



Photosynthetic rate and canopy development in the drought-deciduous shrub *Anthyllis cytisoides* L.

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Seasonal changes in phenology, shoot demography and physiology of the summer-deciduous shrub *Anthyllis cytisoides* L. were monitored at a field site in semi-arid south-eastern Spain. Vegetative growth took place during the cool season and the shrubs were leafless for *c.* 3 months during the dry season. In shrubs which had been supplied with water since late spring, leaf and shoot growth continued in the summer. Photosynthetic rate was limited by low plant water status for most of the observation period. Maximum photosynthetic rates of 14 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ were measured in early April but then declined progressively to practically zero in early July. Shrubs supplied with water maintained the same maximum photosynthetic rate in June. Superimposed on the environmentally controlled seasonal variation in the photosynthetic rate was a change in the leaf to stem area ratio as a result of leaf development, senescence (decrease in leaf nitrogen) and abscission. *Anthyllis cytisoides* is a drought avoider with a predictable, but temporally variable resting period. At various times of the seasonal cycle, the summer-deciduous habit allows only limited phenological and physiological responses to temporally favourable environmental conditions, which constrains carbon gain and productivity.

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Introduction

Sparse vegetation is typical for large areas of abandoned land in semi-arid south-eastern Spain which receive a mean annual rainfall of 200–400 mm and have a dry season of up to 4 months in summer. These abandoned lands were formerly intermittently ploughed and sown with cereals, but arable cultivation ceased several decades ago and the lands now support semi-natural shrublands (Puigdefábregas *et al.*, 1996). These shrublands are presumed to represent only intermediate stages of an old-field succession (Haase *et al.*, 1997), but they do provide substantial cover in these otherwise sparsely vegetated landscapes, thus controlling runoff and soil erosion, and have also become important grazing grounds for the local pastoralism.

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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 shrublands, as well as of other vegetation types, and may become critical for their survival in the drier parts of south-eastern Spain (< 300 mm mean annual rainfall). Substantial mortality of shrubs was already observed after a particularly dry summer in 1994 (Haase *et al.*, 1997). Lower productivity and, therefore, reduced leaf area and cover, accelerates soil degradation and erosion and, ultimately, may lead to mass movement and landscape instability.

Within a wider research project on desertification and land use in the Mediterranean region (MEDALUS II), we conducted ecological research on some regionally dominant perennial species of sparse vegetation types in semi-arid south-eastern Spain. This paper reports the results of measurements of seasonal water relations and gas exchange in the shrub *Anthyllis cytisoides* L. (albaida; Fabaceae; hereafter referred to as *Anthyllis*) with the objective of elucidating the effects of quantitative and qualitative seasonal changes in canopy development on photosynthetic rate. Specific aims of the research were: (1) to determine the seasonal timing and variation of canopy development in relation to environmental variables; (2) to determine the daily and seasonal rates of gas exchange at different canopy structures; and (3) to test the phenological and physiological response of shrubs to continuous availability of water. These results, together with other data, should provide potential insights, allowing predictions of responses of the *Anthyllis* shrublands to changing environmental conditions.

Materials and methods

Field site

The research was carried out in Rambla Honda, a dry valley at the southern slope of the Sierra de los Filabres, 40 km north of Almería, in Spain's southern province of Andalucía (37°08' N 2°22' W, 600–1000 m elevation). Meteorological data have been recorded at the site by an automatic weather station since 1990 (Puigdefábregas *et al.*, 1996). The regional climate is semi-arid; the 5-year period 1990–94 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, sometimes 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. Old fields of irregular shapes and poorly defined margins, depending on the local topography and soil texture, on the lower slopes and terraces of the valley presently support semi-natural shrublands (Puigdefábregas *et al.*, 1996; Haase *et al.*, 1997).

Anthyllis is locally common in grassland dominated by the perennial tussock grass *Stipa tenacissima* L., which covers the mountain slopes and rock outcrops. *Anthyllis* also forms dense and sometimes apparently even-aged stands on the upper parts of the alluvial fans and on the man-made, formerly cultivated terraces on the mountain slopes where fine material has accumulated to form deeper soil profiles. The soils of the mountain slopes and upper parts of the alluvial fans are usually shallow (15–60 cm), with little development of pedogenic horizons, and have been classified as Eutric Leptosols (Puigdefábregas *et al.*, 1996). The sandy valley bottom is covered by shrubland of *Retama sphaerocarpa* (L.) Boiss.

Natural history of Anthyllis cytisoides

Anthyllis cytisoides is a summer-deciduous shrub, up to 1.5 m tall, with a wide distribution along the Mediterranean parts of north-western Africa and the southern and eastern Iberian Peninsula including the Balearic Islands, extending into southern France (de Bolós & Vigo, 1984). *Anthyllis* is particularly common at intermittently disturbed sites, e.g. abandoned fields and along roadsides, where it forms low shrublands of varying density and floristic composition. Its root system penetrates to depths of several metres in loose sediments or into rock fissures, thus potentially exploiting a large soil volume (Domingo *et al.*, 1991). Young stems are green and remain photosynthetically active for two growing seasons. While the shrubs are normally leafless during the summer, field observations suggest that deciduousness in *Anthyllis* is not strictly seasonal, but that its phenology is determined to a large extent by current environmental conditions (L. Gutiérrez, pers. com.; Haase *et al.*, unpublished data).

Anthyllis cytisoides possesses small lanceolate-elliptic leaves on short petioles. The lower leaves of a shoot are unifoliolate and the upper leaves trifoliolate, the terminal leaflet being much larger than the laterals (de Bolós & Vigo, 1984). The inflorescence, which develops in late spring, is a terminal spike with groups of 2–3 yellow florets in the axils of bracts. When environmental conditions are favourable, all long shoots of *Anthyllis* develop a terminal inflorescence which, after seed fall, desiccates in the dry season. The supporting shoot desiccates to a variable length below the inflorescence, probably depending on the severity of the dry season. Axillary buds on the surviving lower part of the shoot produce new shoots in the following growing season.

Seasonal measurement of water potential and gas exchange

Six *Anthyllis* shrubs were selected for monitoring along a *c.* 20-m long transect on an alluvial fan at the western side of the valley in November 1993. Pre-dawn shoot water potential (ψ) of freshly cut, *c.* 1-year-old shoots was measured with a pressure chamber (SKPM 1400, Skye Instruments Ltd., Llandrindod Wells, U.K.) approximately once every month from February to September 1994. Gas exchange of randomly selected attached terminal shoots (7-cm length; below the inflorescence, if present) was measured with a portable infrared gas analyser (model LCA-3, Analytical Development Company Ltd., Hoddesdon, U.K.) and a Parkinson leaf chamber (type PLC-C, cylindrical Plexiglas cuvette). The chamber was exposed to full sunlight and held normal to the solar beam during measurements, which were replicated twice in each of the six shrubs. The same shoots were measured approximately every 2 hours during the day. These measurements began in December 1993 and were carried out every 2 months in winter and spring and monthly in the summer (Table 1).

The sections of the shoots which were in the leaf chamber during the gas exchange measurements were harvested at the end of each day and leaves were detached from the stems. The projected stem and leaf area in the leaf chamber (3–6 cm²) were determined separately with a leaf area measurement system (Mk 2, Delta-T Devices, Cambridge, U.K.). Stems and leaves were then dried at 80°C for 24 h, weighed and ground. The two replicate leaf samples of each shrub were combined and analysed for total nitrogen (PHOSYN Laboratories, York, U.K.).

Gravimetric soil water content (θ) was measured at regular intervals by staff of the Estación Experimental de Zonas Áridas, Almería, in *Anthyllis* shrubland *c.* 200 m south of our experimental site. The data were obtained from soil cores extracted from 15–20 cm depth, which were weighed before and after drying at 105°C (Puigdefábregas *et al.*, 1996).

Table 1. Sampling dates, mean daily air temperature (T), total pre-dawn shoot water potential (ψ), maximum photosynthetic rate (A_{\max}) and maximum diffusive conductance to water vapour (g_{\max}) and leaf nitrogen concentration (N) in shrubs of *Anthyllis cytisoides* (mean \pm S.E. n = 6–12)

Date	T °C	ψ MPa	A_{\max} $\mu\text{mol m}^{-2} \text{s}^{-1}$	g_{\max} $\text{mol m}^{-2} \text{s}^{-1}$	N mg g^{-1}
03 Dec 1993	9.5	no data	5.09 ± 0.75	0.24 ± 0.03	
11 Feb 1994	8.6	-0.48 ± 0.12	6.48 ± 1.20	0.17 ± 0.02	
05 Apr 1994	16.9	-1.48 ± 0.07	13.97 ± 1.11	0.22 ± 0.02	20.3 ± 0.5
04 May 1994	20.4	-2.90 ± 0.12	6.06 ± 0.76	0.08 ± 0.01	15.8 ± 0.7
03 Jun 1994	22.1	-3.51 ± 0.16	3.62 ± 0.35	0.07 ± 0.01	11.1 ± 0.6
04 Jul 1994	34.8	no data	0.08 ± 0.27	0.04 ± 0.01	
20 Sep 1994	21.1	< -5.00			

Experimental watering regime

In a second stand of *Anthyllis*, c. 100 m south, 12 shrubs were selected within a 20×20 -m area in February 1994. Six of these shrubs were supplied with an average of 2 l of water per day for a period of 2 months from late April to late June. Water was applied to the soil surface at the centre of the shrubs with medical gravity dripfeed systems, each connected to a 20-l storage container. The other six shrubs, which served as controls, were located uphill and at a minimum distance of 2 m from the watered shrubs and unlikely to be affected by seepage of water. In each of the 12 shrubs, four shoots of the current season were selected at random and marked with a short section of coloured drinking straw. The length of each marked shoot was measured and the number of green leaves present was counted on 20 March 1994. The marked shoots were inspected at 15-day intervals until 4 July. On 10 June, when the leaves of the control shrubs were beginning to desiccate, shoot water potential and gas exchange of both groups of shrubs were compared in two sets of measurements, one at 08 00 h in the morning at the time of maximum CO_2 assimilation and one at 12 00 h, when pronounced water stress was observed in the control shrubs.

Statistical treatment of results

Results were analysed with the GLM and REG procedures of the SAS statistical package (SAS Institute Inc., 1989). Photosynthetic rate and diffusive conductance were analysed in relation to environmental variables, plant water status and nitrogen concentration. The data obtained during the comparative measurements of watered shrubs and controls were analysed by ANOVA (SAS Institute Inc., 1989) for variation within and between treatments and between the two different times of measurement.

Results

Weather conditions

In 1993 and 1994, the almost rainless dry season lasted for more than four months. After a long dry season in 1993, the soil was recharged with moisture by rainfall in late October

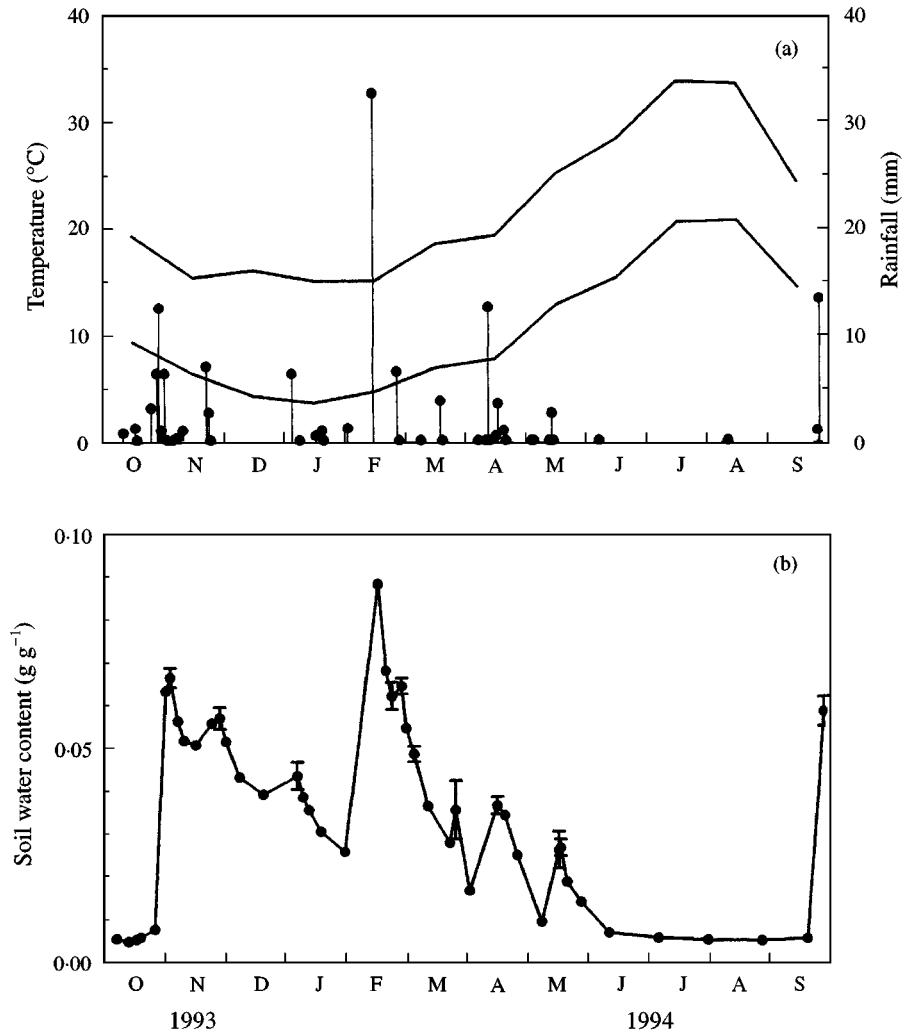


Figure 1. Mean monthly maximum and minimum temperature and daily rainfall (a) and gravimetric soil water content (θ) at 15–20 cm depth (b) at the Rambla Honda field site from October 1993 to September 1994. (All data were collected by staff of the Estación Experimental de Zonas Áridas, Almería, Spain.)

(Fig. 1(a, b)). The cool season remained particularly dry, however, and substantial amounts of rainfall (33 mm; Fig 1(a)) only fell in mid-February. This rainfall increased gravimetric soil water content to a 12-month maximum. θ then again declined and fell below 0.01 g g⁻¹ in early June (Fig. 1(b)). Although the data for soil water content were obtained at some distance of the experimental site and only for one shallow depth, the seasonal trends in soil water content at comparable throughout the larger field site (*cf.* Haase *et al.*, 1999a).

On typical sunny days in summer, PFD reached maxima of about 2000 $\mu\text{mol m}^{-2}\text{s}^{-1}$. In mid-summer, daily maxima of temperature exceeded 40°C while minimum temperatures of -2 to -3°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) were as high as 4–5 kPa.

The mean annual temperature for the 12-month period October 1993 to September 1994 was 16.0°C and total rainfall was 136.5 mm. While the temperature was close to the 5-year mean (15.7°C), the rainfall of the period was approximately 50% below the mean annual rainfall (259 mm).

Phenology

Most *Anthyllis* shrubs at the field site were leafless in the summer of 1993. Bud break occurred in late October following the first autumn rains, but because of low winter rainfall, there was little extension growth until February 1994. On 3 December 1993, 17% of the total photosynthetic area of the shoots measured in the leaf chamber were buds and small leaves (Fig. 2); the remainder was made up by green stems. The proportion of leaf to total shoot area increased to a maximum of 71% in early April, but decreased again and all leaves were shed by early July. The reduction in leaf area was accompanied by an almost 50% reduction in leaf nitrogen concentration from April to June (Table 1).

Diurnal and seasonal water relations and gas exchange

Pre-dawn shoot water potential decreased progressively from February to June 1994 and was below -5.0 MPa in September (Table 1). Daily maxima of the photosynthetic rate (A_{\max}) 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 (Fig. 3, left column). Photosynthetic rate (A) then typically declined until noon, followed by a small recovery late in the afternoon. The diurnal changes in diffusive conductance to water vapour (g ; Fig. 3, right column) were similar to those for A , except that values for the first set of

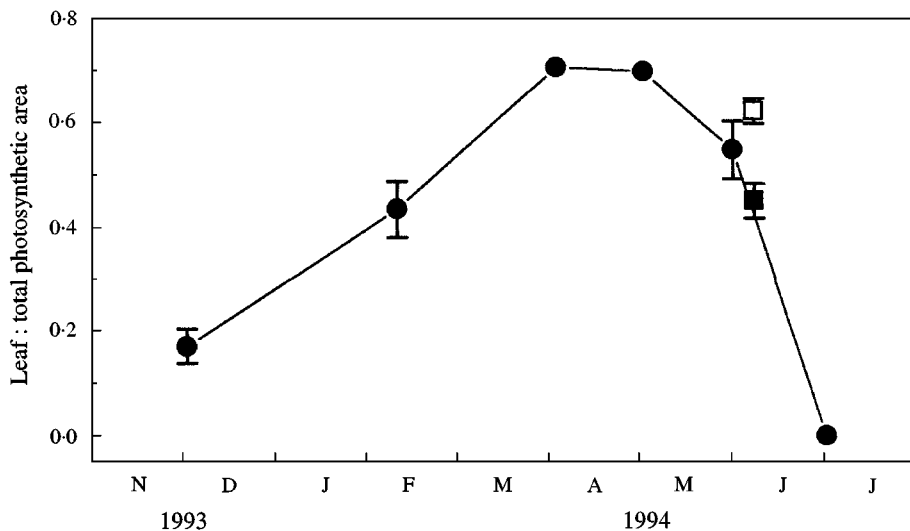


Figure 2. Seasonal variation in green leaf area as a proportion of total photosynthetic area (leaf + shoot) in *Anthyllis cytisoides* from December 1993 to July 1994 (mean \pm S.E. $n = 12$; ●, mean of shrubs measured throughout the period; □, mean for watered shrubs; ■, mean for control shrubs on 10 June 1994).

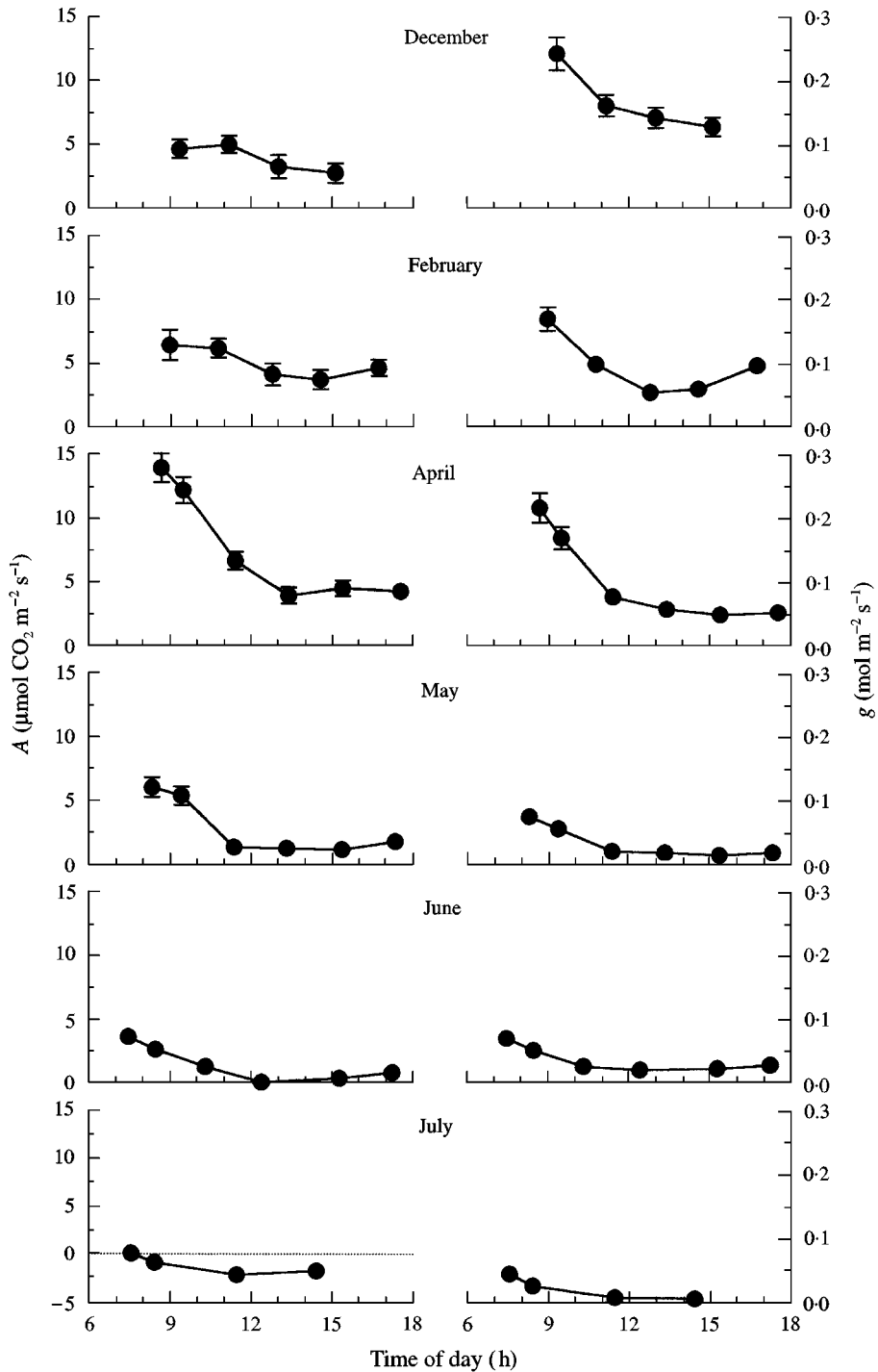


Figure 3. Diurnal changes in the net photosynthetic rate (A) (left column) and diffusive conductance to water vapour (g) (right column) of shoots of *Anthyllis cytisoides*. Top to bottom: 3 December 1993, 11 February 1994, 5 April 1994, 4 May 1994, 3 June 1994, 4 July 1994 (mean \pm S.E. $n = 12$).

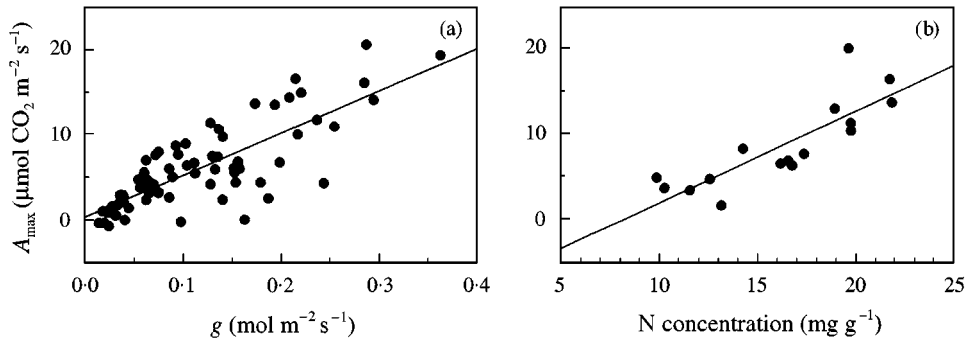


Figure 4. Relations between the daily maximum photosynthetic rate (A_{\max}) and (a) diffusive conductance to water vapour (g) and (b) nitrogen concentration of shoots of *Anthyllis cytisoides*.

measurements in the morning of 3 December and 11 February were much higher than expected by observed rates of A (Fig. 3). PFD was only *c.* 1280 and 930 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, during these measurements, but had increased to *c.* 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in each case 2 hours later. In May and June significant rates of A only occurred in the early morning before 10 00–11 00 h (Fig. 3). In July, A was practically zero in the morning and a net efflux of CO_2 was measured later in the day (Fig. 3). Shoots were inactive or dry in September and gas exchange was not recorded.

The seasonal changes in A and g were apparently a result of changes in environmental conditions, particularly the declining soil water status, but superimposed were the changes in the proportion of the photosynthetic area of leaves and green stems. When photosynthetic stems accounted for most of the photosynthetic area in December and February, maximum photosynthetic rates were 5–6 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ (Table 1), but when leaves accounted for 71% of the total shoot area in April, A_{\max} was 14 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$. There was a substantial decrease in A from April to May (Table 1), even though the leaf to stem area ratio did not change (Fig. 2). This decline was associated with increasingly lower plant water potential and reductions in leaf nitrogen concentration (Table 1). Both g and leaf nitrogen concentration showed linear relationships with A_{\max} ($r = 0.79$, $p < 0.01$, $n = 72$; Fig. 4(a) and $r = 0.83$, $p < 0.01$, $n = 16$; Fig. 4(b), respectively). Most, but not all, *Anthyllis* shrubs produced inflorescences during April and part of the observed decrease in leaf N could have been due to reallocation of nutrients to developing reproductive structures.

Response to continuous availability of water

Shoot extension growth of *Anthyllis* ceased in early April. The shrubs selected for watering initially had a smaller number of leaves per shoot than controls (7.6 ± 0.8 vs. 9.5 ± 0.8 ; mean \pm S.E. Fig. 5). Maximum numbers of green leaves were present in mid-April and then started to decline. Water was applied to one group from 29 April and the first effect was observed in mid-May when leaf abscission in the watered shrubs ceased (Fig. 5). While the number of leaves in controls declined rapidly during May and June due to leaf senescence and abscission, the shoots of watered shrubs retained all present leaves, produced some new leaves on the same shoots, and six of the shoots also produced new axillary short shoots (leaves included in count). A maximum number of 14.7 ± 2.6 leaves per shoot were present in early July when watering and monitoring ceased.

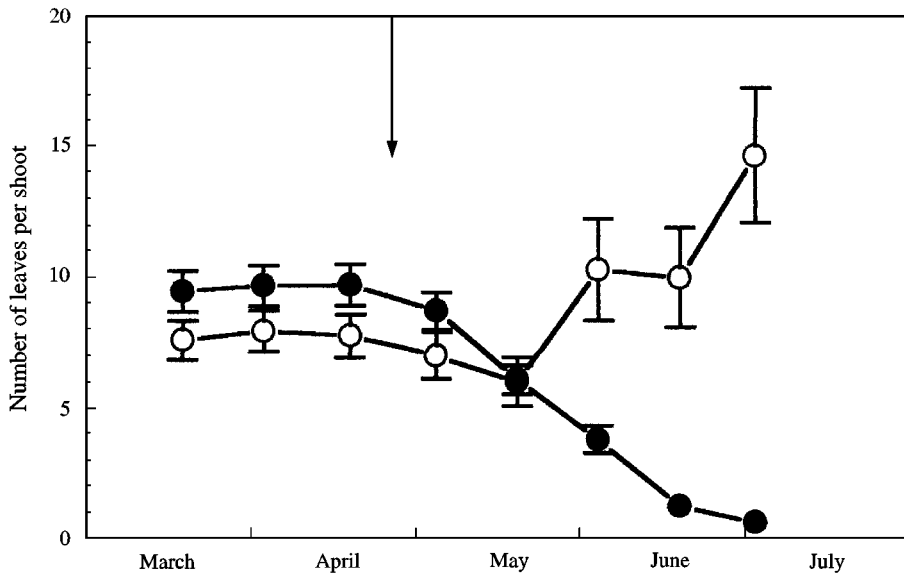


Figure 5. Number of leaves per shoot in watered and droughted shrubs of *Anthyllis cytisoides* from March to July 1994 (mean \pm S.E., $n = 24$; ○, watered shrubs; ●, controls). The arrow indicates the beginning of water supply.

On 10 June, morning shoot potential of the watered shrubs was significantly higher than that of controls ($p < 0.05$; Table 2). By midday, shoot water potential had declined only slightly but significantly ($p < 0.01$) in the watered shrubs, but had dropped below -5.0 MPa in the controls.

When gas exchange was measured on 10 June, leaves made up 62% of the shoot photosynthetic area in watered shrubs and 45% in controls (Fig. 2). The leaf nitrogen concentration of controls was significantly lower compared to the watered shrubs (Table 2). Watered shrubs reached maximum rates of photosynthesis of $> 14 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, both in the morning and at midday, while controls attained only 2.0 and $1.6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively (Table 2). Under natural conditions, the same rate of A ($14 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) had previously been measured during the morning in early April 1994. In the controls, both A and g decreased by 20% between morning and midday. In watered shrubs, g also decreased by 20%, but A by only 2.5% (Table 2).

Table 2. Shoot water potential (ψ), photosynthetic rate (A), diffusive conductance to water vapour (g) and leaf nitrogen concentration (N) in watered and unwatered shrubs of *Anthyllis cytisoides* on 10 June 1994 (mean \pm S.E., $n = 6-12$)

Treatment Variable	Watered		Controls	
	Morning	Midday	Morning	Midday
ψ/MPa	-1.49 ± 0.06	-1.75 ± 0.04	-3.55 ± 0.12	< -5.00
$A/\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	14.74 ± 0.73	14.38 ± 0.60	2.02 ± 0.27	1.62 ± 0.27
$g/\text{mol m}^{-2} \text{ s}^{-1}$	0.35 ± 0.03	0.28 ± 0.02	0.10 ± 0.00	0.08 ± 0.01
$N/\text{mg g}^{-1}$	16.3 ± 0.7		11.2 ± 1.6	

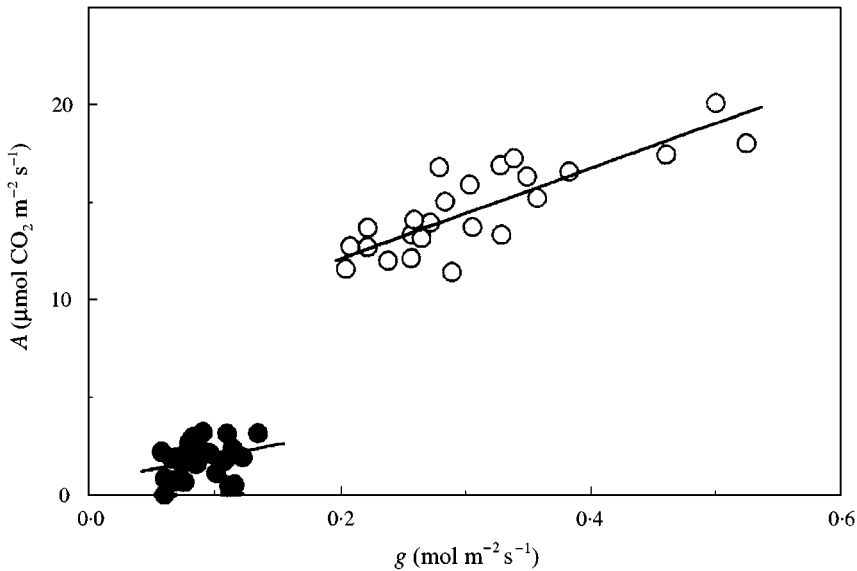


Figure 6. Relations between photosynthetic rate (A) and diffusive conductance to water vapour (g) in shoots of watered and droughted shrubs of *Anthyllis cytisoides* ($n = 24$; ○, watered shrubs; ●, controls).

Correlation between A and g (Fig. 6) was significant in watered shrubs ($r = 0.82$, $p < 0.01$, $n = 24$), but not in controls ($r = 0.25$, $p > 0.1$, $n = 24$), which had much lower rates of A than expected by a linear relationship between A and g . Advanced leaf ageing and possible damage to the photosynthetic apparatus may be implicated. The extent of this effect can be demonstrated by estimating A of the controls from the A - g regression line obtained from the data of the watered shrubs (Fig. 6). At a value of g of $0.1 \text{ mol m}^{-2} \text{ s}^{-1}$, which was determined in the morning, the photosynthetic rate of the controls would be expected to approximate $10 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, but only $2 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ were actually measured.

Discussion

Anthyllis cytisoides can produce two annual cohorts of leaves, the first in autumn and the second in spring (Haase *et al.*, unpublished data). During the 1993/94 growing season, however, only one cohort of leaves was produced. The initiation of distinct flushes of shoot growth appears to depend on environmental conditions, particularly the amount of rainfall. In contrast to the autumn of 1993, when new shoots did not elongate for *c.* 3 months because of lack of rainfall, rapid shoot extension occurred in October–November 1994 after heavy rainfall and at temperatures which were $2\text{--}3^\circ$ above the monthly averages (Haase *et al.*, unpublished data). Such between-year variation, both in the area of green canopy and in the amount of rainfall, can result in large between-year differences in carbon fixation and dry matter production. An observed between-year variation in the length of terminal shoots appears to be related to variation in total amounts of winter rainfall, although only a limited amount of data are available at this stage (Haase *et al.*, unpublished data). Further rainfall in late spring and early summer is less important, because the terminal inflorescence develops at this time and extension growth of the shoot therefore ceases. Early summer rainfall can, however, stimulate the growth of lateral shoots, as suggested by the results of our watering experiment.

Some drought-deciduous desert shrubs can produce several flushes of shoot growth following erratic rainfall events and associated wetting and drying cycles (Comstock & Ehleringer, 1986). If the intervals between successive flushes were short enough, two cohorts of leaves were present in the canopy of *Encelia frutescens* Gray, but leaf life-spans were short, lasting just over 30 days (Comstock & Ehleringer, 1986). Renewed growth did not extend the life-span of leaves of the previous cohort. In our experiment, water was supplied to *Anthyllis* shrubs continuously from late spring to early summer, and a new cohort of shoots was produced and the life span of the old cohort of leaves was extended as well. Availability of water at this time of the growing season can thus maintain and even considerably increase the photosynthetic canopy area and hence, potential carbon gain.

The progressive decline in shoot water potential from February to September 1994 was a result of the low rainfall and a concomitant seasonal decrease in soil water content. In the soils on alluvial and colluvial deposits occupied by *Anthyllis* shrublands, water penetrates deep into the permeable sediment. The comparatively high shoot water potential of *c.* -0.5 MPa in *Anthyllis* in February 1994 suggests that the shrubs' root systems penetrate into these deeper and moister soil horizons. Leaf water potential of the comparatively shallow-rooted tussock grass *Stipa tenacissima*, measured at the same time at a site nearby, was -1.75 MPa (Haase *et al.*, 1999a).

The results of the artificial watering of *Anthyllis* shrubs allow us to predict the effect of rainstorms during late spring and early summer only. If rainstorms occur later in the season, leaves are in an advanced state of senescence and do not recover. Although their life span may be extended, the photosynthetic system appears to have been irreversibly damaged, which constrains photosynthetic rate (Brenner *et al.*, unpublished data). In a similar experiment involving watering of tussocks of *Stipa* in mid-summer, a rapid response was observed — leaf elongation resumed and photosynthetic rate reached a maximum comparable with spring values (Pugnaire *et al.*, 1996). The differential phenological responses of *Stipa* and *Anthyllis* can be explained by their different types of meristem which is of the intercalary type in grasses but terminal in *Anthyllis*. *Anthyllis* therefore needs to initiate a new cohort of shoots after each wetting and drying cycle, while in grasses such as *Stipa*, extension growth of the same leaves simply resumes, thus enabling a much faster and probably repeated response to a series of such cycles.

In perennial plants which possess both green stems and leaves, rates of stem photosynthesis are usually considerably lower than those of leaf photosynthesis (e.g. Ehleringer *et al.*, 1987; Comstock & Ehleringer, 1988). However, stem photosynthesis increases whole-plant gross photosynthesis and decreases the net effect of stem respiration; photosynthesis in stems is also more tolerant of stress than in leaves (Nilsen *et al.*, 1993). Photosynthetic stems also have longer life-spans, particularly in drought-deciduous species where the leaves are shed after only a few months (Comstock & Ehleringer, 1986; Comstock *et al.*, 1988).

In seasonally dry environments, the photosynthetic rate is mainly limited by low plant water status. None of the 19 species of desert shrubs investigated by Comstock *et al.* (1988) were capable of high rates of photosynthesis at low plant water potentials during the dry season, but in those species which maintained a substantial proportion of their canopy area throughout the dry season, previously stressed tissues showed substantial recovery after autumn rains. In most species, the maximum photosynthetic rate was observed at the seasonal maximum development of the canopy and the same was also found for *Anthyllis*.

A strong effect of water deficit on photosynthetic rate has also been found in other studies. Light-saturated photosynthesis of leaves of *Encelia frutescens* decreased from 42.6 to 1.7 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ as leaf water potential decreased from -1.5 to -4.0 MPa (Comstock & Ehleringer, 1984). Both leaf conductance and intrinsic photosynthetic capacity decreased, but the decrease in leaf conductance was proportionally

greater. This was also found in the watered and droughted shrubs of *Anthyllis* (cf. Table 2). In other desert perennials, maximum photosynthetic rate declined to zero at water potentials ranging from -2.1 MPa to -8.0 MPa (Odening *et al.*, 1974; Björkman *et al.*, 1980; Mooney, 1980). In *Anthyllis*, A_{\max} fell to zero between -3.5 and -5.0 MPa. The large difference in photosynthetic rate between watered and droughted shrubs was not due to the low plant water status alone, a contributing factor may have been the more advanced stage of leaf senescence and related decline in photosynthetic capacity, which is also suggested by the 31% decline in leaf nitrogen concentration in droughted shrubs (Table 2).

Anthyllis cytisoides is a drought avoider with a defined, but temporally variable resting period. The summer-deciduous (or drought-deciduous) habit is generally thought to facilitate survival during prolonged periods of drought by eliminating transpiring surface area and by reducing whole-plant respiration during periods of potentially negative carbon balance (e.g. Orshan, 1954; Kozłowski, 1979; Chabot & Hicks, 1982). In *Anthyllis* on the other hand, the summer-deciduous habit only allows a comparatively slow response to rapid improvements in environmental conditions. When unseasonal rainfall temporarily improves soil and plant water status at the onset of the dry season, the already senescent leaves with low photosynthetic capacity limit potential carbon gain. During dry winter months, potential carbon gain is limited by a slow development of the new canopy. *Anthyllis* appears to be less well-adapted to the unpredictable semi-arid climate than other common perennial species growing at the same field site (Haase *et al.*, 1999a, b). Its present abundance is probably a result of recent, large-scale land abandonment and its ability to recover from browsing damage by domestic stock. The high proportion of dead canopy (stems) and mortality of *Anthyllis* shrubs following the severe drought of 1994 (Haase *et al.*, 1997) suggests that populations may be significantly reduced after prolonged periods with low rainfall. Since *Anthyllis* shrublands are important for grazing, their decline would have a significant effect on local pastoralism.

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