into 4-m² squares. We estimated the soil depth by driving a steel stake (0.5 m long) into the ground at each vertex of the grid (36 sampling points) and measuring the length of the stake remaining above ground. The average and the variability coefficient of the soil depth in each plot were used for the affinity analysis (see below).

Analysis of the biomass-density relationship in *S. tenacissima* stands

Stipa tenacissima tussock green biomass (bm) was estimated using an allometric equation fitted by Gasque (1999) in *S. tenacissima* grasslands in SE Spain:

$$bm = 1,027 c^{0.735} \quad (2)$$

where c is the cover area projected by the tussock. To assess the relationship between total green biomass and tussock density where *S. tenacissima* is dominant, a non-linear regression analysis of these variables was performed using Sigma Plot 2000 software (Spss Science, Chicago, Illinois, USA) in plots where *S. tenacissima* cover was >50% of the total plant cover. The average biomass per tussock versus density

relationship in monospecific *S. tenacissima* grasslands (according to de Kroon and Kalliola's 1995 perspective in clonal graminea species) was evaluated within "species boundary lines" (*sensu* Weller 1990) or "population boundary lines" (*sensu* Sackville Hamilton et al. 1995) in the subcatchment using the following equation:

$$\text{Log } \hat{w} = C - b \log N \quad (3)$$

where \hat{w} is the average green biomass per tussock in the plot (g tussock⁻¹), N is the tussock density, C is a constant and $-b$ is the self-thinning slope. The linear fit was found by regression analysis using SPSS v.14 software (SPSS Inc., Chicago, IL, USA).

Correlation and plot ordination

Eighteen variables (11 biotic and seven abiotic), measured and estimated as described above, were analysed. These variables were the total density of *S. tenacissima* tussocks, variability coefficient of the number of *S. tenacissima* tussocks in TSG 0-4, *S. tenacissima* cover, total herbaceous and shrub plant cover, RDFC of *S. tenacissima* in TSG 0, 1, 2 and 3 + 4, Shannon-Weaver species diversity and vertical structure index, plot leaf area index (LAI_{plot}), converted aspect, slope, percentage of gravel and rock, average and variability coefficient of soil depth. The Spearman correlation matrix for the 18 variables in the 15 plots was calculated using Statistica v.5 software (Statsoft Inc., Tulsa, Oklahoma, USA). Plot affinity was assessed by proximity in a multivariate space defined by factors extracted from a principal components analysis (PCA). This enabled us to zone the subcatchment into ecophysiological assessment sectors, from which highly correlated variables (Spearman coefficient value >0.7) were removed for orthogonality. We determined the weight of each orthogonal variable in the classification of the 15 plots by PCA using SPSS v.14 software (SPSS Inc., Chicago, IL, USA).

Gas exchange and chlorophyll fluorescence assessments

One representative plot per sector, as determined by PCA analysis, was taken for ecophysiological assessment in two periods with different water availability, January 15–23, 2004 (early winter, wet season) and August 12–19, 2004 (summer, dry

season). Instantaneous net photosynthesis and transpiration in the *S. tenacissima* leaves were measured using a portable open photosynthesis system (LI-COR 6400 Model, LI-COR Biosciences Inc., Nebraska, USA). A group of three or four leaf sections was placed in the leaf chamber at a fixed photosynthetic photon flux density (PPFD) so that all samples would reflect the same condition. Measurements were taken at 8:00, 12:00 and 16:00 solar time, where the fixed PPFD in the leaf chamber was the average PPFD at the solar time in the study area in the month assessed, that is $PPFD_{8:00} = 425$ and 940 , $PPFD_{12:00} = 890$ and 1999 , $PPFD_{16:00} = 100$ and $998 \mu\text{mol m}^{-2} \text{s}^{-1}$ in January and August, respectively. The other fixed variables in the leaf chamber were air flow rate = $500 \mu\text{mol s}^{-1}$, reference CO_2 concentration = $370 \mu\text{mol CO}_2 \text{mol}^{-1}$. In order to keep the chamber microclimate and leaf temperature from influencing the transpiration rate, we set the same relative humidity (30%) and leaf temperature (24°C) in the chamber for each time of day assessed based on atmospheric information from our study area (meteorological station “Ventos 2”: $38^\circ 27' \text{N}$, $0^\circ 37' \text{W}$). These settings were the mean atmospheric relative humidity and temperature between 8:00 and 16:00 h solar time in winter (December) and summer (August) in previous years (2000–2003). To compare meteorological conditions on the days assessed, we placed a PPFD sensor (HA-LI HOB0, Onset Computer Corporation, USA) with an internal data logger recording outputs every 5 min in each plot evaluated. The PPFD on days assessed were compared by a *t*-test. The gas exchange was analysed in 12 tussocks in three TSGs, 0 + 1 (small), 2 (medium) and 3 + 4 (large). 12, 16 and 32 samples were taken for small, medium and large tussocks, respectively. A two-way ANOVA with repeated time measurements tested the effects of sector and time on gas exchange variables. The gas exchange measures were transformed using a logarithmic function (Zar 1999) to correct for deviation from the norm and heterogeneity of variance.

The individual green leaf area index was found for 32 samples taken from four large tussocks by inserting a metal parallelepiped (0.01 m^2 and 0.3 m high) randomly into the tussocks. The green leaf area inside the parallelepiped was estimated using the allometric functions fitted by Ramírez et al. (2006), and measured by multiplying length by width and scanning *S. tenacissima* leaves.

Due to the fact that *S. tenacissima* grasslands are subjected to maximum water and light stress conditions in summer, resistance to these stresses in the subcatchment sectors defined by PCA analysis were compared for this season, and included chlorophyll fluorescence in the ecophysiological assessment for the same reason. This was done on consecutive days after monitoring the gas exchange using a portable fluorometer (Model PAM-2000, Walz, Effeltrich, Germany) to measure and calculate maximum photosystem II photochemical efficiency (F_v/F_m) at dawn and at midday and relative quantum yield ($\Phi \text{ PSII}$) at 8:00, 12:00 and 16:00 solar time. To assess F_v/F_m at midday, the sampled leaves were adapted to the dark 1 h before measurement. F_v/F_m was estimated by:

$$F_v/F_m = (F_m - F_0)/F_m \quad (4)$$

where F_0 is the minimal fluorescence yield as measured in weak light after adaptation to the dark, F_m is the maximal fluorescence yield after adaptation to the dark. $\Phi \text{ PSII}$ was calculated by the Genty et al. procedure (1989):

$$\Phi \text{ PSII} = (F'_m - F_t)/F'_m \quad (5)$$

where F_t is the fluorescence in natural light and F'_m is the maximum fluorescence during a saturation pulse. Fluorescence was measured in 20 samples per plot, each of which consisted of three to four leaves marked and taped together. TSG sample sizes were:

Large and medium tussocks: 2 cardinal points (N and S) \times 4 tussocks \times 2 TSG = 16 samples

Small tussocks: 1 sample \times 4 tussocks = 4 samples

A one-way ANOVA tested the sector effect on F_v/F_m and $\Phi \text{ PSII}$ at each assessment time.

Soil moisture

One day before the gas exchange and chlorophyll fluorescence assessment, volumetric soil water content (θ) in the plots was measured using Time Domain Reflectometry (TDR) (Model TDR 100, Campbell Scientific Ltd., IK) in ten pairs of steel rods (0.1 m long) randomly inserted into the soil of each plot ($n = 150$). We used the soil calibration equation fitted by Chirino (2003) in our study area: $\theta = -5.41 + 3.06 K - 0.10 K^2 + 0.02 K^3$; $r^2 = 0.99$; $P < 0.01$, where K is the dielectric constant recorded by the TDR.

Results

Stipa tenacissima population structure

We evaluated a total of 1,000 *S. tenacissima* tussocks in the study area. The minimum and maximum percentages of *S. tenacissima* cover – total plant cover were: 3.1% (Plot 2) – 31% (Plot 14) and 44.4% (Plot 9) – 56.6% (Plot 5), respectively (Fig. 2). Tussock size groups (TSG) with $\varnothing < 0.3$ m (TSG 0 and 1) had the highest average density (29.60 ± 5.53 tussocks plot^{-1}) and were dominant in 67.7% of the plots assessed (data not shown). The logistic function was fitted to the ratio of density to projected cover of *S. tenacissima* tussocks in the plot (Fig. 2). This function indicates asymptotic behaviour in *S. tenacissima* projected cover, so for tussock density over 0.9 tussock m^{-2} , the

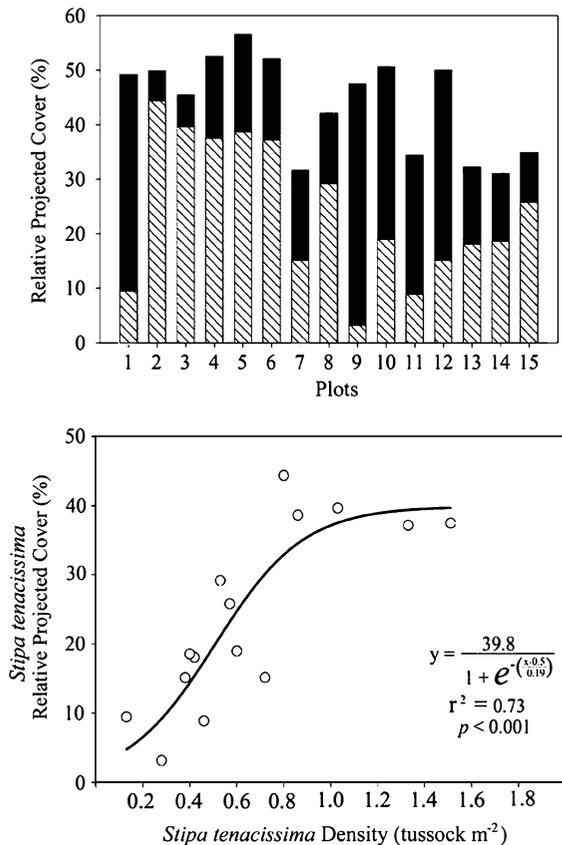


Fig. 2 In the top graph, the black and striped bars indicate relative projected cover of the total plant and *Stipa tenacissima*, respectively, in each plot. The bottom graph shows the relationship between *S. tenacissima* density and relative projected cover

projected cover does not exceed around 40% (Fig. 2), suggesting competition among tussocks.

Analysis of green biomass per m^2 versus total density of *S. tenacissima* tussocks in the plots suggested the same pattern observed in the paragraph above. Changes in green biomass per area are compensated for by changes in density up to 0.9 tussock m^{-2} , where green biomass remains constant (452.2 g m^{-2} approximately, Fig. 3). At high *S. tenacissima* tussock densities, the average tussock size (projected cover per tussock) falls (Fig. 3). The “population boundary line” estimated from monospecific *S. tenacissima* stands in the study area shows a slope of -0.89 (Fig. 4).

Subcatchment zoning

The main relationships among sample variables in the subcatchment found with the Spearman correlation matrix analysis (Table 1) were:

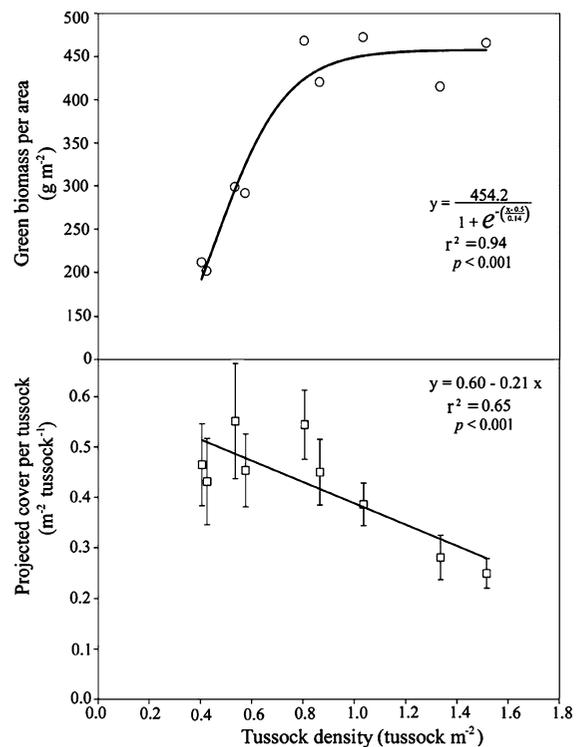


Fig. 3 The top graph shows the relationship between *Stipa tenacissima* tussock density and green biomass per plot area, to which a logistic curve was fitted. The *S. tenacissima* tussock density versus average projected cover per tussock relationship is shown in the graph below, to which a linear function was fitted. Only the plots where the *S. tenacissima* projected cover was $>50\%$ of total plant cover were assessed

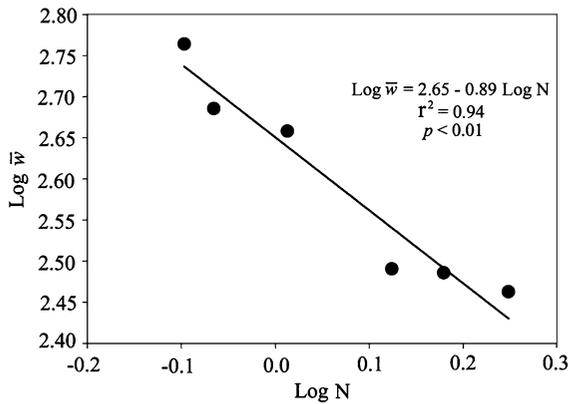


Fig. 4 Species boundary line in monospecific *Stipa tenacissima* stands in the subcatchment studied. Log average green biomass per tussock (Log \bar{w}) versus the log of *S. tenacissima* tussock density in the plot (Log N) was fitted to a linear function. Plots where the *S. tenacissima* projected cover was >80% of the total plant cover were assessed (2, 3, 4, 5, 6 and * plots, see Fig. 1) for this analysis

- In places in the subcatchment with high *S. tenacissima* density and cover, species diversity was low.
- Hillside aspect showed significant relationships to *S. tenacissima* cover, vertical structure diversity, plot leaf area index (LAI_{plot}), and average and variability of soil depth. Thus *S. tenacissima* cover was highest on southeast-facing hillsides, whereas LAI_{plot}, vertical structure diversity and average soil depth were greatest on southwest-facing hillsides where there is little soil variability.

- In the highest places, rock cover on soil and variability of soil depth increased, whereas average soil depth and total plant cover fell. Relative dead foliar (litter) cover was also high in small *S. tenacissima* tussocks ($\varnothing < 0.15$ m).
- Vertical plant structure was high in places characterized by deep soil.

The first three components extracted from the principal component analysis (PCA) explained 69.3% of total variance (Table 2). The first component is determined by altitude and total plant cover, whereas *S. tenacissima* cover, hillside aspect, slope and depth

Table 2 Principal components analysis results

	Comp 1	Comp 2	Comp 3	Comun.
CV	0.24	-0.42	-0.21	0.28
<i>Stipa tenacissima</i> cover	-0.41	0.86	-0.03	0.90
Aspect	0.21	0.81	-0.29	0.78
Total plant cover	-0.77	0.12	0.36	0.73
RDFC TSG-0	0.69	-0.10	0.44	0.68
RDFC TSG-1	0.66	-0.01	0.41	0.59
RDFC TSG-2	0.69	-0.11	0.30	0.57
Vertical structure diversity	-0.57	-0.28	0.64	0.81
Green LAI	-0.30	-0.32	0.81	0.84
Slope	0.12	0.71	0.27	0.56
Altitude	0.75	0.10	0.29	0.67
Depth soil	-0.65	-0.71	0.06	0.90
Eigenvalue	3.65	2.73	1.93	
% Total Variance	30.45	22.78	16.09	69.32

The table shows the weight and communality (Commun.) of each variable belonging to three extracted components (Comp.). In grey, weights > 0.71 and communalities > 0.85. CV = coefficient of variability of the number of *S. tenacissima* tussocks in each tussock size group (TSG: 0–4), RDFC = relative dead foliar (litter) cover of the *S. tenacissima* tussocks

Table 1 The Spearman correlation matrix of biotic and abiotic variables in 15 plots ($P < 0.05$)

	<i>Stipa</i> Density	CV	<i>Stipa</i> Cover	ASP	Plant Cover	RDFC	RDFC TSG 0	RDFC TSG 1	RDFC TSG 1	RDFC TSG 3+4	Hs	Hv	LAI	Slope	Alt	Grav	Rock	Depth
CV	-0.22																	
<i>Stipa</i> Cover	0.81	-0.34																
ASP	0.50	-0.28	0.69															
Plant Cover	0.44	-0.31	0.42	-0.01														
RDFC TSG 0	-0.09	-0.22	-0.29	0.04	-0.08													
RDFC TSG 1	-0.05	0.00	-0.20	0.32	-0.39	0.56												
RDFC TSG 2	-0.28	0.17	-0.29	0.14	-0.09	0.59	0.50											
RDFC TSG 3+4	-0.07	-0.10	-0.21	0.06	0.11	0.89	0.45	0.67										
Hs	-0.71	0.32	-0.94	-0.73	-0.26	0.36	0.21	0.34	0.38									
Hv	-0.05	0.10	-0.06	-0.33	0.51	-0.15	-0.11	-0.04	0.08	0.22								
LAI	-0.11	-0.02	-0.14	-0.59	0.49	0.00	-0.16	-0.26	0.11	0.31	0.62							
Slope	0.29	0.08	0.41	0.25	0.32	-0.12	-0.18	0.14	0.13	-0.23	0.00	0.04						
Alt	-0.45	0.04	-0.36	0.13	-0.66	0.45	0.51	0.32	0.42	0.37	-0.32	-0.27	0.10					
Grav	0.14	-0.07	-0.03	0.06	0.23	-0.04	0.27	-0.21	-0.14	0.02	0.17	0.25	-0.31	-0.32				
Rock	0.06	0.01	0.27	0.34	-0.23	0.15	-0.12	0.22	0.16	-0.30	-0.46	-0.51	0.42	0.57	-0.78			
Depth	-0.05	-0.05	-0.27	-0.70	0.43	-0.29	-0.32	-0.37	-0.29	0.36	0.52	0.64	-0.26	-0.66	0.44	-0.78		
CV Depth	0.06	0.08	0.27	0.59	-0.30	-0.04	0.25	0.12	0.06	-0.31	-0.29	-0.45	0.20	0.60	-0.32	0.57	-0.75	

CV = variability coefficient of the number of *Stipa tenacissima* tussocks in each tussock size group (TSG: 0–4), ASP = aspect, RDFC = relative dead foliar (litter) cover of the *Stipa tenacissima* tussocks in each tussock size group (TSG: 0, 1, 2, 3 + 4), Hs = species diversity Shannon–Weaver index, Hv = vertical structure Shannon–Weaver index, Alt = altitude, Grav = gravel cover, CV Depth = variability coefficient of soil depth

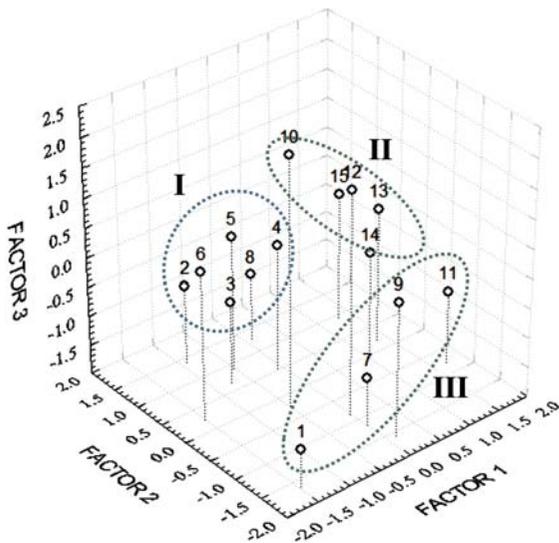


Fig. 5 Subcatchment zoning based on the proximity of the 15 plots in a 3D space from the three factors extracted from the principal components analysis taking 12 orthogonal environmental variables into consideration (see Table 2)

soil were the variables with the most weight in the second component. The third component was mainly influenced by LAI_{plot} . The PCA also indicated that *S. tenacissima* cover and soil depth determined most of the variability in the three components extracted (communality = 0.9), underlining the importance of these variables in the elucidation of environmental gradients in the subcatchment. Three affinity groups were recognized by plot proximity in the 3D space defined by the three factors extracted (Fig. 5). The main characteristics of these groups or “Sectors” were (averages in brackets):

Sector I: Group with the most *S. tenacissima* and total plant cover (37.7% and 49.8%, respectively), and also the least species diversity (1.3 bits/

individual) in the subcatchment. It is located in the lowest zone of the subcatchment (485 m a.s.l.), with steep slope (60.7%) and medium soil depth (0.14 m). *Sector II*: Located in the highest part of the subcatchment (655 m a.s.l.) with steep slope (57.8%), soil depth variability (90.5% variability coefficient) and rock cover on soil (49.0%). This sector had the shallowest soil (0.095 m average). *Sector III*: The least *S. tenacissima* cover (9.2%), highest species diversity (3.0 bits/individual) and deepest soil (0.22 m) in the subcatchment. This sector was spatially highly discontinuous and had the least plot affinity (Figs. 1, 5).

Gas exchange and chlorophyll fluorescence assessment

On the days assessed in early winter, the hourly average PPFD (standard error) from 6 to 18 h solar time was 658.3 (70.7), 543.2 (61.8) and 657.5 (70.4) $\mu\text{mol m}^{-2} \text{s}^{-1}$ in Sectors I, II and III, respectively. A few cloudy periods were observed on 23 January 2004 (assessment of Sector II) (Fig. 6a); however, no significant differences in the hourly PPFD were found for different days in a one-sample *t*-test ($P > 0.05$). In the summer, the hourly average PPFD (standard error) was 937.4 (66.3), 1058.2 (74.9) and 1118.8 (90.6) $\mu\text{mol m}^{-2} \text{s}^{-1}$ on days assessed in Sectors I, II and III, respectively. Summer days assessed were characteristically clear, with PPFD a little higher in Sector III, mainly at midday, than in the other Sectors, because it was at the top of a South–South aspect of the subcatchment and therefore more exposed to the sun in summer (see Plot 13 in Fig. 1). However, as in early winter, no significant differences in the hourly PPFD on different days were found by a

Fig. 6 Hourly photosynthetic photon flux density (PPFD) comparison on days when the ecophysiological assessment was carried out in each Sector in early winter (A) and summer (B). Assessments in Sectors I, II and III were made on 21, 23, 22 January 2004 in early winter, and 12, 10, 11 August 2004 in summer, respectively

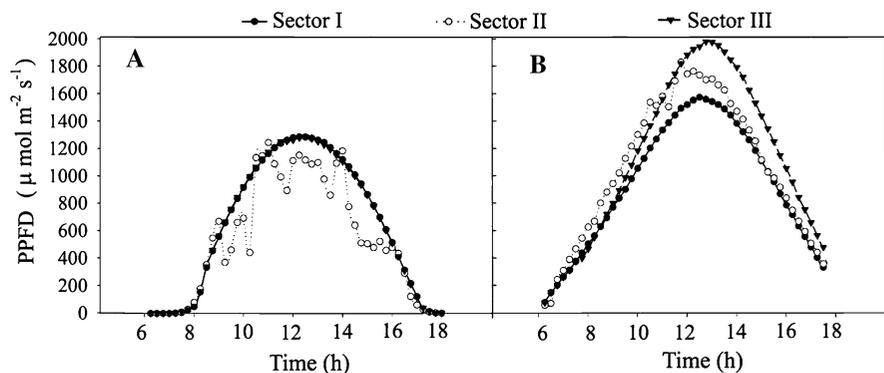


Table 3 Two-way ANOVA *F* values with repeated time factor measurements assessing the gas exchange variables in two seasons

		Early winter <i>F</i>	Summer <i>F</i>
E	Sector	26.4**	166.4**
	Time	307.0**	40.6**
A	Sector	8.1**	46.5**
	Time	524.0**	78.6**

E = transpiration, A = net photosynthesis

** $P < 0.001$ n.s. = no significant differences ($P > 0.05$)

one-sample *t*-test ($P > 0.05$). These results emphasize the similarity in meteorological conditions on days assessed and allowed us to continue with an ecophysiological sector comparison.

A two-way ANOVA analysis detected significant differences in gas exchange variables in the sectors and at times assessed in each period (Table 3). In early winter, soil moisture was relatively high ($\theta = 21.0 \pm 0.8\%$) due to heavy rainfall in the study area in autumn (in October and December 2003, the total rainfall was 145.3 mm or 48.5% of the yearly total precipitation). In this period, there was less gas exchange (transpiration and net photosynthesis) and a lower green leaf area index in Sector I (thick *S. tenacissima* density and wide cover) than in Sectors II and III (Fig. 7). The overall average transpiration, net photosynthesis and individual green leaf area index in the subcatchment were 1.57 ± 0.04 mmol H₂O m⁻² s⁻¹, 5.13 ± 0.16 μmol CO₂ m⁻² s⁻¹ and 4.19 ± 0.27 m² m⁻², respectively. However, in summer, with severe water stress ($\theta = 5.8 \pm 0.3\%$), the gas exchange in the *S. tenacissima* stands in Sector I was higher than in Sectors II and III. In this period, we also detected significant differences between Sector II (with medium *S. tenacissima* cover and shallow soil) and Sector III (with little *S. tenacissima* cover) (Fig. 7). The green leaf area index was higher in Sector III than in Sectors I and II in summer (Fig. 7). The overall average transpiration, net photosynthesis and individual green leaf area index in the subcatchment were 0.67 ± 0.02 mmol H₂O m⁻² s⁻¹, 1.29 ± 0.05 μmol CO₂ m⁻² s⁻¹, and 2.15 ± 0.12 m² m⁻², respectively. As we had set the same relative humidity and leaf temperature in the portable photosynthesis system chamber (30% and 24°C, respectively) for

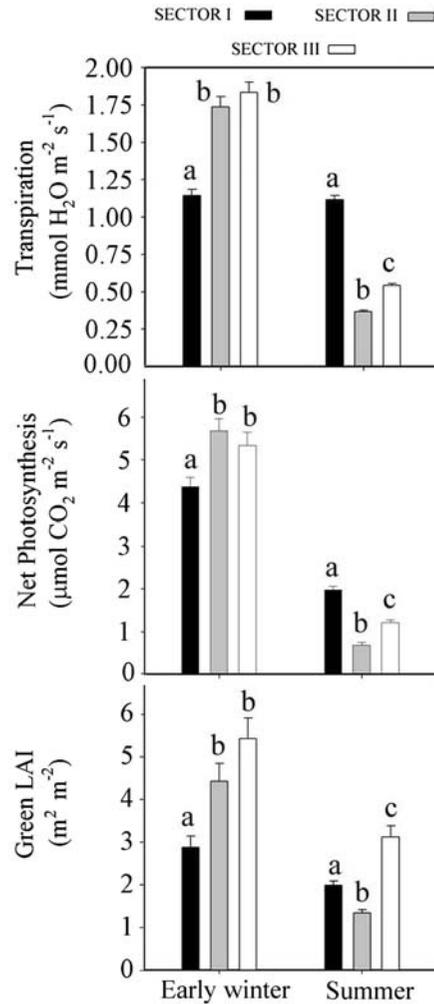


Fig. 7 Ecophysiological comparison of sectors in early winter and summer. Different letters in daily average gas exchange measurements (transpiration* and net photosynthesis) and individual green leaf area index (green LAI) comparisons mean significant differences among sectors detected by a Tukey HSD test ($P < 0.05$) of one-way ANOVA in each period assessed. Plots 5 (Sector I), 10 (Sector II) and 11 (Sector III) were assessed in early winter, whereas Plots * (Sector I), 13 (Sector II) and 11 (Sector III) were assessed in summer. *The transpiration rate was measured at a simulated constant VPD (by setting the same relative humidity and leaf temperature in the chamber for each time of day). The rates shown therefore do not reflect real transpiration

each time of day analysed, VPD simulated in the chamber was constant, and therefore, the transpiration rates in this study do not reflect real transpiration.

Other ecophysiological measurements in the high-stress season partly corroborated the gas exchange evaluation (Sector I > Sector III > Sector II), in which

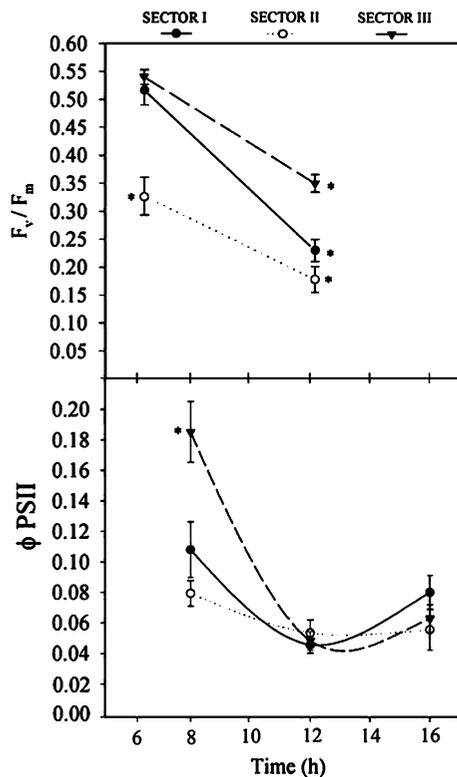


Fig. 8 Chlorophyll fluorescence during the high water-stress period (summer 2004). The sector hourly average maximum photosystem II (F_v/F_m) photochemical efficiency and relative photosystem II (Φ PSII) quantum yield were compared. An * next to the hourly average means significant differences detected by Tukey HDS test ($P < 0.05$) of one-way ANOVA

maximum photosystem II photochemical efficiency (F_v/F_m) in Sector II was lower at dawn and at midday (0.33 ± 0.03 and 0.18 ± 0.02 , respectively) (Fig. 8). F_v/F_m in Sector III at midday was found by the Tukey HDS test to be highly significant ($P < 0.05$). The relative quantum yield of photosystem II (Φ PSII) was high at 8:00 solar time, falling at midday with a slight recovery at 16:00 solar time (Fig. 8). Sector III Φ PSII was also significantly higher at 8:00 solar time (0.19 ± 0.02 , Fig. 8); however, no significant sector differences (Tukey HDS test, $P < 0.05$) were found at midday or 16:00 solar time.

Discussion

This article emphasizes the importance of considering population structure and soil connectivity in order to understand the heterogeneity of ecophysiological attributes in *S. tenacissima* grasslands. We found

evidence of density-dependency in *S. tenacissima* stands, possibly promoted by an intraspecific competition mechanism, where the slope of the population boundary line is close to -1 , meaning that the system is nearly at its maximum green biomass limit. In very dense *S. tenacissima* stands, this competition acts as a water consumption control factor, reducing gas exchange when soil water content is high. On the other hand, in the high water-stress season, the ecophysiological status of *S. tenacissima* stands on shallow soil, with rock outcrops and heavy stone cover, is significantly lower (less gas exchange and more photoinhibition) because of the poor connection between the root system and non-rainfall water gains from bare soil close to the tussock.

Density-dependent regulation by limitation of tussock size was observed in the *S. tenacissima* tussock population with maximum cover and 40%, or approximately 452 g m^{-2} , biomass in the subcatchment assessed (Figs. 3, 4). This could be caused by intraspecific competition due to limited resources. This argument is backed by mechanisms reported in *S. tenacissima* grasslands. Puigdefábregas and Sánchez (1996) suggested water competition among tussock tillers. They observed a significant increment in leaf growth and water content in soil close to the tussock when the tussock transpiration surface was small. Armas (2003) confirmed competition for soil resources, mainly water, among tussocks and tussock clones. Puigdefábregas and Sánchez (1996) suggest that strong competition among tillers is responsible for the smaller size of *S. tenacissima* tussocks during aging, when the tussock, which ages gradually from the centre outward, separates into new tussocks around the edges.

Assessment of the individual green leaf area index suggests self-thinning in *S. tenacissima* stands where tussocks in the plots with the lowest density (Sector III) are large and leafy (Fig. 7). In our study area, the *S. tenacissima* stand had been subjected to past management practices such as planting and pruning to increase productivity (Bonet 2004) due to the socio-economic importance of *S. tenacissima* fibre as a raw manufacturing material for paper paste, thread, baskets and jute. However, these activities ceased in the second half of the last century in SE Spain (Servicio del Esparto 1953). Stands in inaccessible (high) and inappropriate (with large rock outcrops) zones not subjected to management practices are therefore the oldest (Sectors II and III except Plots 1

and 7). This self-thinning was also observed by Armas and Pugnaire (2005) in mixed populations of *Cistus clusii* and mature *S. tenacissima* in Almería, SE Spain. In high-density gramineae populations, a reduction in reproductive capacity and tiller production is reported to be caused by intraspecific competition (Raventós and Silva 1995). Kays and Harper (1974) found that intraspecific competition caused a decrease in the number of tillers per genet in manipulative experiments with “rye grass” (*Lolium perenne*). De Kroon and Kalliola (1995) also found a rise in the individual leaf area index and stem volume per unit of ground area with low shoot density in *Gynerium sagittatum* (giant reed) under natural conditions in the Peruvian Amazonia.

The population boundary line slope (b) on hillsides where *S. tenacissima* tussocks are dominant (Sector I) in our subcatchment was close to -1 , which means that these zones are close to the maximum biomass that habitat resources can support. This process, common in modular organisms, is called the “law of constant final yield” (Kira et al. 1953), whereby density-dependent growth loss (and size) in individuals is proportionately compensated by increased density, resulting in a constant final yield. In “dynamic thinning line” (*sensu* Weller 1990) assessments, a -1 slope was found in gramineae species (*Festuca pratensis*, *Lolium perenne* and *Vulpia fasciculata*) by Lonsdale and Watkinson (1983) and Watkinson (1984), where self-thinning went from $-3/2$ to -1 when the populations reached their maximum stable growth or production. A -1 self-thinning slope was also found when populations of *Lolium perenne* were subjected to low radiation from self-shading by tillers where light was a limiting resource (Kays and Harper 1974; Lonsdale and Watkinson 1982). De Kroon and Kalliola (1995) found a -1 self-thinning slope in monospecific populations of *Gynerium sagittatum*, which they attributed to perennial shoots.

On hillsides with very dense *S. tenacissima* close to the “constant final yield” (or environmental carrying capacity), resource input (water pulses) could promote development of intraspecific competition among tussocks, which might explain the ecophysiological pattern found in the wet season (early winter). This process thus plays an important role in the control of water resource acquisition in high-density *S. tenacissima* stands in the subcatchment (Sector I) and might also explain the low gas exchange responses in Sector I

in the wet season (Fig. 7). On the other hand, the higher physiological potential in other sectors might be due to fewer tussocks or competitors for water resources. In the high water-stress season (summer), however, water loss in *S. tenacissima* is known to be reduced through such mechanisms as leaf folding and stomatal closure (Pugnaire et al. 1996; Balaguer et al. 2002). The “law of constant final yield” in the sector where *S. tenacissima* is dominant involves dependence on environmental resource supply, whilst competition is of less consequence under resource shortage conditions (Harper 1977). In the water-stress season, less competition among tussocks is therefore expected. Gas exchange in the sector with the densest *S. tenacissima* tussocks (Sector I) was higher than in the other sectors assessed. The range of stomatal conductance (21.8 – 43.1 mmol H₂O m⁻² s⁻¹) in Sector I was higher than reported in *S. tenacissima* stands in summer (0 – 0.08 mmol H₂O m⁻² s⁻¹; Pugnaire and Haase 1996; Balaguer et al. 2002). Ramírez et al. (2007) studied soil water vapour adsorption (WVA) in the study area, finding close correspondence between soil water gains from WVA and stand transpiration in summer. These authors suggest that *S. tenacissima* in our study area makes use of WVA for water gains. However, the use of this water by a shallow root system would require a connection between the tussock and the bare soil nearby. The soil in this study area, like Mediterranean rangelands, is shallow and discontinuous with poor structure and rock outcrops (Vallejo et al. 2000). Soil is shallower and more variable on the steeper hillsides (Table 1). The *S. tenacissima* tussocks in these areas are confined to “soil pockets” surrounded by rock outcrops, where the connection between the root system and bare soil is interrupted, and use of non-rainfall soil water gains (WVA) by the plant is impossible. This explains the low gas exchange and chlorophyll fluorescence responses in Sector III and Sector II (0.11 ± 0.01 and 0.09 ± 0.02 m soil depth and 70.3 and 44.6% rock cover, respectively, in the plots assessed) in the summer (see Figs. 6, 7).

The maximum photosystem II photochemical efficiency (F_v/F_m) found at dawn and the hourly pattern of relative photosystem II (Φ PSII) quantum yield are in close agreement with the results of Balaguer et al. (2002) in summer in *S. tenacissima* grasslands in SE Spain. The higher individual green leaf area index in *S. tenacissima* tussocks in Sector III (Fig. 7) could promote more self-shading, attenuating the negative

effect of high radiation and causing a higher F_v/F_m at midday and Φ PSII at 8:00 solar time (Fig. 8). Self-shading caused by tussock architecture is a key photoprotection factor in *S. tenacissima* (Valladares and Pugnaire 1999), especially in summer. Chlorophyll fluorescence confirmed the higher stress of the *S. tenacissima* population near the top of the sub-catchment (mainly Sector II). The excellent coherence of the ecophysiological descriptors (gas exchange and chlorophyll fluorescence) indicates that water availability spatially varies significantly in the study area, depending mainly on the interaction between the soil connection between tussocks and surrounding bare soil (soil availability) and *S. tenacissima* density. However as the ecophysiological variables tested in this study are instantaneous measurements, an integral physiological assessment would be required to test our hypothesis. Some advances have been made from this perspective. Maestre and Cortina (2006), for example, found that the local condition of bare soil, specifically a water infiltration indicator, was a key factor in the isotopic natural abundance of nitrogen ($\delta^{15}\text{N}$, an integral physiological indicator) in *S. tenacissima* stands in SE Spain.

In conclusion, we have found intraspecific competition and rock outcrops around the tussock (microsite)

to be the main factors responsible for spatial and temporal heterogeneity of ecophysiological status in *S. tenacissima* stands. Due to the extensive *S. tenacissima* grasslands in semiarid zones in the Iberian Peninsula, precaution must be taken in scaling or extrapolating water and carbon fluxes in these ecosystems, because significant differences in the ecophysiological condition of stands may be found in a relatively small area (in this case 19 ha). We recommend evaluation of integral physiological performance in *S. tenacissima* stands, including descriptors (soil depth, rock outcrops) of bare soil surrounding tussocks and the soil connection between them, because of their importance to gas exchange and chlorophyll fluorescence responses in semiarid steppes.

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Appendix 1 List of species sampled in the 15 plots assessed

Species	Life form	Func. group	Species	Life form	Func. group
<i>Anthyllis cytisoides</i>	P	Wd	<i>Helichrysum stoechas</i>	Ch	Wd
<i>Asparagus horridus</i>	P	Wd	<i>Helictotrichon filifolium</i>	Gh	G
<i>Asperula aristata</i>	H	F	<i>Juniperus oxycedrus</i>	P	Ws
<i>Asphodelus ramosus</i>	Gh	F	<i>Osyris quadripartita</i>	P	Ws
<i>Atractylis humilis</i>	Ch	F	<i>Paronychia suffruticosa</i>	Ch	Wd
<i>Brachypodium retusum</i>	H	G	<i>Phlomis lychnitis</i>	Ch	F
<i>Bupleurum fruticosum</i>	Ch	Wd	<i>Pinus halepensis</i>	P	Ws
<i>Carex halleriana</i>	H	F	<i>Polygala rupestris</i>	Ch	Wd
<i>Centaurea intybacea</i>	Ch	Wd	<i>Quercus coccifera</i>	P	Ws
<i>Cistus albidus</i>	P	Wd	<i>Rhamnus lycioides</i>	P	Ws
<i>Coronilla minima</i>	Ch	Wd	<i>Rosmarinus officinalis</i>	P	Wd
<i>Dianthus broteri</i>	Ch	F	<i>Ruta angustifolia</i>	Ch	Wd
<i>Erica multiflora</i>	P	Ws	<i>Sedum sediforme</i>	Ch	F
<i>Fumana ericoides</i>	Ch	Wd	<i>Sideritis leucantha</i>	Ch	Wd
<i>Fumana hispidula</i>	Ch	Wd	<i>Spartium junceum</i>	P	Wd
<i>Fumana laevipes</i>	Ch	Wd	<i>Stipa offneri</i>	H	G
<i>Fumana thymifolia</i>	Ch	Wd	<i>Stipa tenacissima</i>	H	G
<i>Galium fruticosum</i>	Ch	F	<i>Teucrium carolipau</i>	Ch	Wd

Appendix 1 continued

Species	Life form	Func. group	Species	Life form	Func. group
<i>Globularia alypum</i>	Ch	Wd	<i>Teucrium homotrichum</i>	Ch	Wd
<i>Helianthemum cinereum</i>	Ch	Wd	<i>Teucrium pseudochamaepitys</i>	Ch	F
<i>Helianthemum syriacum</i>	Ch	Wd	<i>Thymelaea argentata</i>	Ch	Wd
<i>Helianthemum violaceum</i>	Ch	Wd	<i>Thymelaea tinctoria</i>	Ch	Wd

The letters near to each species give the Life form: chamaephyte (Ch), hemicryptophyte (H), phanerophyte (P), geophyte (Gh); and Functional group (Func. group): perennial forb (F), perennial grass (G), woody (Wd = dwarf scrub, Ws = shrub) following Mateo and Crespo's (2001) review

References

- Armas C (2003) Balance de la interacción entre plantas superiores en ambientes semiáridos: mecanismos y procesos. PhD thesis, Universidad Autónoma de Madrid, Spain.
- Armas C, Pugnaire FI (2005) Plant interactions govern populations dynamics in a semi-arid plant community. *J Ecol* 93:978–989. doi:10.1111/j.1365-2745.2005.01033.x
- Balaguer L, Pugnaire FI, Martínez-Ferri E, Armas C, Valladares F, Manrique E (2002) Ecophysiological significance of chlorophyll loss and reduced photochemical efficiency under extreme aridity in *Stipa tenacissima* L. *Plant Soil* 240:343–352. doi:10.1023/A:1015745118689
- Bertiller MB, Zaixso P, Irisarri MP, Brevedan ER (1996) The establishment of *Festuca pallescens* in arid grasslands in Patagonia (Argentina): the effect of soil water stress. *J Arid Environ* 32(2):161–171. doi:10.1006/jare.1996.0014
- Bonet A (2004) Secondary succession of semi-arid Mediterranean old-fields in south-eastern Spain: insights for conservation and restoration of degraded lands. *J Arid Environ* 56:213–233. doi:10.1016/S0140-1963(03)00048-X
- Chirino E (2003) Influencia de las precipitaciones y de la cubierta vegetal en el balance hídrico superficial y en la recarga de acuíferos en clima semiárido. PhD thesis, University of Alicante, Spain
- de Kroon H, Kalliola R (1995) Shoot dynamics of the giant grass *Gynerium sagittatum* in Peruvian Amazon floodplains, a clonal plant that does show self-thinning. *Oecologia* 101:124–131. doi:10.1007/BF00328909
- Domingo F, Gutiérrez L, Brenner AJ, Aguilera C (2002) Limitation to carbon assimilation of two perennial species in semi-arid south east Spain. *Biol Plant* 45(2):213–220. doi:10.1023/A:1015136421445
- Ferrer-Castán D, Calvo JF, Esteve-Selma MA, Torres-Martínez A, Ramírez-Díaz L (1995) On the use of three performance measures for fitting species responses curves. *J Veg Sci* 6:57–62. doi:10.2307/3236256
- Gasque M (1999) Colonización del esparto (*Stipa tenacissima* L.) en sectores degradadas del clima semiárido. PhD thesis, Universidad Politécnica de Valencia, Escuela Técnica Superior de Ingenieros Agrónomos, Spain
- Genty B, Briantais JM, Baker NR (1989) The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *Biochim Biophys Acta* 99:87–92
- Guijarro JA (1981) Aproximación al clima de Alicante y su comarca. In: Excmo. Ayuntamiento de Alicante, (ed) El medio físico de la comarca de Alicante, Ayuntamiento de Alicante, Spain, pp 248–277
- Haase P, Pugnaire FI, Clark SC, Incoll L (1999) Environmental control of canopy dynamics and photosynthetic rate in the evergreen tussock grass *Stipa tenacissima*. *Plant Ecol* 145:327–339. doi:10.1023/A:1009892204336
- Harper JL (1977) Population biology of plants. Academic Press Inc., San Diego, CA, pp 857
- Ivans CY, Leffler AJ, Spaulding U, Stark JM, Ryel RJ, Caldwell MM (2003) Root responses and nitrogen acquisition by *Artemisia tridentata* and *Agropyron desertorum* following small summer rainfall events. *Oecologia* 134:317–324
- Kays S, Harper JL (1974) The regulation of plant and tiller density in a grass Sward. *J Ecol* 62(1):97–105. doi:10.2307/2258882
- Kira T, Ogawa H, Shinozaki N (1953) Intraspecific competition among higher plants. 1. Competition-density-yield inter-relationship in regularly dispersed populations. *J Inst Polytech Osaka Univ Ser D* 4:1–16
- Kurc S, Small EE (2004) Dynamics of evapotranspiration in semiarid grassland and shrubland ecosystems during the summer monsoon season, central New Mexico. *Water Resour Res* 40:1–15. doi:10.1029/2004WR003068
- Lázaro R, Rodrigo FS, Gutiérrez L, Domingo F, Puigdefábregas J (2001) Analysis of a 30-year rainfall record (1967–1997) in semi-arid SE Spain for implications on vegetation. *J Arid Environ* 48:373–395. doi:10.1006/jare.2000.0755
- Le Houérou HN (2001) Biogeography of the arid steppeland north of the Sahara. *J Arid Environ* 48:103–128. doi:10.1006/jare.2000.0679
- Lonsdale WM, Watkinson AR (1982) Light and self-thinning. *New Phytol* 90:431–445. doi:10.1111/j.1469-8137.1982.tb04476.x
- Lonsdale WM, Watkinson AR (1983) Tiller dynamic and self-thinning in grassland habitats. *Oecologia* 60(3):390–395. doi:10.1007/BF00376857
- Maestre FT (2006) Linking the spatial patterns of organisms and abiotic factor to ecosystems function and management: insights from semi-arid environments. *Web Ecol* 6:75–87
- Maestre FT, Cortina J (2004a) Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. *Proc R*

- Soc Lond B Biol Sci 271:S331–S333. doi:[10.1098/rsbl.2004.0181](https://doi.org/10.1098/rsbl.2004.0181)
- Maestre FT, Cortina J (2004b) Insights into ecosystem composition and function in a sequence of degraded semiarid steppes. *Restor Ecol* 12(4):493–501. doi:[10.1111/j.1061-2971.2004.03106.x](https://doi.org/10.1111/j.1061-2971.2004.03106.x)
- Maestre FT, Cortina J (2006) Ecosystem structure and soil-surface condition drive the variability in the foliar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of *Stipa tenacissima* in semiarid Mediterranean steppes. *Ecol Res* 21:44–53. doi:[10.1007/s11284-005-0091-4](https://doi.org/10.1007/s11284-005-0091-4)
- Maestre FT, Bautista S, Cortina J (2003) Positive, negative, and net effects in grass-shrub interactions in Mediterranean semiarid grasslands. *Ecology* 84(12):3186–3197. doi:[10.1890/02-0635](https://doi.org/10.1890/02-0635)
- Mateo G, Crespo MB (2001) Manual para la determinación de la flora valenciana, 2nd edn. Moliner 40-Gómez Coll S. L., Valencia-Spain, pp 503
- Puigdefábregas J, Sánchez G (1996) Geomorphological implications of vegetation patchiness on semi-arid slopes. In: Anderson MG, Brooks SM (eds) *Advances in hillslopes processes*, vol 2. John Wiley, New York, pp 1027–1060
- Puigdefábregas J, Sole A, Guitierrez L, del Barrio G, Boer M (1999) Scales and processes of water and sediment redistribution in drylands: results from the Rambla Honda field site in Southeast Spain. *Earth Sci Rev* 48:39–70. doi:[10.1016/S0012-8252\(99\)00046-X](https://doi.org/10.1016/S0012-8252(99)00046-X)
- Pugnaire FI, Haase P (1996) Comparative physiology and growth of two perennial tussock grass species in a semi-arid environment. *Ann Bot (Lond)* 77:81–86. doi:[10.1006/anbo.1996.0010](https://doi.org/10.1006/anbo.1996.0010)
- Pugnaire FI, Haase P, Incoll L, Clark SC (1996) Response of tussock grass *Stipa tenacissima* to watering in a semi-arid environment. *Funct Ecol* 10:265–274. doi:[10.2307/2389852](https://doi.org/10.2307/2389852)
- Ramírez DA (2006) Estudio de la transpiración del esparto (*Stipa tenacissima* L.) en una cuenca del semiárido alicantino: un análisis pluriescalar. PhD thesis, University of Alicante, Spain
- Ramírez DA, Valladares F, Blasco F, Bellot A (2006) Assessing transpiration in the tussock grass *Stipa tenacissima* L.: the crucial role of the interplay between morphology and physiology. *Acta Oecol* 30(3):386–398. doi:[10.1016/j.actao.2006.06.006](https://doi.org/10.1016/j.actao.2006.06.006)
- Ramírez DA, Bellot J, Domingo F, Blasco A (2007) Can water responses in *Stipa tenacissima* L. during the summer season be promoted by non-rainfall water gains in soil? *Plant Soil* 291:67–79. doi:[10.1007/s11104-006-9175-3](https://doi.org/10.1007/s11104-006-9175-3)
- Raventós J, Silva JF (1995) Competition effects and responses to variable numbers of neighbors in two tropical savanna grasses in Venezuela. *J Trop Ecol* 11(1):39–52
- Reynolds JF, Kemp PR, Ogle K, Fernandez RJ (2004) Modifying the “pulse reserve” paradigm for deserts of North America: precipitation pulses, soil water and plant responses. *Oecologia* 141:194–210. doi:[10.1007/s00442-004-1524-4](https://doi.org/10.1007/s00442-004-1524-4)
- Sackville Hamilton NR, Matthew C, Lemaire G (1995) In defence of the $-3/2$ boundary rule: a re-evaluation of self-thinning concepts and status. *Ann Bot (Lond)* 76:569–577. doi:[10.1006/anbo.1995.1134](https://doi.org/10.1006/anbo.1995.1134)
- Sánchez G, Puigdefábregas J (1994) Interactions of plant growth and sediment movement on slopes in a semi-arid environment. *Geomorphology* 9:243–260. doi:[10.1016/0169-555X\(94\)90066-3](https://doi.org/10.1016/0169-555X(94)90066-3)
- Servicio del Esparto (1953) *Estudios y Experiencias sobre el Esparto*, vol II. Ministerios de Industria y Comercio y de Agricultura, Madrid
- Sher AA, Goldberg DE, Novoplansky A (2004) The effect of mean and variance in resource supply on survival of annual from Mediterranean and desert environments. *Oecologia* 141:353–362. doi:[10.1007/s00442-003-1435-9](https://doi.org/10.1007/s00442-003-1435-9)
- Schwinnig S, Sala OE (2004) Hierarchy of responses to resources pulses in arid and semi-arid ecosystems. *Oecologia* 141:211–220
- Silvertown JW (1982) *Introduction to plant population ecology*. Longman Inc., New York, pp 209
- Tongway DJ, Cortina J, Maestre FT (2004) Heterogeneidad espacial y gestión de medios semiáridos. *Ecosistemas* 2004/1 (URL: <http://aet.org/ecosistemas/041/revision5.htm>)
- Valentini C, d’Herbes JM, Poesen J (1999) Soil and water components of banded vegetation patterns. *Catena* 37:1–24. doi:[10.1016/S0341-8162\(99\)00053-3](https://doi.org/10.1016/S0341-8162(99)00053-3)
- Valladares F, Pugnaire FI (1999) Tradeoffs between irradiance capture and avoidance in semi-arid environments assessed with a crown architecture model. *Ann Bot (Lond)* 83:459–469. doi:[10.1006/anbo.1998.0843](https://doi.org/10.1006/anbo.1998.0843)
- Vallejo VR, Serranoles I, Cortina J, Seva JP, Valdecantos A, Vilagrosa A (2000) Restoration strategies and actions in Mediterranean degraded lands. In: Enne G, Zanolla Ch, Peter D (eds) *Desertification in Europe: mitigation strategies land-use planning*. EC DGXII Environment and Climate Program, European Commission, Brussels, pp 211–233
- Watkinson AR (1984) Yield-density relationship: the influence of resource of availability on growth and self-thinning in population of *Vulpia fasciculata*. *Ann Bot (Lond)* 53:469–482
- Weller D (1990) Will the real self-thinning rule please stand up?—a reply to Osawa and Sugita. *Ecology* 71(3):1204–1207. doi:[10.2307/1937389](https://doi.org/10.2307/1937389)
- White J, Harper JL (1970) Correlated changes in plant size and number in plant populations. *J Ecol* 58:467–485. doi:[10.2307/2258284](https://doi.org/10.2307/2258284)
- Yoda K, Kira T, Osawa H, Hozumi H (1963) Intraspecific competition among higher plants. XI Self-thinning in overcrowded pure stands under cultivated and natural conditions. *J Inst Polytech Osaka City Univ* 14:107–129
- Zar JH (1999) *Biostatistical analysis*, 4th edn. Prentice-Hall Inc., New Jersey, pp 931