

## Comparative Physiology and Growth of Two Perennial Tussock Grass Species in a Semi-Arid Environment

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The physiology and growth of *Lygeum spartum* and *Stipa tenacissima*, two perennial tussock grasses which dominate wide areas of semi-arid south-eastern Spain, were compared at times of high and low availability of water, in autumn and summer respectively, to study the adaptation of this growth form to arid environments. The two species differed in morphological and physiological traits. *Stipa* tussocks were larger and had opportunistic growth, and *Stipa* leaves had a smaller specific area and lower diffusive conductance to water vapour. The two grasses were similar in maximum photosynthetic rate, leaf nitrogen concentration, and in the response to high light conditions but had different tissue water relations. *Stipa* was better suited to cope with drought and erratic rainfall, because of its more effective control of water loss and its growth patterns. *Lygeum* seems to be adapted to less dry conditions and more saline soils. The tussock growth form provides an adaptive advantage in these infertile environments by reducing radiation absorbance.

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**Key words:** Adaptation, growth, leaf extension, *Lygeum spartum*, perennial grassland, photosynthesis, semi-arid environments, *Stipa tenacissima*, tussock grass, water relations.

### INTRODUCTION

Perennial grasses are the most widespread species of herbs (McNaughton, 1991). Among them, those forming tussocks are present in the most infertile regions of the world, from arctic tundra (Miller, 1968) to dry environments (e.g. Distel and Fernández, 1988; Busso and Richards, 1993; Haase, Pugnaire and Incoll, 1995), suggesting that the tussock growth form may enhance survival under stressful conditions. Most tussock grasses are clonal plants with slow growth rates and relatively small root systems, in contrast to other perennial plants growing in the same environments, usually shrubs with high root-to-shoot ratios (Chapin, 1980; Rundel, 1991). Tussock grasses can form mounds of organic debris and fine soil particles which retain more water (Sánchez and Puigdefábregas, 1994) and have higher nutrient content than the soil between tussocks (Jackson and Caldwell, 1992; Ryel, Beyschlag and Caldwell, 1994; Puigdefábregas *et al.*, 1995). The upright leaves of the tussock also reduce light interception by the canopy at midday (Werk and Ehleringer, 1984), lowering the potential photoinhibition and damage of the photosynthetic apparatus (Ryel, Beyschlag and Caldwell, 1993) especially in arid environments with high irradiance.

In this paper we compare two tussock grass species, *Lygeum spartum* L. and *Stipa tenacissima* L., found in the driest environments of the Mediterranean basin. *Lygeum* has a wider geographical range and spreads throughout the Mediterranean basin (Tutin, 1980), while *Stipa* is restricted to the Iberian Peninsula and North Africa (Maire, 1968;

Martinovský, 1980). In south-east Spain, where both species are called *esparto*, they are widespread over uncultivated land and abandoned fields. Their predominance was documented in Roman times by Plinius, who called the region of Cartagena, close to our field site, *campus spartarius* (Freitag, 1971). Although they occur in the same geographical region, the two species generally occupy different sites. *Lygeum* is thought to be tolerant of saline soils (Freitag, 1971), and usually grows in washes and lower areas, while *Stipa* is more widespread and occupies higher altitudes and drier sites. Yet both are morphologically similar, and constitute one of the dominant growth forms in these environments. In this paper we compared the physiology and growth of these two species under favourable and unfavourable conditions to test their convergent adaptation to dry habitats.

### FIELD SITE

The field site was at the Ramblilla de Genaro, near Tabernas, Almería Province, Spain (37°01' N, 2°25' W, 300 m altitude) at the foot of the Sierra Alhamilla, 20 km north of Almería. The climate is semi-arid with a mean annual precipitation of less than 250 mm and a pronounced dry season from Jun. to Sep. Mean annual temperature over 25 years at Tabernas (490 m altitude, 3 km to the east) is 17.9 °C with mean maximum temperatures of 10.7 °C in January and 34.7 °C in August (R. Lázaro, unpublished). Environmental conditions (air temperature and humidity, wind velocity and direction, and irradiance) during the period of our experiment were recorded by an automatic weather station at the Rambla Honda, 9 km north of the field site and at 340 m higher altitude.

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## METHODS

Six tussocks of *Lygeum spartum* and six of *Stipa tenacissima* were selected at random in a mixed stand along the bank of a dry stream. Extension of four juvenile, not fully elongated leaves (each in a different tiller) per plant was measured weekly over two periods of 4 weeks. To compare plant traits during the wet and dry seasons, measurements were carried out in Nov.–Dec. 1993 and in May–Jun. 1994 on the same tussocks. All marked leaves were sampled in Jun., and extension growth and dry mass production between the two dates was determined for each tiller.

Physiological measurements were carried out on 2 Dec. 1993, after autumn rains in Oct. (24.8 mm) and Nov. (19.8 mm), when leaf growth was at a maximum, and again on 2 Jun. 1994, when growth was about to cease, as shown by continuous measurements of *Stipa* at the Rambla Honda. Gas exchange of fully developed, attached leaves was measured in the early morning and at midday with a portable gas exchange system and leaf chamber [LCA-3 and PLC-3(N), ADC Ltd., Hoddesdon, UK]. Six leaves were held together by a clip and enclosed in the leaf chamber and the chamber was orientated at a right angle to the solar beam. Measurements were replicated twice in each of six tussocks of each species. Photosynthetic rate ( $A$ ), leaf conductance to water vapour ( $g_l$ ), photon flux ( $PF$ ), and air temperature ( $T_a$ ) were measured and recorded automatically. The system also calculated leaf temperature ( $T_l$ ) by the leaf energy balance method, and specific gas exchange efficiency was calculated as  $A/g_{CO_2}$  (Farquhar, O'Leary and Berry, 1987). All gas exchange measurements were made at full sunlight. After the measurements were completed, the leaf segments enclosed by the chamber were harvested and leaf area was determined by an area meter (Mk2, Delta T Devices, Burwell, UK).

Chlorophyll fluorescence was measured at midday on randomly chosen leaves with a chlorophyll induction fluorometer (PEA, Hansatech, Kings Lynn, UK). Leaves were acclimated in darkness for at least 30 min prior to measurement. Fluorescence yield of PSII with all primary electron acceptors fully oxidised (minimum fluorescence,  $F_0$ ) as well as maximum fluorescence yield ( $F_m$ ) after applying a pulse of saturating light, were recorded. Variable fluorescence ( $F_v$ ) and the photochemical efficiency of PSII reaction centres were calculated as  $F_m - F_0$  and as the  $F_v/F_m$  ratio respectively (Genty, Briantais and Da Silva, 1987).

Chlorophyll concentration was determined following Arnon's method (1949) after extraction with 80% acetone and was expressed per unit leaf area. Total nitrogen (N) concentration was determined by Kjeldahl analysis and phosphorus (P) concentration by colorimetry (Watanabe and Olsen, 1965) of extracts from oven-dried samples of a set of leaves (two per tussock) harvested after gas exchange measurements had been completed in June. Nutrient pools were calculated as the product of nutrient concentration and mass per unit area of lamina.

Relative water content (RWC) which was measured at the same time as gas exchange, was determined by the method of Barrs and Weatherley (1962).

In another set of *Lygeum* leaves, the changes in the angle

between the two halves of the lamina and in RWC were determined on fully rehydrated leaves ( $n = 3$ ) which were allowed to dry out on a laboratory bench at room temperature and in low light. As the leaves dried, imprints of the cross sections of cut leaf segments were made consecutively on blocks of plasticine and the angle between the halves of the lamina was measured under a dissecting microscope.

Dawn and midday leaf water potentials ( $\psi_l$ ) were measured by a pressure chamber (SKPM 1400, Skye Instruments Ltd., Powys, UK). Tissue water relations were determined by the pressure-volume technique (Tyree and Hammel, 1972; Davis and Mooney, 1986).

Repeated measurements on the same tussock were averaged, and differences in means between species were compared by *t*-tests.

## RESULTS

*Climate*

After a dry summer (Jun.–Sep. rainfall = 0.7 mm) the autumn rains began in Oct. 1993 and lasted until late Nov., producing a total of 45 mm of rain in the Rambla Honda, our reference station. The 5-year average available shows a mean rainfall of 100 mm for these months. The following winter of 1993–94 was particularly dry (77.1 mm rainfall between Jan. and Jun. *vs.* an average of 147.8 mm), so that the water stress was accentuated in spring and summer of 1994. Temperature was lower than average by 1 °C in autumn and 1 °C above average between Jan. and Jun.

*Growth*

*Stipa* tussocks were taller and had longer, heavier leaves of smaller specific leaf area (Table 1) than those of *Lygeum*. Both species had the same number of green leaves per tiller; thus individual tiller mass was also greater in *Stipa*.

In late autumn, when water was available, the extension

TABLE 1. *General plant and leaf characteristics of Lygeum spartum and Stipa tenacissima in Almería, Spain. Nutrient determinations were made in June 1994; all others in December 1993*

	<i>Lygeum</i>		<i>Stipa</i>
Tussock height, cm	73.8 ± 6.5	*	80.4 ± 2.3
Leaf length, cm	53.5 ± 0.2	*	60.0 ± 0.1
Leaf dry mass, g	0.20 ± 0.01	**	0.46 ± 0.01
SLA, cm <sup>2</sup> g <sup>-1</sup>	27.1 ± 1.3	***	15.8 ± 0.3
Total Chl, g m <sup>-2</sup>	2.80 ± 0.59	**	4.06 ± 0.45
Chl a/b ratio	4.0 ± 0.4	ns	3.3 ± 0.1
N, mg g <sup>-1</sup> dry mass	7.8 ± 0.3	***	5.6 ± 0.2
P, mg 100 g <sup>-1</sup> dry mass	3.8 ± 0.5	ns	4.6 ± 1
N pool, g m <sup>-2</sup>	2.22 ± 0.07	***	6.25 ± 0.26
P pool, mg m <sup>-2</sup>	15.5 ± 2.6	*	36.8 ± 3.4

Values are mean ± 1 s.e. Differences between means (*t*-test) indicated by \*, \*\* and \*\*\* for  $P < 0.05$ ,  $P < 0.01$  and  $P < 0.001$ , respectively (n.s.: Not significant).

TABLE 2. Growth characteristics of *Lygeum spartum* and *Stipa tenacissima*, and leaf water potential ( $\psi_l$ ) and relative water content (RWC) at early morning and midday in December 1993 and June 1994

	November			May			
	<i>Lygeum</i>		<i>Stipa</i>	<i>Lygeum</i>		<i>Stipa</i>	
Extension rate, mm d <sup>-1</sup>	4.4 ± 0.5	*	6.3 ± 2.7	0.12 ± 0.03	n.s.	0.07 ± 0.02	
Total leaf extension, mm	112.1 ± 25.3	*	176.2 ± 9.8	2.48 ± 0.65	n.s.	1.56 ± 0.41	
$\Delta$ mass, g	0.42 ± 0.09	*	1.35 ± 0.07	0.01 ± 0.00	n.s.	0.01 ± 0.00	
$\psi_l$ , MPa							
	Morning	-0.47 ± 0.10	n.s.	-0.54 ± 0.09	-4.64 ± 0.11	n.s.	-5.00 ± 0.20
	Midday	-1.25 ± 0.11	n.s.	-1.21 ± 0.15	ND	ND	ND
RWC							
	Morning	0.90 ± 0.01	n.s.	0.93 ± 0.01	0.72 ± 0.01	*	0.75 ± 0.01
	Midday	0.88 ± 0.01	*	0.91 ± 0.01	0.69 ± 0.01	n.s.	0.72 ± 0.01

Means ± 1 s.e. ( $n = 6$ ); statistics as in Table 1 (ND: not determined).

TABLE 3. Tissue water relations of *Lygeum spartum* and *Stipa tenacissima* in December 1993. Statistics as in Table 1

	<i>Lygeum</i>		<i>Stipa</i>
$\psi_\pi$	-4.18 ± 0.50	*	-1.85 ± 0.33
Leaf water potential at turgor loss, $\psi_{tlp}$ , MPa	-7.20 ± 0.68	**	-2.67 ± 0.24
Relative water content at turgor loss, RWC <sub>tlp</sub>	0.83 ± 0.02	n.s.	0.85 ± 0.01
Apoplasmic bound water, $R_a$	0.67 ± 0.08	n.s.	0.70 ± 0.07
Modulus of elasticity, $\epsilon$ , MPa	17.8 ± 2.0	n.s.	16.2 ± 1.9
$m_s/m_a$	2.07 ± 0.02	*	1.57 ± 0.01

rate was greater in *Stipa* leaves (Table 2). *Stipa* produced 1.35 g dry mass of leaf per tiller in 4 weeks against 0.42 g in *Lygeum*, meaning a much higher relative growth rate in *Stipa* (53 mg g<sup>-1</sup> d<sup>-1</sup> vs. 29 mg g<sup>-1</sup> d<sup>-1</sup>). By May 1994 the lack of water almost stopped leaf growth in both species. In the 4-week period to 2 Jun., only 2.5 ± 0.7 mm had been achieved in *Lygeum* and 1.6 ± 0.4 mm in *Stipa*, equivalent to an increase of 0.01 g of dry mass of leaf in both cases.

Between 4 Nov. 1993 and 2 Jun. 1994 the combined length of monitored leaves ( $n = 4$  per tussock) increased 92.2 ± 6.7 cm per tiller in *Lygeum* and 49.2 ± 5.8 cm in *Stipa* but because of the lower SLA of *Stipa* leaves there was no significant difference in the calculated increase in dry matter of leaves (3.44 ± 0.25 g and 3.76 ± 0.44 g, respectively).

#### Plant water relations

In Dec., after the autumn rains, leaf water potential ( $\psi_l$ ) at dawn was around -0.5 MPa in both *Lygeum* and *Stipa* tussocks (Table 2) and decreased to -1.2 MPa at midday in both grasses. The RWC in both species was high, and did not change significantly at midday (Table 2).

After a very dry spring, dawn  $\psi_l$  had decreased to -4.6 MPa in *Lygeum* and to almost -5 MPa in *Stipa* in early Jun. (Table 2) while midday  $\psi_l$  was below the measuring range of our equipment. The relative water contents of the

leaves of both species were also much lower (Table 2); differences between species and between time of day paralleled those of the autumn values.

*Lygeum* had a lower osmotic potential at saturation ( $\psi_{sat}$ ) and lost turgor at lower leaf water potential ( $\psi_{tlp}$ ) than *Stipa*, but both species had similar RWC at the turgor loss point, bound water in the apoplasm ( $R_a$ ), and bulk modulus of elasticity ( $\epsilon$ ) (Table 3). The saturated/dry mass ratio ( $m_s/m_a$ ) was also higher in *Lygeum* (Table 3).

The angle between the two halves of the lamina changed little with RWC in *Lygeum*. The leaf was completely folded (angle = 0°) at a RWC of 0.86 and when turgid (RWC = 1) the angle was 17.7° ( $y = 128x - 110$ ;  $r = 0.95$ ;  $P > 0.01$ ). In *Stipa* the angle varied from 0° to approx. 100° when RWC varied from 0.7 to 1 (Pugnaire *et al.*, 1996).

#### Gas exchange

In December both species had similar photosynthetic rates ( $A$ ) in the early morning (Table 4), which did not change significantly by midday. Nevertheless, *Stipa* had twice the leaf conductance to water vapour ( $g_l$ ) of *Lygeum*. Conductance did not change, however, between early morning and midday in either species. The two species differed also in the internal CO<sub>2</sub> concentration, which was slightly higher in *Stipa*. Internal CO<sub>2</sub> concentration remained constant in *Stipa* and *Lygeum* between early morning and midday measurements (Table 4). The efficiency of gas exchange ( $A/g_{co_2}$ ) was much higher in *Stipa*.

In the summer, the maximum photosynthetic rate reached early in the morning in Jun. was about half that attained in Dec. in both species, and decreased a further 50% by midday. Leaf conductance was higher in *Lygeum* in the early morning but equal in both species at midday (Table 4). In Jun., early morning  $g_l$  was lower than in Dec. in both *Lygeum* (28%) and *Stipa* (73%) but midday  $g_l$  decreased by 78% and 90%, respectively. Even though  $g_l$  was much lower,  $C_i$  in *Stipa* remained higher in Jun. than in Dec., suggesting a non-stomatal reduction of CO<sub>2</sub> fixation which was also denoted by a much lower efficiency of gas exchange (Table 4).

TABLE 4. Gas exchange parameters for *Lygeum spartum* and *Stipa tenacissima* at early morning and midday in November 1993 and June 1994. Means  $\pm 1$  s.e. (n = 6)

	<i>Lygeum</i>		<i>Stipa</i>			
	Morning	Midday	Morning	Midday		
Dec. 1993						
$g$ , mmol m <sup>-2</sup> s <sup>-1</sup>	0.12 $\pm$ 0.01	n.s.	0.12 $\pm$ 0.01	0.22 $\pm$ 0.01	n.s.	0.22 $\pm$ 0.02
$A$ , $\mu$ mol m <sup>-2</sup> s <sup>-1</sup>	14.2 $\pm$ 1.0	n.s.	13.2 $\pm$ 0.7	15.7 $\pm$ 0.5	n.s.	14.6 $\pm$ 1.2
$C_i$ , $\mu$ mol mol <sup>-1</sup>	175 $\pm$ 3	n.s.	176 $\pm$ 5	201 $\pm$ 7	n.s.	191 $\pm$ 7
$A/g_{CO_2}$	0.67 $\pm$ 0.09	n.s.	0.71 $\pm$ 0.09	2.26 $\pm$ 0.14	n.s.	2.24 $\pm$ 0.35
Jun. 1994						
$g$ , mmol m <sup>-2</sup> s <sup>-1</sup>	0.11 $\pm$ 0.01	**	0.05 $\pm$ 0.01	0.08 $\pm$ 0.01	**	0.04 $\pm$ 0.01
$A$ , $\mu$ mol m <sup>-2</sup> s <sup>-1</sup>	8.31 $\pm$ 0.48	**	4.36 $\pm$ 0.66	7.09 $\pm$ 0.65	**	3.89 $\pm$ 0.43
$C_i$ , $\mu$ mol mol <sup>-1</sup>	204 $\pm$ 6	**	168 $\pm$ 8	184 $\pm$ 5	**	147 $\pm$ 8
$A/g_{CO_2}$	0.46 $\pm$ 0.07	**	0.10 $\pm$ 0.04	0.31 $\pm$ 0.06	**	0.06 $\pm$ 0.01

$g$ , stomatal conductance;  $A$ , photosynthetic rate;  $C_i$ , internal CO<sub>2</sub> concentration.

TABLE 5. Fluorescence emission and photochemical efficiency of *Lygeum spartum* and *Stipa tenacissima* at midday in December 1993 and June 1994. Means  $\pm 1$  s.e. (n = 6). Statistics as in Table 1

	<i>Lygeum</i>		<i>Stipa</i>			
	December 1993	June 1994	December 1993	June 1994		
$F_0$	17.2 $\pm$ 0.9	*	21.8 $\pm$ 1.3	14.7 $\pm$ 0.8	n.s.	16.9 $\pm$ 0.2
$F_m$	67.5 $\pm$ 4.3	n.s.	61.0 $\pm$ 4.3	61.0 $\pm$ 4.3	n.s.	53.1 $\pm$ 5.8
$F_v$	50.3 $\pm$ 3.5	n.s.	40.7 $\pm$ 6.7	46.3 $\pm$ 3.5	n.s.	36.0 $\pm$ 4.6
$F_v/F_m$	0.74 $\pm$ 0.01	*	0.63 $\pm$ 0.04	0.75 $\pm$ 0.01	n.s.	0.67 $\pm$ 0.03

### Fluorescence

Minimum fluorescence ( $F_0$ ) at midday in Dec. did not differ significantly between species (Table 5), nor did the efficiency of photosystem II, measured as the ratio of variable to maximum fluorescence.

In Jun., minimum fluorescence ( $F_0$ ) had increased by 27% in *Lygeum* ( $t$ -test,  $P < 0.03$ ) and by 15% in *Stipa* (n.s.; Table 5) and efficiency of PSII had fallen significantly in *Stipa* ( $P < 0.05$ ) but not in *Lygeum* ( $P = 0.08$ ).

### Nutrition

Total chlorophyll concentration in Dec. was higher in *Stipa* leaves, and chlorophyll a/b ratio did not differ significantly between species (Table 1). In Jun. the concentration of N was significantly higher in *Lygeum* leaves than in *Stipa* leaves but concentrations of P were similar. Because of differences in SLA, the pools of N and P (mass per unit area of leaf) were both higher in *Stipa* leaves (Table 1).

## DISCUSSION

Growth patterns differed in *Lygeum* and *Stipa*. Both species produced the same amount of dry matter of leaf per tiller between Nov. and Jun., but during the 4-week period in Nov. in which we monitored growth, *Stipa* completed 36% of its total leaf production for the year, against 12% of *Lygeum*. A dry and cooler period followed the autumn

rains, during which leaf extension in *Stipa* was much lower than in Nov. (P. Haase, unpubl. res.). Leaf extension and growth of semi-arid grasses is sensitive to temperature fluctuations, and may stop when temperature falls below a certain threshold (Busso and Richards, 1993). It is also sensitive to availability of water (Boyer, 1970; Pugnaire *et al.*, 1996), suggesting that *Stipa* had a plastic response to environmental conditions, maximising growth whenever they were adequate. *Lygeum*, on the other hand, had a steadier rate of growth throughout the season, and was less responsive to adverse conditions. Because *Stipa* has greater biomass per shoot than *Lygeum*, with a similar average growth rate, it has greater net primary production, and since nutrient uptake is determined by productivity (Chapin, 1993), the intermittent, opportunistic growth of *Stipa* is better suited to utilize the pulses of nutrients characteristic of this kind of environment.

The thicker leaves of *Stipa* determine higher pools of N, P and chlorophyll than in *Lygeum*. This did not lead, though, to a proportional increase of photosynthetic rate in *Stipa* (Table 4) as could be expected since  $A$  and N are usually coupled across species (Field and Mooney, 1986). Differences in  $A$  may be explained by the morphological features. Stomata in *Stipa* are located in deep grooves in the upper side of the lamina, but the long leaves are always twisted around their axis so that the adaxial surface is in the abaxial position. When a certain amount of water is lost (approx. at a RWC of 0.73) the leaf is tightly folded and gas exchange is restricted (Pugnaire *et al.*, 1996). Thus in

Jun. the leaf was folded up and stomata were completely concealed in the grooves;  $g_l$  was reduced to 25% of the value in Nov. and  $A$  had decreased by 50% (Table 4).  $\text{CO}_2$  fixation was limited by  $C_p$ , and the efficiency of gas exchange decreased by 86% (Table 4).

*Lygeum*, in contrast, showed a photosynthetic rate similar to that of *Stipa* when water was not limiting, with a lower leaf conductance (Table 4) which decreased less markedly than in *Stipa* in Jun. Stomata in *Lygeum* are on the abaxial leaf surface, i.e. facing outside, making the mechanisms of leaf movement less effective than in *Stipa*. In *Lygeum* the angle formed by the two halves of the lamina changed from  $0^\circ$  at a RWC of 0.86 to only approx.  $18^\circ$  at saturation, while in *Stipa* the angle varied from  $0^\circ$  to approx.  $100^\circ$  when RWC varied from 0.7 to 1 (Pugnaire *et al.*, 1996). Although RWC of *Lygeum* in Jun. was low enough to completely close the leaf by folding, the internal diffusion of  $\text{CO}_2$  appeared not to be restricted.

Overall, gas exchange results suggest that *Stipa* is better suited to cope with water shortage than *Lygeum*, being more responsive to water loss. The rate of carbon fixation is mediated by its morphological traits, allowing a very plastic response of the photosynthetic system whenever water is available.

Tissue water relations suggest that *Lygeum* may be better suited to cope with saline soils because of its lower osmotic potential at saturation (Table 3). Both have, nevertheless, inelastic cell walls (high  $\epsilon$ ), which implies a rapid fall of  $\psi_l$  with a small loss of water. This mechanism avoids excess transpiration when the demand for water is not met by uptake by the roots, which would frequently occur in these shallow-rooted grass species (Sánchez and Puigdefábregas, 1994). Differences in the saturated/dry mass ratio (Table 3) anticipate that, for a given amount of water loss, the relative change will be higher in *Stipa*, prompting an earlier leaf folding. On the other hand, a small increase in water gain would increase RWC further in *Stipa* than in *Lygeum*, inducing a faster response of the photosynthetic system.

Fluorescence emission patterns were very similar in both species (Table 5), though  $F_0$  was always lower in *Stipa*. In addition to the lack of water, maximum irradiance had increased from approx. 1500 to approx. 2100  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , and maximum temperature from 26 to 37  $^\circ\text{C}$  from Dec. to Jun. There was an increase in  $F_0$  between Dec. and Jun. and a simultaneous decrease in the efficiency of PSII in both species. The change in  $F_0$  was significant only in *Lygeum*, and may denote impairment of photosynthesis.  $F_0$  depends on the functional integrity of PSII reaction centres (Krause and Weiss, 1991) and increases also as a consequence of a decreased photochemistry. Nevertheless, compared with the 40–50% decrease in  $A$ , the increase in  $F_0$  would mean that excess energy is dissipated by other means, probably by light reflection through leaf folding. Hence the higher capacity for leaf folding of *Stipa* would be responsible for the smaller increase in  $F_0$ . Variable ( $F_v$ ) and maximum ( $F_m$ ) fluorescence decreased in both species with drought, but the ratio  $F_v/F_m$  was far from the optimum value of 0.83 (Table 5). Values of  $F_v/F_m$  as low as 0.57 have been measured in *Stipa* in midsummer (Pugnaire *et al.*, 1996), so the slow decrease in this value in spite of combined stresses may

reflect rather strong photoprotective mechanisms in these two species.

The decrease in  $A$  at midday between the two dates (approx. 70%) was not paralleled by the decrease in the  $F_v/F_m$  ratio (approx. 11–13%), and points to the physical properties of the leaf of both grasses as another way of dissipating energy. Steeply inclined leaves absorb less radiation (Werk and Ehleringer, 1984, Ehleringer and Cooper, 1992) and by folding the leaf exposes less area to sunlight and decreases the angle of incident light, which is reflected more efficiently. Leaf characteristics and canopy structure of semi-arid tussock grasses thus combine to absorb less radiation (Ryel *et al.*, 1993, 1994). These characteristics provide the means by which *Lygeum* and *Stipa* dominate this high-light, seasonally dry environment. Nevertheless, the specific mechanisms of resistance to several months of adverse conditions clearly deserve further investigation.

In conclusion, the opportunistic growth patterns of *Stipa*, along with its resistance to drought allows this species to dominate wide areas of semi-arid SE Spain. *Lygeum* seems to be better adapted to saline soils and probably needs more mesic conditions than *Stipa*, such as higher water and N availability, and is therefore less able to cope with the harsh environmental conditions of these ecosystems.

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