



Environmental control of canopy dynamics and photosynthetic rate in the evergreen tussock grass *Stipa tenacissima*

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Abstract

Seasonal changes in leaf demography and gas exchange physiology in the tall evergreen tussock grass *Stipa tenacissima*, one of the few dominant plant species in the driest vegetation of Europe, were monitored over a period of two years at a field site in semi-arid south-eastern Spain. Three age-classes of leaves – young, mature and senescent – were distinguished in the green canopy. Production of new leaves and extension growth of older leaves occurred exclusively from October–November to May–June. The rate of extension was significantly correlated with gravimetric soil water content. Leaf growth ceased after gravimetric soil water content fell below 0.015 g g⁻¹ at the beginning of the dry season which corresponded to pre-dawn leaf water potentials of -3.0 MPa. Leaf senescence and desiccation reduced green leaf area by 43–49% during the dry season. Diurnal changes in the net photosynthetic rate of all three cohorts of leaves were bimodal with an early morning maximum, a pronounced midday depression and a small recovery late in the afternoon. Maximum photosynthetic rates of 10–16 μmol CO₂ m⁻² s⁻¹ were attained from November 1993 to early May 1994 in young and mature leaves. Photosynthetic rate declined strongly during the dry season and was at or below compensation in September 1994. Gas exchange variables of young and mature leaves were not significantly different, but photosynthetic rate and diffusive conductance to water vapour of senescing leaves were significantly lower than in the two younger cohorts. Leaf nitrogen content of mature leaves varied seasonally between 2.9 and 5.2 g m⁻² (based on projected area of folded leaves), but was poorly correlated with maxima of the photosynthetic rate. There was a stronger linear relationship between the daily maxima of leaf conductance and pre-dawn leaf water potential than with atmospheric water vapour saturation deficit. Seasonal and between-year variation in daily carbon assimilation were caused mainly by differences in climatic conditions and canopy size whereas the effect of age structure of canopies was negligible. Since water is the most important limiting factor for growth and reproduction of *S. tenacissima*, any future rise in mean temperature, which might increase evapotranspiration, or decrease in rainfall, may considerably reduce the productivity of the grasslands, particularly at the drier end of their geographical distribution.

Introduction

Stipa tenacissima L. (esparto), a tall perennial tussock grass with long narrow evergreen leaves, is one of the few dominant species in the driest vegetation types of the Mediterranean Basin. It occurs where annual rainfall is between 100 and 500 mm and is abundant and forms the characteristic tussock grasslands between the 200 and 400 mm isohyets (White

1983). The extensive *S. tenacissima* grasslands in semi-arid south-eastern Spain (200–400 mm) have been exploited to supply raw material for cellulose and paper-making from historical times until the 1960s (see Johnston 1871; Freitag 1971). This commercial exploitation has almost ceased, but the *S. tenacissima* grasslands do provide substantial cover in these otherwise sparsely vegetated landscapes thus control-

ling runoff, soil erosion and, therefore, slope stability (Sánchez & Puigdefábregas 1994).

The predicted rise in mean temperature, higher potential evapotranspiration and, probably, more erratic rainfall in the Mediterranean Region as a result of global warming (Le Houérou 1990) will have adverse effects on the long-term productivity of these grasslands and may become critical for their survival at the drier end of their climatic range in south-eastern Spain (<250 mm mean annual rainfall). Lower productivity and, therefore, reduced leaf area and cover, will accelerate soil degradation and erosion and, ultimately, may lead to mass movement and landscape instability.

Before the extent of the potential effects of changing regional climatic conditions on the *S. tenacissima* grasslands can be assessed, however, the phenological and physiological responses of the species to present climate regimes must be investigated. The climate of dry Mediterranean and semi-arid regions is highly variable between years and can potentially lead to high variation in annual plant productivity (Mooney et al. 1974; Mooney 1981; Mooney & Kummerow 1981). Such variation particularly affects annual leaf area production and plant canopy size. Since leaves of *S. tenacissima* persist for more than one year (White 1983), large canopies in one year followed by little new growth in the next, and vice versa, will also affect the age structure of the canopy. Since physiological properties, in particular photosynthetic rate, may change with increasing age of leaves, the potential whole-plant carbon gain depends not only on the absolute amount of green canopy area, but also on the proportions made up by different age-classes of leaves. Demographic and ecophysiological research aiming to predict potential whole-plant carbon gain must therefore consider the effects of ageing and seasonal turnover of canopies in relation to within- and between-year variation in climatic variables, particularly the availability of water (see also Haase et al. in press).

Specific aims of the research were (1) to determine the seasonal timing and rates of leaf emergence (leaf birth) and leaf extension and the environmental variables which influence them; (2) to identify different age classes of leaves and their relative proportions in the canopy, and to monitor seasonal and long-term variation in canopy size and age structure; (3) to determine the rates of gas exchange of the different age classes of leaves and their dependence on environmental variables; (4) to estimate the seasonal variation in daily carbon assimilation in relation to leaf

age, canopy dynamics and environmental conditions. These results, together with other data, should provide potential insights, allowing accurate predictions of responses of the *S. tenacissima* grasslands to changing climatic conditions.

Methods

Field site

The field site is in the Rambla Honda, a dry valley at the southern slope of the Sierra de los Filabres, 40 km north of Almería, Andalucía, Spain (37°08' N, 2°22' W, 600–1000 m a.s.l.) Climatic data have been recorded by an automatic weather station, located c. 200 m south of our sampling site, since 1990 (Puigdefábregas et al. 1996). The regional climate is semi-arid; the 5-year period 1990–1994 has a mean annual temperature of 15.7 °C (January 7.5 °C, August 25.4 °C) and mean annual rainfall of 259 mm (R. Lázaro, unpublished data). The records show a pronounced dry season from May to September, often with practically no rainfall from June to August.

The local bedrock is mica-schist with some quartzite beds and supports a thin regolith soil with abundant rock debris. Weathering and erosion has produced extensive alluvial fan systems and colluvial deposits at the base of the mountain slopes (Puigdefábregas et al. 1996). The valley bottom is filled with thick and poorly sorted fluvial deposits, mainly sands and plate-shaped pebbles.

In the Rambla Honda, *S. tenacissima* grassland covers the mountain slopes up to the ridges at 800–1000 m and also occurs on some small outcrops of bedrock in the valley bottom, while the lower parts of the valley are occupied by various types of shrublands. These *S. tenacissima* grasslands are moderately dense, ground cover by the tussocks accounted for 27% (in September 1993), smaller proportions were covered by annual species (7%) and by the summer-deciduous shrub *Anthyllis cytisoides* L. (4%) (P. Haase, unpublished). Puigdefábregas et al. (1996) reported a mean seasonal LAI of 0.98 for *S. tenacissima* grasslands at the field site.

Monitoring of canopy dynamics

Leaf area dynamics was monitored from May 1993 to May 1995. Ten tussocks were selected along a 40-m transect on the lower western slopes of Rambla Honda at 640 m a.s.l. In each of the 10 tussocks,

four to six tillers were randomly selected and marked at the base with a short section of coloured drinking straw. Leaves of each marked tiller were classified as *young* (in their first growing season), *mature* (in their second growing season), *senescent* (orange to yellow colour) and *dry* (dead), and their length was measured. The measurements were repeated at 15-day intervals during the 1993–1994 growing season and at monthly or longer intervals during the dry season. The length and projected area of harvested leaves was allometrically related with the regression equation $\ln y = 1.4224 \ln x - 4.0339$ ($r^2 = 0.98$, $n = 106$). This equation was used for the conversion of leaf length, which was measured non-destructively in the field, into leaf area, and to calculate the proportions of the canopy area of the different age classes of leaves at each observation date.

Ecophysiological measurements

Ecophysiological measurements were carried out from May 1993 to September 1994. In order to prevent damage to the tussocks selected for long-term monitoring, water relations and gas exchange of leaves were measured in six different tussocks along the same transect. Xylem leaf water potential (ψ_l) was measured with a pressure chamber (SKPM 1400, Skye Instruments Ltd., Llandrindod Wells, UK; range to -5 MPa) at pre-dawn and at solar noon at approximately monthly intervals during the period of field work. Gravimetric soil water content (θ) was measured at regular intervals, in particular after each rainfall event, by staff of the Estación Experimental de Zonas Áridas, Almería, in *S. tenacissima* grassland ca. 200 m south-west of our sampling site. We used the means of six samples, taken at 15–20 cm soil depth, to estimate the soil water status at our transect.

Diurnal gas exchange of attached leaves was measured with a portable infrared gas analyser (model LCA-3, Analytical Development Company Ltd., Hoddesdon, UK) and a Parkinson leaf chamber (type PLC-3(N), window dimension 20×58 mm). Three leaves of a particular cohort (age-class), held together by a clip, were enclosed in the chamber which was held normal to the full solar beam during measurements. Photon flux density (PFD) and air temperature in the chamber (T_a) were measured and recorded automatically by the instrument. The system calculated net photosynthetic rate (A) and diffusive leaf conductance to water vapour (g_l) (Anon 1990). The same leaves were measured approximately every two hours during

the day. These routine measurements were carried out approximately once a month from spring to early summer and every two months during the remainder of the year.

The leaf segments used in the gas exchange measurements were harvested at the end of each day and their projected area was determined with a leaf area measurement system (Mk 2, Delta-T Devices, Cambridge, UK). The leaf segments were then dried at 80°C , weighed, and ground in a hammer-mill. The two replicate samples from each tussock were combined and analysed for total nitrogen (PHOSYN Laboratories, York, UK) which was expressed on a leaf area basis.

The ability of *S. tenacissima* to fold its leaves (Pugnaire et al. 1996) posed a particular problem for the determination of leaf area as a basis for calculations of the photosynthetic rate (A) and diffusive conductance to water vapour (g_l). While most of the diurnal measurements were carried out in dry conditions when the leaves were completely folded into a cylinder, the angle of leaf-folding and, therefore, the exposed surface area of the leaves changed in the course of the day between November and May. Since harvested leaves fold rapidly as a result of loss of water, the only feasible method was to determine their projected area when completely closed.

Using calculated proportions of projected canopy area (folded leaves) and measured photosynthetic rates of the three cohorts of leaves, their relative contributions to daily carbon fixation were assessed by integration of the determined diurnal curves of the net photosynthetic rate for four key times of the season (February, April, June, September). These calculations were repeated with data for different canopy area and age structure to estimate the relative effect of these variables on daily carbon gain.

The results of the gas exchange measurements were analysed separately for each annual cohort in relation to climatic variables, water potential of leaves, and their nitrogen status.

Results

Environmental conditions

In both years, 1993 and 1994, the almost rainless dry season exceeded four months (Figure 1). The ecologically most important difference in the pattern of rainfall between the two years was the much

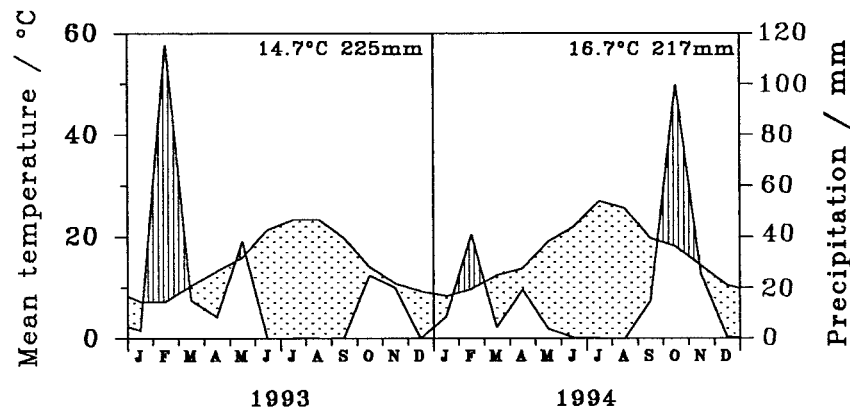


Figure 1. Ecological climate diagrams (cf. Walter 1973) for the Rambla Honda field site near Tabernas, south-eastern Spain, for 1993 and 1994. The scaling of mean monthly temperature and monthly precipitation ($10\text{ }^{\circ}\text{C} = 20\text{ mm}$) gives a good representation of potential evapotranspiration and thus water balance. The dotted area represents the relatively arid, vertical hatching the relatively humid season. The vertical extent of both areas indicates the intensity of aridity/humidity.

lower rainfall during the cool season (October–March) 1993–1994 (Figure 1). On typical sunny days in summer, photon flux density (PFD) reached maxima of about $2000\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$. In mid-summer, daily maxima of temperature exceeded $40\text{ }^{\circ}\text{C}$ while minimum temperatures of -2 to $-3\text{ }^{\circ}\text{C}$ occurred on a few days in winter. During the summer, with high temperatures and low absolute humidities, atmospheric water vapour saturation deficits (D ; vapour pressure deficit, calculated from air temperature and humidity data of the climatic records) were as high as 4–5 KPa. Gravimetric soil water content (15–20 cm depth) varied widely throughout the observation period. Values of 0.10 – $0.14\ \text{g g}^{-1}$ were measured after rainfall, but θ dropped below $0.01\ \text{g g}^{-1}$ for almost four months during the dry seasons of 1993 and 1994 (Figure 2).

Seasonal canopy dynamics

Individual tillers of *Stipa tenacissima* have an average of 2–3 green leaves but also retain several senesced and dead leaves in various stages of decomposition. Young leaves emerged and older, not yet fully grown leaves resumed extension growth exclusively from autumn to late spring. The 48 tillers marked in mid-May 1993 produced 62 new leaves in 1993–1994 and 84 new leaves in 1994–1995. These numbers include the (intravaginal) production of one and three new tillers in 1993–1994 and 1994–1995, respectively. Three tillers died during the 1994–1995 growing season. The mean number of green leaves per tiller varied from 3.1 ± 0.1 (mean \pm SE) in mid-May 1993 and early April 1995 to 2.1 ± 0.1 in September 1994. Leaves of

all three age-classes – young, mature and senescent – were distinguishable during the growing season from October–November to May–June when they had distinct colours: fresh green, mat green and mat green with a yellowish to orange tinge, respectively. During the dry season leaves became extremely discoloured (pale green) and a distinction of cohorts on the basis of leaf colour was no longer possible.

In 1993, leaf extension ceased in the second week of June and no further growth was detected during the dry season (Figure 2). After the autumn rains started in mid-October, leaf extension resumed for the 1993–1994 growing season and reached maximum rates of 4 – $5\ \text{mm d}^{-1}$. During the period October 1993 to June 1994, the mean daily extension rate was significantly correlated with gravimetric soil water content ($r^2 = 0.61$, $P < 0.01$, $n = 16$).

At the beginning of the dry season, when soil water content declined to low levels, leaf extension growth of *S. tenacissima* slowed down and eventually ceased leaving leaves in various stages of development. Leaves which emerged early in the growing season completed most of their extension growth in their first season while growth of late emerging leaves was soon arrested and resumed in their second season. The tissue of the same leaf may therefore differ widely in age depending on its position along the length of the lamina which makes the separation of leaves into particular age-classes difficult.

Leaf senescence was observed during and particularly just after the end of the growing season. The senescent phase was comparatively short and only lasted 1–2 weeks in individual leaves. Complete life

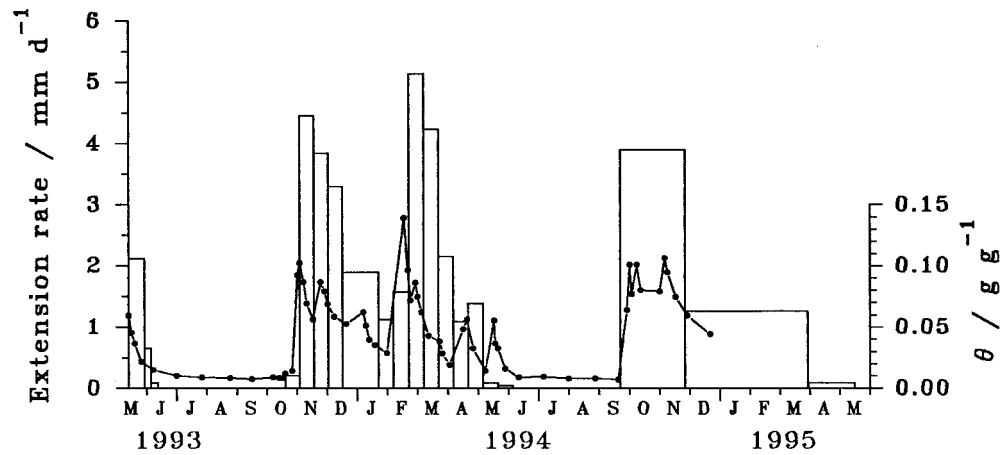


Figure 2. Mean daily extension rate of leaves of *Stipa tenacissima* (open bars) and gravimetric soil water content (θ) at 15–20 cm depth at the Rambla Honda field site from May 1993 to May 1995.

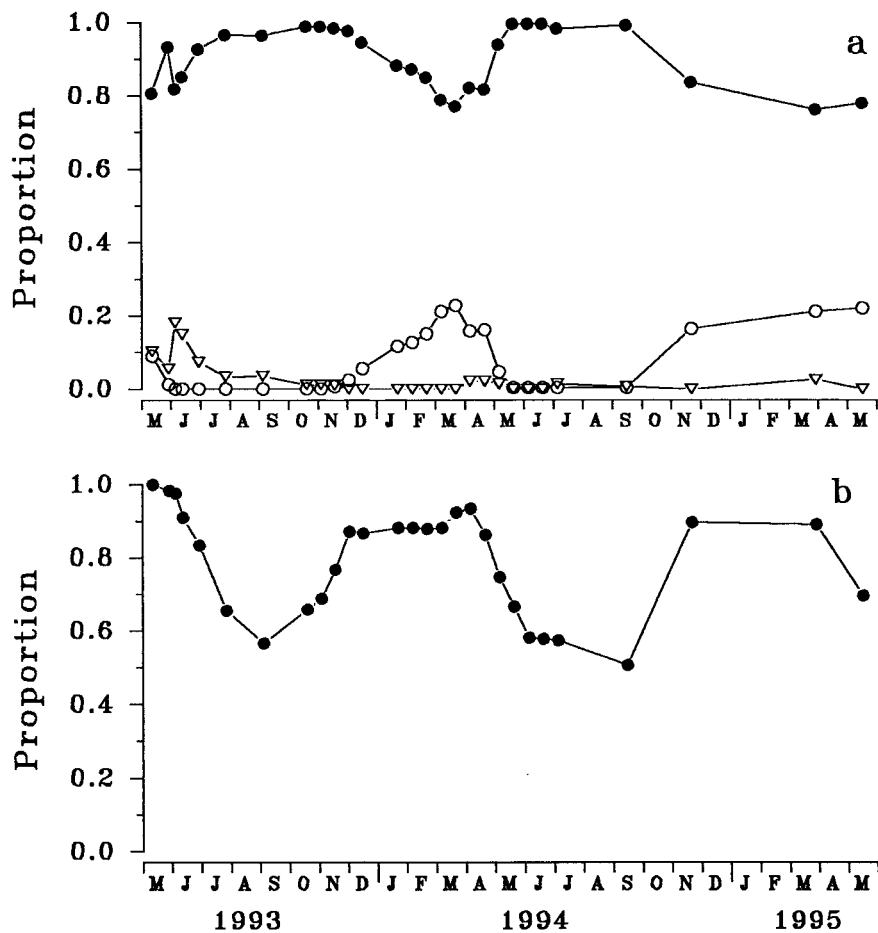


Figure 3. Seasonal changes in the proportions of green leaf area of three cohorts of leaves of *Stipa tenacissima* (a) (○, young; ●, mature; ▽, senescent leaves) and variation in total green leaf area as a proportion of the maximum area measured in May 1993 (b).

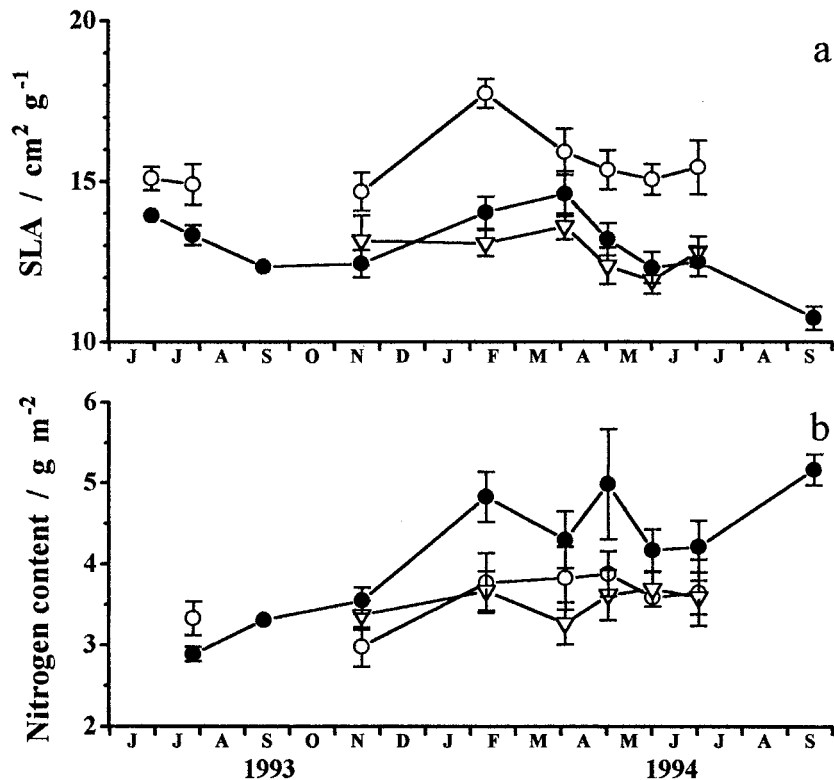


Figure 4. Seasonal changes in specific leaf area (SLA) (a) and nitrogen content (b) of three cohorts of leaves of *Stipa tenacissima* from July 1993 to September 1994 (○, young; ●, mature; ▽, senescent leaves; mean \pm SE, $n = 4-12$).

histories (birth to death) are only available for 23 of the 302 monitored leaves. Inclusion of other leaves ($n = 176$), which were either born or died during the observation period, gave a mean life span of 454 ± 11 days. Since an unknown part of the life history of the latter group of leaves is missing, this figure is an underestimate and we assume that the mean life span of *S. tenacissima* leaves is between 15 and 24 months.

Because of their larger number and size, mature leaves accounted for most of the photosynthetic area at any time (Figure 3a). Young and/or senescent leaves contributed a significant proportion to the photosynthetic area only in spring (Figure 3a). Total green leaf area of the marked tillers, which was at a maximum when first determined in mid-May 1993, declined to 57% in September (Figure 3b). Similar relative maximum (97%) and minimum proportions (51%) of green leaf area were estimated in April and September 1994, respectively (Figure 3b).

Dynamics of leaf nitrogen

Specific leaf area (SLA; based on projected area of folded leaves) generally declined with increasing age of the cohorts (Figure 4a), but the difference between mature and senescent leaves was never significant (Table 1). Maxima of SLA were attained in February (juvenile leaves; $17.4 \pm 0.5 \text{ cm}^2 \text{ g}^{-1}$) and early April 1994 (mature and senescent leaves; 14.6 ± 0.7 and $13.6 \pm 0.4 \text{ cm}^2 \text{ g}^{-1}$, respectively), while annual minima occurred in September of both years (mature leaves recognised only; Figure 4a).

Seasonal variation in mean leaf nitrogen content was largest in mature leaves where it ranged from $2.9 \pm 0.1 \text{ g m}^{-2}$ in July 1993 to $5.2 \pm 0.2 \text{ g m}^{-2}$ in September 1994 (Figure 4b). Young and senescent leaves usually had lower nitrogen contents than mature leaves, but significant differences were only determined on few occasions and the two former cohorts showed comparatively little seasonal variation (Table 1, Figure 4b). Mature leaves showed an overall rise in leaf nitrogen content throughout the period of sampling (July 1993 to September 1994); contents

Table 1. Sampling dates (gas exchange), mean daily air temperature (T) and number of leaf cohorts distinguished in *Stipa tenacissima* tussocks. Significant differences between cohorts ($P < 0.05$; 1 = young, 2 = mature, 3 = senescent) in specific leaf area (SLA), leaf nitrogen content (N), photosynthetic rate (A) and diffusive leaf conductance (g_l) are indicated by different letters (ANOVA).

Date	$T/^\circ\text{C}$	Number of cohorts	SLA	N	A	g_l
2 June 1993	19.8	(3)	no data	no data	1 ^a 2 ^b 3 ^b	
30 June 1993	23.7	2	1 ^a 2 ^b	no data		
28 July 1993	25.0	2	1 ^a 2 ^b	1 ^a 2 ^b		
14 September 1993	17.2	1				
19 November 1993	8.4	3	1 ^a 2 ^b 3 ^{ab}		1 ^a 2 ^b 3 ^c	1 ^a 2 ^b 3 ^b
11 February 1994	8.6	3	1 ^a 2 ^b 3 ^b	1 ^a 2 ^b 3 ^a	1 ^a 2 ^a 3 ^b	1 ^a 2 ^a 3 ^b
5 April 1994	16.9	3	1 ^a 2 ^{ab} 3 ^b	1 ^{ab} 2 ^a 3 ^b	1 ^a 2 ^b 3 ^c	1 ^a 2 ^b 3 ^c
4 May 1994	20.4	3	1 ^a 2 ^b 3 ^b			
3 June 1994	22.1	3	1 ^a 2 ^b 3 ^b		1 ^a 2 ^b 3 ^a	
4 July 1994	34.8	3	1 ^a 2 ^b 3 ^b			
20 September 1994	21.1	1				

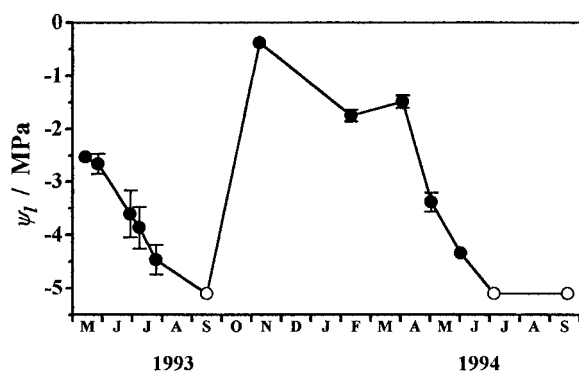


Figure 5. Pre-dawn water potential (ψ_l) of leaves of *Stipa tenacissima* from May 1993 to September 1994 (mean \pm SE, $n = 3-6$; open symbols indicate values < -5.0 MPa).

measured in July and September 1994 were significantly higher ($P < 0.05$, $P < 0.001$, t -test) than those for the same months in 1993.

Plant water relations

Pre-dawn leaf water potential declined steeply from late spring to summer in both dry seasons and fell below -5.0 MPa in August 1993 and early July 1994 (Figure 5). The decline was steeper in 1994 (0.048 MPa d^{-1}) than in 1993 (0.027 MPa d^{-1}). After soil moisture had been recharged by the autumn rains, pre-dawn leaf water potential rose to a measured maximum of -0.38 ± 0.02 MPa in November 1993.

Gas exchange

The daily maxima of the photosynthetic rate (A) and leaf diffusive conductance (g_l) normally occurred in the morning at approximately 08:00 h local standard time in the summer and at 09:00 h in winter and early spring (Figure 6a-h). Both rates then typically declined until midday to mid-afternoon followed by a small recovery late in the afternoon. This diurnal trend was observed in all of the three age-classes of leaves. Mature leaves usually had slightly higher photosynthetic rates than young leaves, while senescent leaves had considerably lower rates. Under dry and hot conditions during the dry season of 1994, the recorded daily maximum photosynthetic rate was close to compensation (Figure 6d).

Daily maxima of the photosynthetic rate (A_{max}) of $10-16$ $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ were measured in early June 1993 and from November 1993 to early May 1994 in young and mature leaves, while A_{max} of senescent leaves never exceeded 10 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. In 1994 the daily maxima of the photosynthetic rate declined continuously from early April to practically zero after early July in relation to increasingly drier soils. Daily maxima of A were thus constrained by environmental conditions during most of the observation period and only the measurements of November 1993 and April 1994 yielded true A_{max} values obtained under (near) optimum moisture conditions. These in-

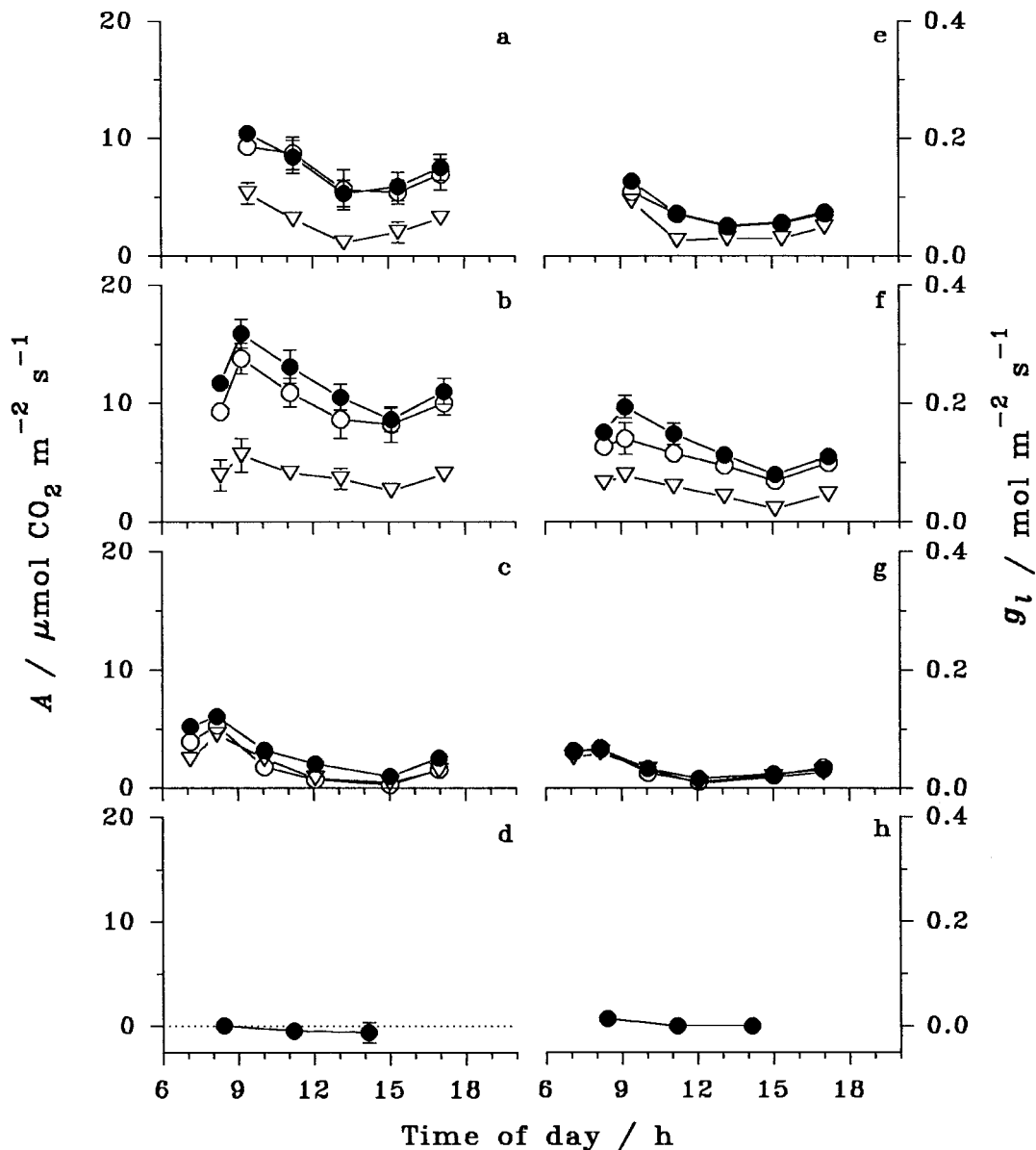


Figure 6. Diurnal changes in the net photosynthetic rate (A) (a–d) and diffusive leaf conductance to water vapour (g_l) (e–h) of three cohorts of leaves of *Stipa tenacissima*. Top to bottom: 11 February 1994, 5 April 1994, 3 June 1994, 20 September 1994 (○, young; ●, mature; ▽, senescent leaves; mean \pm SE, $n = 6$ –12).

dividual A_{\max} values showed weak but insignificant correlations with leaf nitrogen content.

Daily maxima of diffusive conductance ($g_{l\max}$) of mature leaves were significantly correlated with pre-dawn water potential ($r^2 = 0.89$, $P < 0.001$; Figure 7a), but only a weak (negative) correlation was found with the current vapour pressure deficit ($r^2 = 0.22$, $P > 0.1$, $n = 10$; Figure 7b).

Carbon assimilation in relation to canopy demography

When canopy development had attained 88% of its observed seasonal maximum (11 February 1994), the combined projected leaf area of the monitored *S. tenacissima* tillers (Table 2) fixed carbon at a calculated rate of $0.035 \text{ mol CO}_2 \text{ day}^{-1}$ (product of columns 2 and 3 in Table 2). Given the same en-

Table 2. Sampling dates (gas exchange), total green leaf area of 48 monitored tillers and integrated daily carbon gain in *Stipa tenacissima*.

Date	Leaf area (m ²)	Carbon gain (mol m ⁻² day ⁻¹)
2 June 1993	0.076	0.292
30 June 1993	0.065	0.138
28 July 1993	0.051	0.020
14 September 1993	0.045	0.025
19 November 1993	0.060	0.658
11 February 1994	0.068	0.508
5 April 1994	0.075	0.893
4 May 1994	0.060	0.714
3 June 1994	0.047	0.254
4 July 1994	0.044	-0.235
20 September 1994	0.040	-0.011
11 February 1995	0.069	no data
1 April 1995	0.069	no data

environmental conditions and photosynthetic rates, but assuming the size and age structure of the canopy as observed in April, June and September 1994, this daily rate would have varied from +8% to -41% (Table 3). This variation was mostly accounted for by the changes in area alone, the effect of the different age structure was negligible. The daily rates of carbon assimilation actually measured in April, June and September varied even more from those measured in February (Table 3, Figure 6) because of different environmental conditions.

During the two years of observation, there was large seasonal but comparatively small between-year variation in the canopy size and, therefore, potential daily carbon gain of the monitored tillers (Table 2). One exception are the considerably lower daily rates in early June 1994 compared with 1993 (Table 4, left column) which were the result of the earlier onset of leaf desiccation and hence, reduction in canopy area (cf. Table 2). Variation in canopy demography (size and age structure) caused only minor to moderate between-year variation in daily carbon assimilation at the later dates (September, February and April; Table 4). Except in February, the effect of variation in canopy area was much larger than that of the different age structure (Table 4).

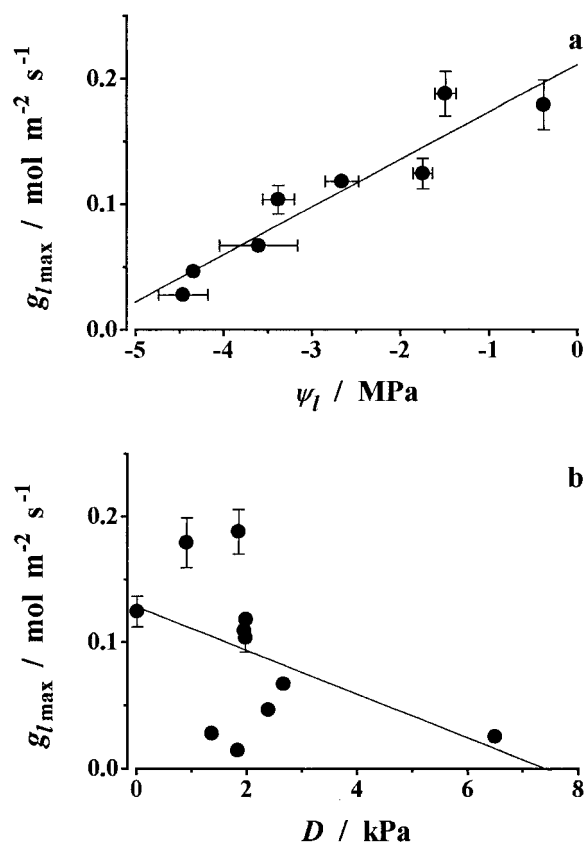


Figure 7. The relations between mean daily maximum diffusive leaf conductance ($g_{l_{\max}}$) and pre-dawn water potential (ψ_l) (a) and vapour pressure deficit (D ; relevant hourly means) (b) in *Stipa tenacissima* (mean \pm SE, $n = 6-12$).

Discussion

Effect of soil and plant water status on canopy dynamics

The presented data on leaf extension growth and gas exchange suggest a strictly seasonal activity of *S. tenacissima*, but this is only the result of the two successive rainless dry seasons during the period of field work. Like many other plants of dry, resource-limited environments, where growth is constrained mainly by availability of water (e.g., Le Houérou 1984; Pugnaire et al. 1993), *S. tenacissima* has adapted to use sporadic pulses of resources. Its ability to enhance physiological activity, rapidly increase the rate of carbon fixation and resume growth as soon as water is available has been demonstrated by watering droughted tussocks (Pugnaire et al. 1996). When plants were watered, leaves extended at rates

Table 3. Effects of within-year variation in canopy area, canopy age structure and environment (daylength, climate and soil water) on daily net photosynthesis in *Stipa tenacissima*.

Reference day	11 Febr. 1994		
Canopy of	5 April 1994	3 June 1994	20 Sept. 1994
Effect of variation in			
Area	+9.7%	-31.5%	-40.6%
Age structure	-1.2%	+0.4%	±0.0%
Area & age structure	+8.3%	-31.2%	-40.6%
The above & environment	+99.5%	-64.0%	-103.1% ¹

¹Negative net photosynthetic rate.

Table 4. Effects of between-year variation in canopy area, canopy age structure and environment (climate and soil water) on daily net photosynthesis in *Stipa tenacissima*.

Reference day	2 June 1993	14 Sept. 1993	11 Febr. 1994	5 April 1994
Canopy of	3 June 1994	20 Sept. 1994	11 Febr. 1995	1 April 1995
Effect of variation in				
Area	-38.4%	-10.4%	+1.4%	-7.8%
Age structure	-0.2%	±0.0%	-1.2%	-1.1%
Area & age structure	-38.5%	-10.4%	+0.2%	-8.8%
The above & environment	-33.9%	-141.4% ¹	no data	no data

¹Negative net photosynthetic rate.

that were directly related to the current water status of the soil and plant (Pugnaire et al. 1996).

The strong dependence of the growth rate on plant and soil water status and hence, rainfall, was also found by the present, longer term research. When leaf extension ceased at the onset of the dry season, pre-dawn leaf water potential was at or below -3.0 MPa and soil water content was 0.015 g g⁻¹ in both years (by interpolation of data presented in Figures 5 and 2, respectively). High soil and plant water status were re-established so rapidly in October 1993 that measurement of the values of these variables when leaf growth resumed was not possible. Re-initiation of leaf growth may, however, require different threshold values from those for cessation of growth (e.g., Comstock & Ehleringer 1992). Gravimetric soil water content, which can be calculated from precipitation, hydraulic properties of the soil and potential evapotranspiration, appears to be the most valuable predictor for estimating both the seasonal timing and the mean rate of leaf extension growth in *S. tenacissima*. The critical lower limits of ψ_l and θ below which roots, tillers or leaves are irreparably damaged are not known

and remain to be investigated, preferably under controlled experimental conditions. Minimum values of θ of 0.0074 g g⁻¹ and 0.0071 g g⁻¹ were determined in mid-September 1993 and 1994, respectively, but all monitored tussocks fully recovered after both dry seasons.

Reductions in canopy area during the annual dry season through desiccation and shedding of photosynthetic organs are common in plants of arid environments (e.g., Orshan 1954; Comstock et al. 1988). The reduced green canopy area, which in *S. tenacissima* amounted to 43% and 49% in 1993 and 1994, respectively, considerably decreases water use by evapotranspiration. A smaller canopy also requires less carbon allocation for maintenance respiration of leaves which might have a predominantly negative carbon balance under typical annual dry season conditions which last 3–4 months.

As a result of the comparatively low SLA (folded leaves), nitrogen contents of *S. tenacissima* leaves are higher than in other large tussock grasses from similar environments (Anderson et al. 1995; Pugnaire & Haase 1996). The reverse applies to nitrogen concen-

tration. The significant overall rise in nitrogen content of young and mature leaves during the observation period (Figure 4b) may be explained by the phenological history of the stand. When sampling was initiated in the early summer of 1993, *S. tenacissima* had just completed a growing season with particularly high reproductive growth (Haase et al. 1995) which probably limited nutrient allocation to other plant parts. There was virtually no flowering in 1994, which may have allowed a recovery of the resources, including nitrogen. The comparatively steep rise in nitrogen concentration after November 1993 is presumably the result of rapid uptake of nitrogen which became available through increased decomposition and mineralisation of organic matter under the moister conditions of the cool season or of re-allocation of nitrogen reserves stored in below-ground plant parts.

Effect of water status and leaf age on gas exchange

Leaf rolling (or folding) is a common indication of water deficit in Gramineae (Shields 1951; O'Toole & Cruz 1979; Redmann 1985) and also in some woody perennials (e.g., Kyprisiss & Manetas 1993). Loss of turgor is generally considered to induce leaf rolling, the response time being a matter of minutes (Redmann 1985). *Stipa tenacissima* leaves respond to loss of turgor by folding along their long axis, the folding angle being directly proportional to the relative water content of the leaves (Pugnaire et al. 1996). Below a mean relative water content of 0.7, the upper leaf surface, where stomata are located in deep grooves, was completely concealed and the leaf formed a tightly closed cylinder (Pugnaire et al. 1996). Further water loss through transpiration is thus minimised, but at the same time photosynthesis is severely restricted as well. Once the leaves are completely folded, leaf conductance can no longer respond to changes in vapour pressure deficit on a linear basis, which only explained 22% of the variation in g_l (Figure 7b).

Leaf conductance and, hence, photosynthetic rate in comparatively shallow-rooted species like *S. tenacissima* (Freitag 1971) largely depends on the water status of the upper soil layer (e.g., Nobel 1980; Anderson et al. 1995). Even when soils are at field capacity, a temporary decrease in gas exchange due to stomatal closure or leaf folding occurs at noon when the evaporative demand of the atmosphere at high temperatures with accompanying vapour pressure deficits cannot be met by the rate of uptake of water (Ludlow & Ng 1976). A longer term and much more

pronounced decline in the rate of gas exchange occurs seasonally when the soils dry out in the summer. Either precipitation which increases soil moisture, or cloudiness and low temperatures, which conserve soil moisture by reducing evaporation and transpiration, can greatly enhance the photosynthetic rate during the dry season (e.g., Pugnaire et al. 1996). Although in dryland ecosystems of temperate regions a substantial proportion of the total carbon gain occurs during the usually moist winter months (Emmingham & Waring 1977; Waring & Franklin 1979), the evergreen habit enables species such as *S. tenacissima* to exploit sporadic rain storms during summer drought or during extended periods when rainfall is scarce (e.g., Pugnaire et al. 1996).

The perennial species of the genus *Stipa* mainly occur in semi-arid regions of the temperate zones and possess the C_3 photosynthetic pathway (e.g., Redmann 1985); this has also been confirmed for *S. tenacissima* (Winter et al. 1976). At times when soil moisture was not a limiting factor, we measured maximum rates of photosynthesis of 14–16 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for young and mature *S. tenacissima* leaves under field conditions which is within the range 10–30 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ reported for other drought-resistant C_3 grasses (e.g., Doley & Yates 1976; Knapp 1993; Anderson et al. 1995).

Carbon assimilation in relation to canopy demography

Although the photosynthetic area of *S. tenacissima* tussocks is made up of varying proportions of leaves of different (chronological) age and phenology, this appears to have little effect on the overall pattern of carbon gain. Young and mature leaves, which account for most of the photosynthetic area at any time, usually had similar rates of leaf conductance and photosynthesis. Although gas exchange of senescent leaves was significantly lower than that of the two younger cohorts, the former cohort usually comprised a rather small proportion (<5%) of the photosynthetic area. The within and between-year variation in canopy age structure generally had a negligible effect on daily carbon assimilation compared with that of the seasonal changes in total canopy area. The same was concluded for another, physiognomically very different species, the stem-photosynthetic shrub *Retama sphaerocarpa* (L.) Boiss., growing at the same field site (Haase et al., in press).

The figures for daily carbon gain (Table 2) are presented for comparative purposes only. They are based on theoretical maxima calculated by integration of the measured diurnal curves. Between February and June 1994, these daily rates ranged from 0.25 to 0.89 mol CO₂ m⁻² day⁻¹ (Table 2) which compares well with 0.26–1.05 mol CO₂ m⁻² day⁻¹ attained by the tall tussock grass *Leymus cinereus* in early summer under varying soil moisture conditions (Anderson et al. 1995). These and our data are not corrected for variation in the angle of incident light and mutual shading of leaves in dense compact tussocks, however. Ryel et al. (1994) suggested that mutual shading reduced daily carbon gain by 40% and 60% in the tussock grasses *Pseudoroegneria spicata* and *Agropyron desertorum*, respectively, compared with evenly spaced tillers. Estimates for the seasonal or annual carbon balance of *S. tenacissima* would also have to consider night respiration and carbon allocation to roots and reproductive structures, but such data are not available at this stage.

Possible effects of climatic change on grassland productivity

Global Circulation Models predict a rise in mean temperature of 3.0 ± 1.5 °C for the Mediterranean Region (e.g., Le Houérou 1990). Even without considering associated changes in rainfall, this predicted rise in temperature will lead to an increase in potential evapotranspiration and, hence, water demand of vegetation, which will particularly affect the regions with less than 350 mm of mean annual rainfall (Le Houérou 1990). The increased potential evapotranspiration may result in increasing aridity of these regions and thus in considerable reductions in plant productivity and vegetative cover.

At present densities, *S. tenacissima* grasslands provide a comparatively high and well distributed cover on moderate to steep slopes of many hills and mountains. Our research suggests that availability of water determines both the length and timing of the growing season, the rate of leaf extension, and also strongly affects the photosynthetic rate in *S. tenacissima*. Any decrease in rainfall will result in higher water stress which will limit assimilation and reduce productivity. Likewise, depending on seasonality of warmth patterns and associated distribution of rainfall, the nitrogen status of the tussocks may deteriorate because of reduced decomposition rates. If decreases in the present densities of the grasslands result in ac-

celerated soil erosion and, possibly, mass movement on steep slopes, *S. tenacissima* may be unable to re-colonise such disturbed sites since it requires stable substrates for successful establishment and growth (Freitag 1971). Under the predicted drier conditions, besides producing less biomass and providing less cover, *S. tenacissima* may no longer be able to flower and reproduce from seed (White 1983; Haase et al. 1995) and become limited to vegetative reproduction which will also affect its future genetic diversity.

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