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Diurnal variations of photosynthesis and dew absorption by leaves in two evergreen shrubs growing in Mediterranean field conditions

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SUMMARY

The effects of summer drought, dew deposition on leaves and autumn rainfall on plant water relations and diurnal variations of photosynthesis were measured in two evergreen shrubs, rosemary (*Rosmarinus officinalis*) and lavender (*Lavandula stoechas*), grown in Mediterranean field conditions. Withholding water for 40 d caused a similar decrease in predawn shoot water potential (ψ_{pd}) from *c.* −0.4 to *c.* −1.3 MPa in both species, but a 50% decrease in the relative leaf water content in *L. stoechas* compared with 22% in *R. officinalis*. A similar decrease in CO_2 assimilation rates by *c.* 75% was observed in water-stressed plants of both species, although *L. stoechas* showed smaller photosynthesis: stomatal conductance ratio than *R. officinalis* (35 vs 45 μmol CO_2: mol H_2O). The relative quantum efficiency of photosystem II photochemistry also decreased by *c.* 45% at midday in water-stressed plants of both species. Nevertheless, neither *L. stoechas* nor *R. officinalis* suffered drought-induced damage to photosystem II, as indicated by the maintenance of the ratio $F_v:F_m$ throughout the experiment, associated with an increase in the carotenoid content per unit of chlorophyll by *c.* 62% and *c.* 30%, respectively, in water-stressed plants. Only *L. stoechas* absorbed dew by leaves. In this species the occurrence of 6 d of dew over a 15-d period improved relative leaf water content by *c.* 72% and shoot water potential by *c.* 0.5 MPa throughout the day in water-stressed plants, although the photosynthetic capacity was not recovered until the occurrence of autumn rainfall. The ability of leaves to absorb dew allowed *L. stoechas* to restore plant water status, which is especially relevant in plants exposed to prolonged drought.

Key words: diurnal cycles, drought, *Lavandula stoechas*, leaf dew absorption, photosynthesis, plant water relations, *Rosmarinus officinalis*, stress.

INTRODUCTION

Mediterranean climate conditions induce several stresses that plants have to cope with, especially during summer months when high temperature and radiation levels along with low water availability in the soil prevail for long periods (Munné-Bosch & Alegre, 1999). Variation in physiological traits such as photosynthesis and plant water status and their association with morphological characters can play an important role in the adaptability of the species to environmental constraints (Sandquist & Ehleringer, 1997). The most important strategy of plants in response to environmental stresses is to survive and persist under adverse conditions and to be able to recover rapidly after autumn rainfalls (Volaire *et al.*, 1998). Nevertheless, most attention has been given to performance during the summer drought, and little information is available on recovery from stress, and even less on the protective effect of dew in plants subjected to drought.

The effect of drought on leaf gas exchange in Mediterranean plants has been reviewed by Schulze & Hall (1982), Tenhunen *et al.* (1987) and Pereira & Chaves (1993). These studies show that drought not only affects the rate of gas exchange, but also results in diurnal changes in activity. Thus, the impact of stress on plants growing in Mediterranean field conditions should be assessed by examining the evolution of their diurnal variations on leaf gas exchange (Körner, 1995; Mäkelä *et al.*, 1996).

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The importance of dew for the survival of plants should be considered, especially in summer. Some studies have shown that direct water absorption by leaves can improve plant water relations in several species (Katz *et al.*,1989; Ourcival *et al.*, 1994; Boucher *et al.*, 1995; Yates & Hutley, 1995). There is evidence that water can enter leaves from the surface (Kerstiens, 1996) but it is not clear to what extent plants growing in field conditions may take benefit from dew and whether or not plant water relations, or even photosynthesis, can be improved by leaf dew absorption. Previous studies have shown that simulated dew can avoid the depression of photosynthesis associated with drought (Grammatikopoulos & Manetas, 1994) or even improve plant water relations and photosynthesis in water-stressed plants (Munné-Bosch & Alegre, 1999). Nevertheless, data confirming the role of dew in the recovery of water-stressed plants in realistic situations are still lacking.

Rosmarinus officinalis and *Lavandula stoechas* are native Mediterranean evergreen half-shrubs that can survive drought and which differ in their morphology (*R. officinalis* is more sclerophyllous than *L. stoechas*) as well as in their hormonal responses to water-stress (López-Carbonell *et al.*, 1996).

Here we study the photosynthetic response of *R. officinalis* and *L. stoechas* to summer drought, dew deposition on leaves and autumn rainfall, in plants growing in Mediterranean field conditions. Emphasis is laid on the protective effect of dew in plants subjected to drought.

MATERIALS AND METHODS

Two native Mediterranean evergreen shrubs of the *Labiatae* family were used: lavender (*Lavandula stoechas* L.) obtained from seeds, and rosemary (*Rosmarinus officinalis* L.) obtained from cuttings.

Plant growth conditions and experimental site

Seeds of lavender germinated on moist filter paper, and seedlings were transferred to 0.5-l pots containing a mixture of soil:peat:perlite (1:1:1 v/v). The pots were maintained in a glasshouse with controlled temperature (24/18°C, day/night). The plants were watered twice a week, once with water and once with Hoagland solution. Cuttings of rosemary were rooted and grown in pots in the same conditions as described for lavender plants. After 1 yr of growth, rosemary and lavender plants of the same height (35 cm) were transplanted to the Experimental Fields.

The experimental area consisted of four plots of 4.5 m^2 each of calcic Luvisol (FAO) in Barcelona, Northeast Spain, homogenized artificially 10 yr ago. The plots and their surroundings were always maintained clear of vegetation that could interfere in the growth of *R. officinalis* and *L. stoechas*. Before the plants were transferred, the soil was ploughed and treated with N:P:K (1:1:1) fertilizer at the rate of 100 kg N ha^{-1}. Plants were transplanted during April 1996 and 16 plants per plot were distributed homogeneously in a square, 1 m apart, so all plants had the same orientation to sun. Until August 1996, they were watered with 15 mm twice weekly. Twelve shrubs of each species per treatment, of approximately the same size, were chosen for this study.

Between 16 August and 26 September two watering regimes were imposed: (1) plants watered twice a week with 10 mm (irrigated (IR) plants), equivalent to the average rainfall during this period over the last 40 yr but distributed in a regular way, and (2) plants not irrigated at all (water-stressed (WS) plants). During this period when rainfall was expected, all plants were covered with a clear polyvinyl chloride (PVC) sheet. Between 27 September and 11 October dew occurred in the morning during 6 d (28, 29 and 30 Sept., and 1, 6 and 10 Oct.). This period was very humid ($>80\%$ rh at night) and was characterized by cloudy days (11 out of 15 d), although no rainfall occurred. Major rainfall occurred during 13 and 14 October (18.8 and 89.5 mm, respectively, Fig.1). Measurements were taken every 10 d and the data from the following representative days were selected: 16 August (beginning of the experiment), 26 September (imposed water deficit), 11 October (dew) and 31 October (rainfall). The imposed water deficit during summer and the occurrence of dew and rainfall when plants were water-stressed allowed us to evaluate the photosynthetic response to summer drought and recovery by dew and rainfall in *R. officinalis* and *L. stoechas* growing in the field.

Climatological measurements

Environmental conditions were monitored by a weather station (Delta-T Devices, Newmarket, UK) that was situated 8 m from the experimental plot. Measurements of photosynthetically-active photon flux density (PPFD), air temperature and relative humidity were taken at 1-min intervals, and 5 min means were logged. The PPFD (μmol m^{-2} s^{-1}) was measured with a Quantum Sensor (Li-Cor, Lincoln, NE, USA), air temperature and relative humidity were measured with a Vaisala thermocouple (Vaisala, Helsinki, Finland) and the precipitation (mm) was measured with a standard rain gauge. Vapour pressure deficit (VPD) was determined according to Nobel (1991). The environmental conditions during the experiment were typical of a Mediterranean summer and autumn (Fig. 2). Maximum PPFD decreased from *c.* 1760 to 1130 μmol m^{-2} s^{-1}, maximum diurnal temperature decreased from 27 to 18°C and maximum VPD decreased from 2.1 KPa on 16 August to 1.2 KPa on 31 October (Fig. 2).

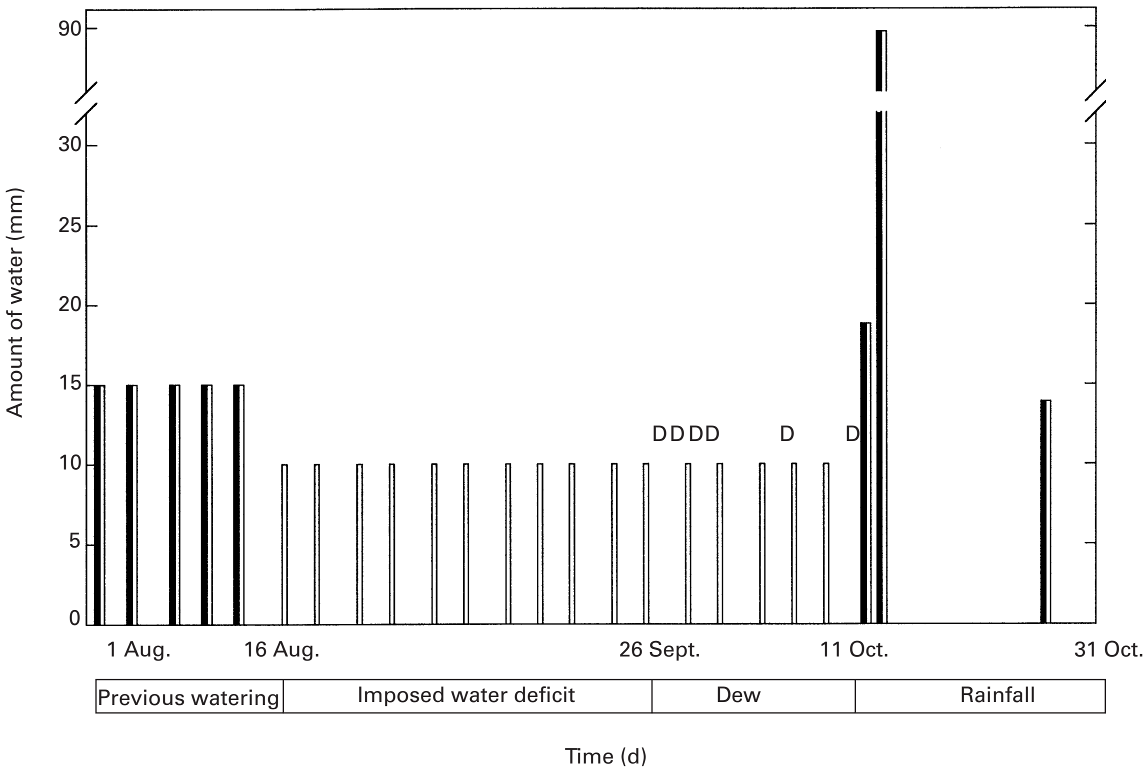

Fig. 1. Watering regimes for irrigated (open bars) and water-stressed (closed bars) plants of both *Rosmarinus officinalis* and *Lavandula stoechas* during the measurement period (Aug.–Oct. 1996). The boxes immediately under the abscissa indicate the four subperiods in water-stressed plants during the experiment: (1) previous watering before the measurement period, (2) imposed water deficit from 16 August to 26 September, (3) recovery by dew from 27 September to 11 October (the days when dew occurred are indicated by (D)) and (4) recovery by rainfall from 12 October to 31 October.

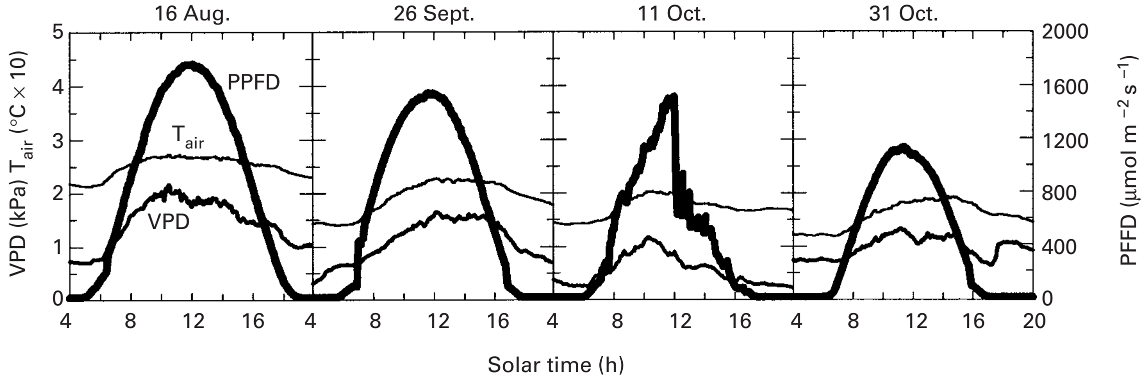

Fig. 2. Diurnal time courses of photosynthetically-active photon flux density (PPFD), air temperature (T_{air}) and vapour pressure deficit in the air (VPD) during the measurement days at the Experimental Fields of the University of Barcelona.

Plant and soil water status

Shoot water potential (ψ) of apical non-woody shoots ($N = 4$) was measured throughout the day at 3-h intervals from predawn to sunset using a pressure chamber (ARIMAD-2, ARI Far Charuv-Water Supply Accessories, Israel) containing damp paper at the base. Relative water content of fully developed young leaves ($N = 6$) was measured on plants taken before sunrise as RWC (%) = (FW − DW)/(TW − DW) × 100 (FW, fresh weight; DW, dry weight after drying samples to constant weight in an oven at *c.* 85°C; TW, turgid weight, after rehydrating samples for 24 h (Turner, 1981)). The gravimetric soil water content of the upper surface (0–20 cm depth) was measured as grams of water per gram of oven-dried soil.

Photosynthetic performance in the field

A LI-6200 portable measuring system (Li-COR Inc., Lincoln, NE, USA) was used to estimate diurnal CO_2 assimilation (A) and stomatal conductance (g_s) rates of 10 cm long attached apical non-woody shoots ($N = 4$) in the field, using equations developed by von Caemmerer & Farquhar (1981). Steady-state modulated chlorophyll fluorescence of single attached leaves ($N = 4$) was measured using a portable fluorimeter (mini-PAM, Walz, Effeltrich, Germany). The relative quantum efficiency of PSII photochemistry (ϕ_{PSII}) was estimated following Genty *et al.* (1989) as $(F'_m–F'_s)/F'_m$, (F'_m is the maximal fluorescence yield obtained at steady-state photosynthesis and F_s’ is the fluorescence yield at steady-state photosynthesis). Measurements of the maximum quantum yield of PSII photochemistry were made from the ratio of variable to maximal fluorescence yield ($F_v:F_m$) of dark-adapted leaves. Correction for changes in the internal temperature of the mini-PAM that affected the output of the measuring beam during the course of the day was applied to the fluorescence data according to Demmig-Adams & Adams III (1996).

Photosynthetic (chlorophyll $a+b$ and carotenoid) pigments from leaves ($N = 6$) of apical non-woody shoots were measured spectrophotometrically in 80% acetone (v/v) extracts using the equations described by Lichtenthaler (1987).

Fluorescence microscopy

Fluorescence microscopy studies were carried out to determine whether *L. stoechas* and *R. officinalis* were able to absorb water directly by leaves. Ten leaves of both species were detached and their adaxial surface was sprayed with a 0.1% (w/v) aqueous solution of fluorescent brightener-20 (Aldrich 29,418–7) (Grammatikopoulus & Manetas, 1994). Fluorescent brightener is an apoplastic tracer (Fahn, 1986) that binds to polysaccharides of the cell wall and emits a strong, pale blue fluorescence under an excitation wavelength of 350 nm (O’Brien & McCully, 1981). After 30 min, the leaves were washed in distilled water. Hand-cut transverse sections from the middle of blades were mounted in water and observed under a fluorescence microscope Leica DMRB (Leica UK Ltd, Milton Keynes, UK) at an excitation wavelength of 350 nm. Fluorescent controls were carried out by spraying leaves with distilled water. The experiment was repeated three times, and for each species an average of 95 randomly chosen mesophyll cells were examined.

Statistical analysis

Statistical differences between measurement days and treatments were analysed by ANOVA using SPSS (version 8, Chicago, IL, USA). Differences between treatments were considered significant when $P < 0.05$.

RESULTS

Water relations

The RWC and ψ did not show significant differences during the experiment in IR *R. officinalis* plants whereas IR *L. stoechas* plants showed a RWC decrease of *c.* 20% (26 Sept.) and ψ_{pd} fell from *c.* -0.4 to -0.7 MPa (16 Aug.–26 Sept., Table 1 and Fig.3). The relationship between RWC and ψ was different in the two species, and *L. stoechas* displayed much lower RWC than *R. officinalis* at the same ψ. A drought of 40 d caused an RWC decrease of *c.* 22 and 50% in *R. officinalis* and *L. stoechas* leaves, respectively. The ψ of both species decreased during the morning, as the water demand increased, to recover again during the afternoon to similar pre-dawn values (Fig. 3). Drought caused a decrease in ψ_{pd} from *c.* -0.4 to -1.5 MPa and from -0.4 to -1.3 MPa in water-stressed *R. officinalis* and *L. stoechas* leaves, respectively.

Six d of dew between 27 September and 11 October restored plant water status in *L. stoechas*, but not in *R. officinalis*. Both IR and WS *L. stoechas* plants showed a significant increase in RWC of *c.* 12 and 72% between 26 September and 11 October (Table 1). Shoot water potential was also restored during this period depending on the time of the day. Shoot water potential recovered by *c.* 0.3 and 0.5 MPa in IR and WS *L. stoechas* plants, respectively, at predawn and late in the afternoon; however, no differences were observed at midday ($P < 0.05$) (Fig. 3).

The gravimetric soil water content decreased from *c.* 5% to *c.* 4.3% between 26 September and 11 October in plots of WS plants of both species, thus corroborating that plant water recovery was due to dew and not to an improvement of soil water content.

Observations with the fluorescence microscope confirmed the results obtained on leaf dew absorption. Fluorescence micrographs showed that only *L. stoechas* was able to absorb water by leaves. Fig. 4 shows leaf cross sections of *L. stoechas* (a,b,c) and *R. officinalis* (d,e) observed under a fluorescence microscope at an excitation wavelength of 350 nm. *Lavandula stoechas* leaves sprayed with distilled water (fluorescence control) did not show blue fluorescence on mesophyll cell walls (Fig. 4a), whereas those sprayed with an aqueous solution of fluorescent brightener did (Fig. 4b,c). However, in *R. officinalis* no fluorescence was observed even when an aqueous solution of fluorescent brightener was sprayed (Fig. 4d,e). These results indicate that surface water enters mesophyll cell walls throughout the epidermis in *L. stoechas* but not in *R. officinalis*.

With the arrival of autumn rainfall, plant water relations returned to similar pre-drought values in both species (31 Oct., Table 1 and Fig. 3). Besides, higher water potential values were obtained at

Table 1. *Predawn relative leaf water content* (*RWC*) *of irrigated* (*IR*) *and water-stressed* (*WS*) Rosmarinus officinalis *and* Lavandula stoechas *plants from 16 August to 31 October*

	RWC (%) *R. officinalis*		*L. stoechas*	
	IR	WS	IR	WS
16 Aug.	81.0 ± 1.3	80.3 ± 0.9	76.3 ± 4.2	72.6 ± 1.3
26 Dept.	75.7 ± 4.9	62.8 ± 3.0ab	60.0 ± 0.4b	36.2 ± 4.8ab
11 Oct.	73.6 ± 6.5	62.0 ± 4.2a	70.1 ± 3.7c	62.5 ± 4.4c
31 Oct.	83.0 ± 4.1	81.5 ± 3.9	75.9 ± 5.5	69.4 ± 1.1

Letters next to a value indicate: a, significant difference at $P < 0.05$ (probability level) comparing IR with WS plants; b, comparing 26 September with 16 August; c, comparing 11 October with 26 September. Each value is a mean ± SE, $n = 6$. Plant water recovery by dew (dashed line) or rainfall (solid line).

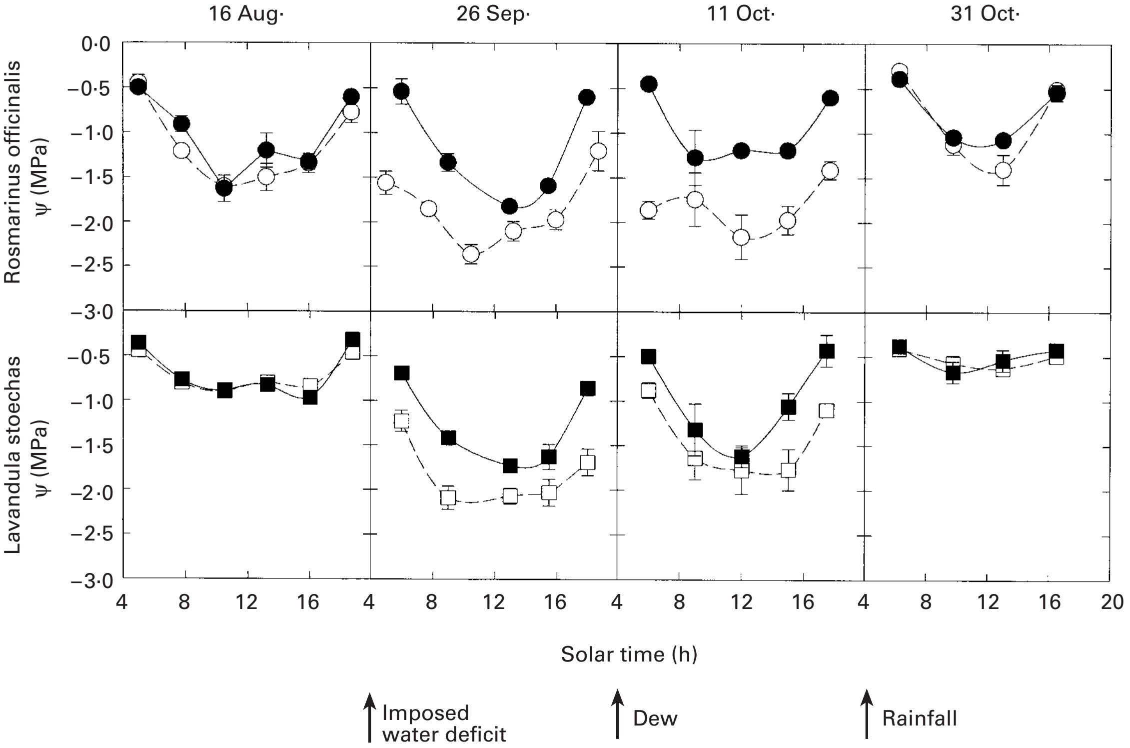

Fig. 3. Diurnal time courses of shoot water potential (ψ) of irrigated (closed symbols) and water-stressed (open symbols) *Rosmarinus officinalis* and *Lavandula stoechas* plants. Imposed water deficit and occurrence of dew and rainfall are indicated by arrows. Each value is a mean ± SE, $n = 4$.

midday in both species due to the lower evaporative demand during 31 October.

Diurnal variations of photosynthesis

The A, g_s and ϕ_{PSII} of irrigated (IR) and water-stressed (WS) *R. officinalis* and *L. stoechas* are shown in Figs 5 and 6. At the beginning of the measuring period (16 Aug.) *R. officinalis* and *L. stoechas* had a typical one-peaked diurnal time course of photosynthesis, with a maximum peak of CO_2 assimilation and stomatal conductance rates in the morning. In drought conditions (26 Sept.), maximal CO_2 assimilation rates decreased by *c.* 70% and 78% in *R. officinalis* and *L. stoechas* plants, respectively. Leaf gas exchange in IR *R. officinalis* plants remained unchanged between 16 August and 26 September, but IR *L. stoechas* plants showed a depletion of *c.* 25% in A and g_s (Fig. 6, 26 Sept.). During the morning ϕ_{PSII} decreased with changes in PPFD to increase again during the afternoon. Midday ϕ_{PSII} decreased by *c.* 43% and 50% during the summer drought in WS *R. officinalis* and *L. stoechas* plants, respectively (26 Sept., Figs 5, 6).

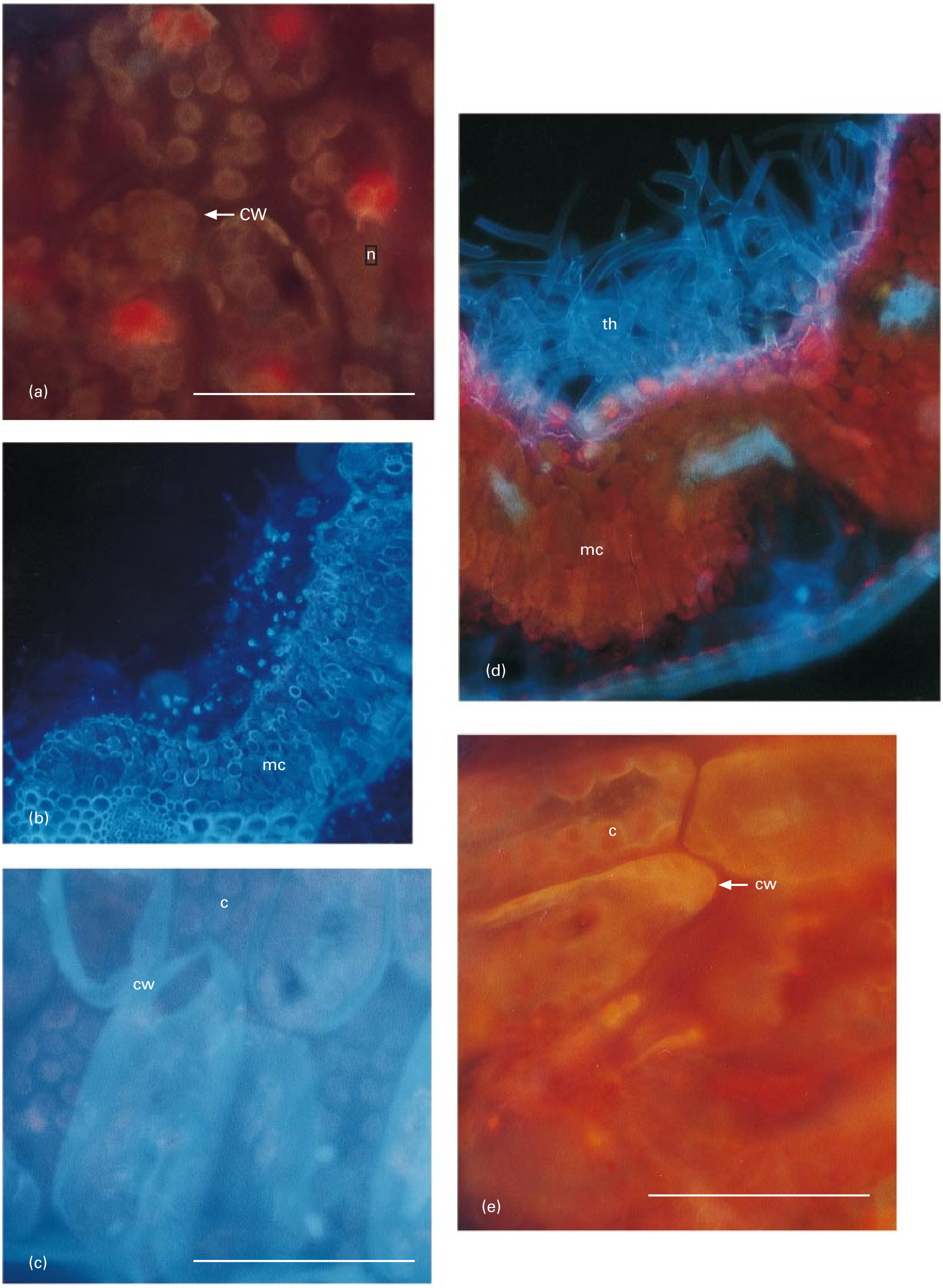

Fig. 4. Cross sections of *Lavandula stoechas* (a,b,c) and *Rosmarinus officinalis* (d,e) observed with a fluorescent microscope at an excitation λ of 350 nm. (a) *L. stoechas* mesophyll cells sprayed with distilled water (fluorescent control) did not show blue fluorescence on mesophyll cell wall. (b) *L. stoechas* mesophyll cells treated with fluorescent brightener-20. Fluorescent brightener is an apoplastic tracer that binds to polysaccharides of the cell wall and emits a strong, pale blue fluorescence (c) leaf cross section of *L. stoechas* treated with fluorescent

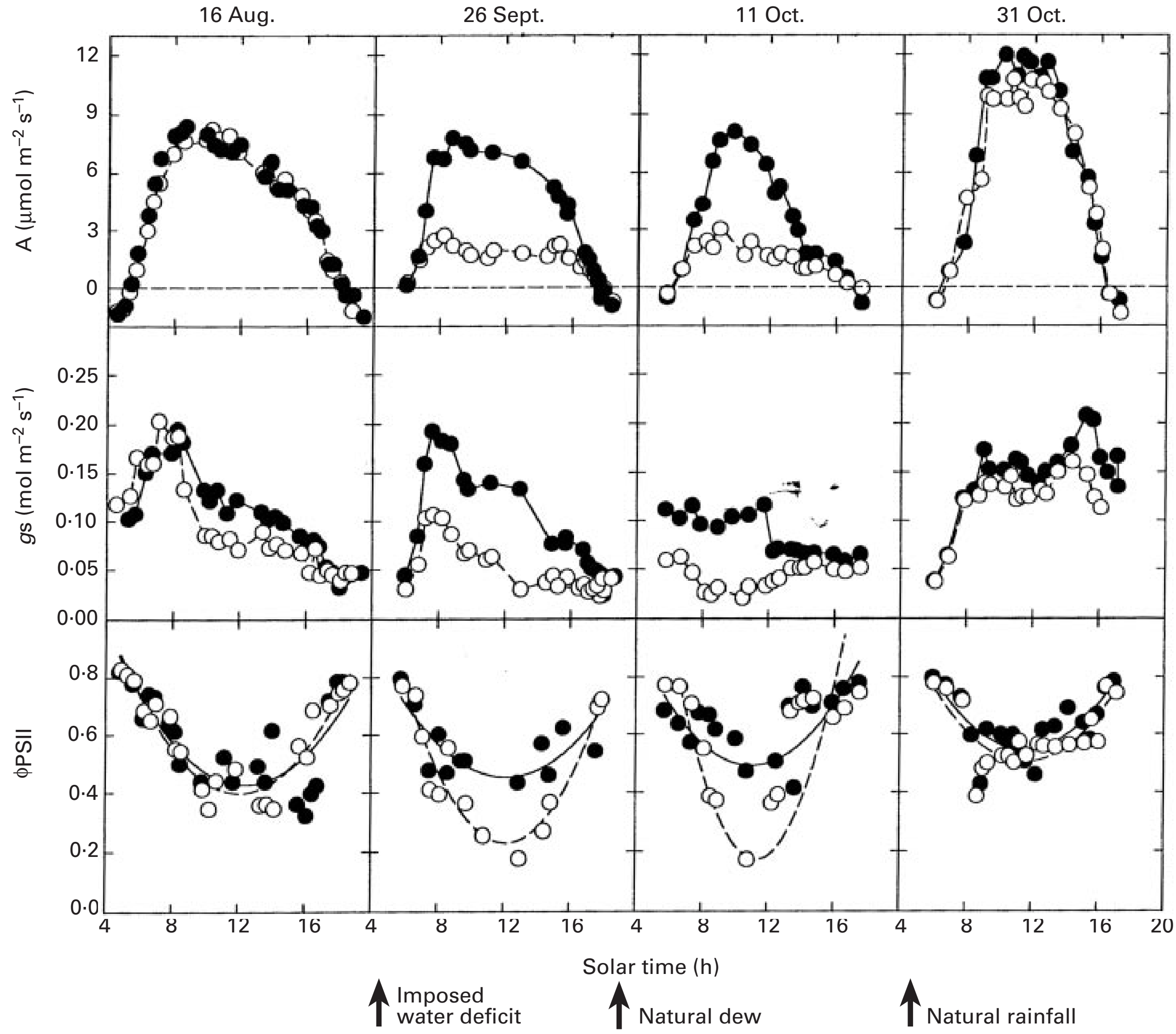

Fig. 5. Diurnal time courses of net CO_2 assimilation rate (A), stomatal conductance (g_s) and relative quantum efficiency of photosystem II photochemistry (ϕ_{PSII}) of irrigated (closed symbols) and water-stressed (open symbols) *Rosmarinus officinalis* shrubs. Imposed water deficit and occurrence of dew and rainfall are indicated by arrows. Each value is a mean of 4 measurements; the SE were $< 10\%$ of the mean values in all cases.

It is clear that plant water status was improved in *L. stoechas* by leaf dew absorption. Nevertheless, no effect of dew was observed in the photosynthetic performance of this species. The A and ϕ_{PSII} were unchanged between 26 September and 11 October in both irrigated and water-stressed *L. stoechas* plants (Fig. 6). Only g_s followed a different pattern on 11 October. However, any effect of dew on stomatal conductance may be masked by the different environmental conditions during 11 October. With the arrival of autumn rainfall, the photosynthetic capacity of plants recovered completely in both species (31 Oct., Figs 5, 6). The maximum diurnal net CO_2 assimilation rates on 31 October were higher than those obtained during 16 August in both species but, total CO_2 assimilation during the day was very similar (*c.* 80 vs 76 mmol m^{-2} d^{-1}).

Although ϕ_{PSII} decreased in drought conditions in both species, the ratio F_v : F_m remained constant at *c.* 0.75 at midday and did not show significant differences between 16 August and 26 September either between species or between IR and WS plants (Table 2).

Table 3 shows the effects of drought on the chlorophyll $a+b$ (Chl) and carotenoid (Car) leaf contents of IR and WS plants of both species. Overall, chlorophyll concentration was significantly decreased by *c.* 30% and 71% from 16 August to 26

brightener-20 (detail of b); notice the blue cell wall. (d) Leaf cross section of *R. officinalis* sprayed with distilled water (fluorescent control); blue fluorescence was not observed on mesophyll cell wall. Red and far-red chlorophyll fluorescence is emitted by the chl *a* molecules in the antenna and reaction centre of the photosynthetic photosystems of the chloroplasts of the mesophyll cells. (e) *Rosmarinus officinalis* mesophyll cells treated with fluorescent brightener-20; blue fluorescence was not observed on mesophyll cell walls. c, chloroplast; cw, cell wall; mc, mesophyll cells; n, nucleus; th, trichomes. Bar, 10 μm.

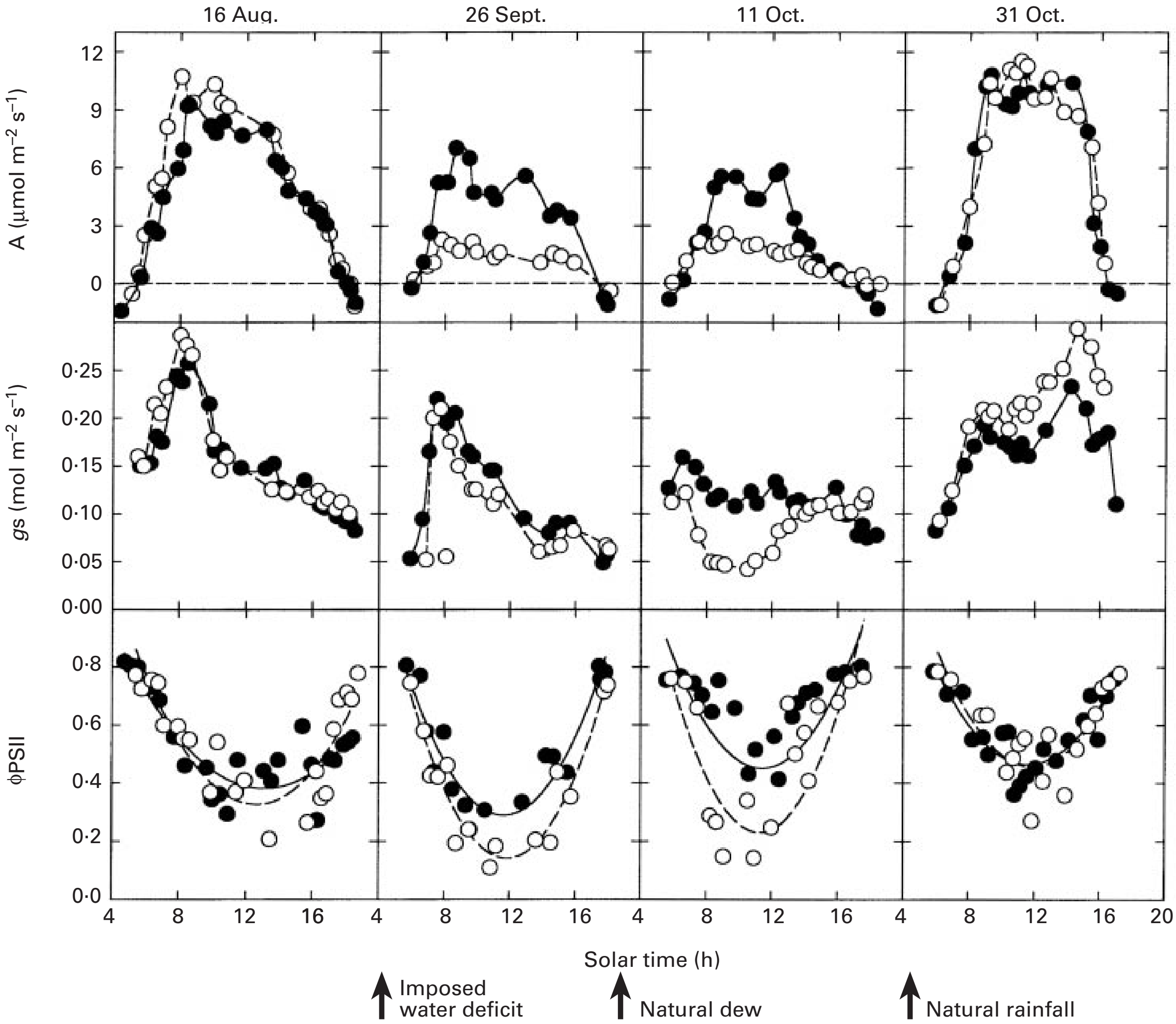

Fig. 6. Diurnal time courses of net CO_2 assimilation rate (A), stomatal conductance (g_s) and relative quantum efficiency of photosystem II photochemistry (ϕ_{PSII}) of irrigated (closed symbols) and water-stressed (open symbols) *Lavandula stoechas* shrubs. Imposed water deficit and occurrence of dew and rainfall are indicated by arrows. Each value is a mean of 4 measurements; the SE were $< 10\%$ of the mean values in all cases.

Table 2. *Maximum quantum efficiency of PSII photochemistry* ($F_v : F_m$) *at midday of irrigated* (*IR*) *and water-stressed* (*WS*) Rosmarinus officinalis *and* Lavandula stoechas *plants from 16 August to 31 October*

			$F_v : F_m$			
			R. officinalis		*L. stoechas*	
	T (°C)	PPFD (μmol m^{-2} s^{-1})	IR	WS	IR	WS
16 Aug.	27.3	1762	0.75 ± 0.01	0.74 ± 0.02	0.76 ± 0.02	0.76 ± 0.03
26 Sept.	25.2	1804	0.74 ± 0.02	0.74 ± 0.01	0.72 ± 0.02	0.72 ± 0.04
11 Oct.	20.4	1504	0.75 ± 0.01	0.74 ± 0.03	0.77 ± 0.01	0.78 ± 0.03
31 Oct.	19.3	1130	0.76 ± 0.02	0.75 ± 0.02	0.75 ± 0.01	0.77 ± 0.01

Each value is a mean ± SE of at least four measurements. Air temperature (T) and photosynthetically-active photon flux density (PPFD) are also given. Plant water recovery by dew (dashed line) or rainfall (solid line). No significant differences were found at $P < 0.05$ (probability level), comparing IR with WS plants or comparing different days.

Table 3. *Chlorophyll content and carotenoid*:*chlorophyll at midday of irrigated* (*IR*) *and water-stressed* (*WS*) Rosmarinus officinalis *and* Lavandula stoechas *plants from 16 August to 31 October*

	Chl a+b (μg cm^{-2})				Car:Chl			
	R. officinalis		*L. stoechas*		*R. officinalis*		*L. stoechas*	
	IR	WS	IR	WS	IR	WS	IR	WS
16 Aug.	40.5 ± 2.8	36.1 ± 2.4	45.2 ± 2.0	46.8 ± 4.0	0.37 ± 0.03	0.37 ± 0.02	0.32 ± 0.03	0.31 ± 0.02
26 Sept.	41.8 ± 1.4	25.1 ± 5.9ab	45.8 ± 3.5	13.2 ± 1.5ab	0.35 ± 0.03	0.46 ± 0.03ab	0.31 ± 0.02	0.50 ± 0.03ab
11 Oct.	41.7 ± 3.4	25.4 ± 1.5a	45.9 ± 0.7	14.5 ± 1.4a	0.33 ± 0.03	0.43 ± 0.02a	0.32 ± 0.02	0.47 ± 0.04a
31 Oct.	41.0 ± 2.1	39.5 ± 1.6	46.0 ± 1.6	41.4 ± 2.1	0.34 ± 0.02	0.35 ± 0.02	0.34 ± 0.3	0.33 ± 0.03

Letters next to a value indicates: a, a significant difference at $P < 0.05$ (probability level) comparing IR with WS plants; b, comparing 26 September with 16 August. No differences were found at $P < 0.05$ (probablity level) comparing 11 October with 26 September. Each value is a mean ± SE, $n = 6$. Plant water recovery by dew (dashed line) or rainfall (solid line).

September in water-stressed *R. officinalis* and *L. stoechas* plants, respectively. Neither IR *R. officinalis* plants nor IR *L. stoechas* plants showed significant changes during this period. The decrease in the carotenoid concentration was smaller than that for chlorophyll, which resulted in increases in the ratio Car: Chl in response to drought by *c.* 30% and 62% in WS *R. officinalis* and *L. stoechas* plants, respectively (26 Sept., Table 3). The maximum quantum efficiency of photosystem II photochemistry (F_v:F_m) and the pigment content of leaves remained unchanged between 26 September and 11 October in both IR and WS *L. stoechas* plants (Tables 2, 3). With the arrival of autumn rainfall F_v:F_m and the pigment content of leaves returned to similar pre-drought levels in both species (31 Oct., Tables 2, 3).

DISCUSSION

Plant water status and photosynthetic performance in irrigated *R. officinalis* and *L. stoechas*, although they may seem low, are consistent with the data reported by Körner (1995) and Kyparissis *et al.* (1995) for Mediterranean shrubs under field conditions in the absence of water stress. *Lavandula stoechas* showed a lower photosynthesis: stomatal conductance ratio than *R. officinalis* (A : g_s of *c.* 35 and *c.* 45 μmol CO$_2$: mol H$_2$O, respectively), and was less hydrated throughout the experiment, as shown by the RWC. Besides, when plants were exposed to a watering regime of 80 mm month^{-1}(IR plants), *L. stoechas* suffered a significant decrease in RWC, A and g_s, whereas *R. officinalis* did not. These results suggest that although both species were of the same age, *L. stoechas* had a higher water demand than *R. officinalis* growing under the same environmental conditions.

Water stress reduced the maximum diurnal stomatal conductance as shoot water potential decreased (Schulze & Küppers, 1979; Gollan *et al.*, 1985; Pereira & Chaves, 1993). In WS *R. officinalis* and *L. stoechas* plants maximum stomatal conductance decreased by *c.* 50% and *c.* 25%, respectively (26 Sept., Figs 5, 6) when ψ_{pd} fell below *c.* −1.3 MPa. Both species showed one-peaked diurnal time courses of photosynthesis during the summer. A small depletion of A was observed at midday in IR *L. stoechas* plants on 26 September and 11 October but it was not significant (ANOVA, $P < 0.05$). These results confirm previous studies (Körner, 1995; Mäkelä *et al.*, 1996), which show that water-stressed plants avoid water losses by closing stomata during midday and afternoon, when VPD increases.

In WS plants of both species, although ϕ_{PSII} decreased in response to water deficit, the photosynthetic system function was unlikely to be damaged by dehydration (Cornic & Massacci, 1996), despite the interaction of water deficit, high light and high temperature during the summer. Although the F_v:F_m values obtained at midday were slightly smaller than those obtained at predawn (0.75 vs 0.80), the maintenance of constant F_v:F_m values at midday throughout the experiment demonstrates the lack of drought-induced damage to PSII photochemistry, as already reported for many species (Genty *et al.*, 1987; Cornic, 1994). This was accompanied by a decrease in chlorophyll, but also by an increase in the ratio Car: Chl, which partly explains the absence of drought-induced damage to PSII (Demmig-Adams & Adams III, 1996).

The two species studied displayed different drought responses. At the same ψ *R. officinalis* (a sclerophyllous shrub) was able to maintain higher values of RWC than *L. stoechas*, which could indicate a higher osmotic adjustment in *R. officinalis* than in *L. stoechas* (Bowman & Roberts, 1985). It is a general concern that the Scholander pressure bomb does not always measure xylem water tension correctly (Tyree, 1997) and might overestimate it (Zimmerman *et al.*, 1993). However, recent studies on the hydraulic architecture of woody plants have provided strong support for the cohesion-tension theory and have demonstrated that the Scholander pressure bomb is one of the most useful tools to measure xylem water tension correctly under many circumstances.

Only *L. stoechas* absorbed water directly by leaves. *L. stoechas* has amphistomatic leaves protected by trichomes, glands and a cuticular thickening of 2–2.5 µm. However, *R. officinalis* has hypostomatic leaves protected by trichomes and an adaxial epidermis with a cuticular thickening similar to *L. stoechas*, *c.* 2 µm but covered with cuticular waxes of 5 µm thickness (Pastor, 1996). The pathway of direct water entrance through leaves is not yet clearly understood and further research is needed. Our hypothesis is that the polar fluorescent brightener and, by implication, dew, can enter directly through the epidermis and also through the stack cells of the glands and trichomes by diffusion. The abundance of trichomes observed in *L. stoechas* would retain dew, thus increasing leaf surface wetness. Franke (1967) and Kramer & Boyer (1995) pointed out that a significant amount of water could enter plants through the leaves because the cuticle is moderately permeable when wet. The absence of trichomes and the presence of thick cuticular waxes in *R. officinalis* would offer more resistance to water entrance through the epidermis. On the other hand, neither *L. stoechas* nor *R. officinalis* showed cracks in the epidermis.

Clearly, dew absorption by leaves during 6 d over a 15-d period played a major role in water-stressed *L. stoechas* improving RWC by *c.* 72% and ψ by *c.* 0.5 MPa at predawn and late in the afternoon. No effect of dew was observed in *R. officinalis*. Our results with *L. stoechas* are in accordance with Garrat & Segal (1988), who reported that dew provides significant amounts of water especially relevant in water-stressed plants. Although water precipitated on the leaf surface causes an immediate depletion of leaf gas exchange (Smith & McClean, 1989; Ishibashi & Terashima, 1995; Brewer & Smith, 1997), once dew water is absorbed from the leaf surface, the photosynthetic performance of water-stressed plants can be improved through increased plant water status (Grammatikopoulos & Manetas, 1994; Munné-Bosch & Alegre, 1999). Nevertheless, this assumption depends on the amount of water that plants absorb. The amount of dew absorbed by *L. stoechas* in the present study is not comparable to the large amounts of simulated dew that plants received in the previously cited studies. The absorption of dew could result in improved photosynthesis in water-stressed plants growing in field conditions only if long periods of dew occurred. In *L. stoechas*, dew improved plant water status, which is especially important in water-stressed plants than can suffer damage to the photosynthetic system under prolonged drought.

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