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Seasonal changes in photosynthesis and stomatal conductance of five plant species from a semiarid ecosystem

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Abstract

In order to determine whether stomatal closure alone regulates photosynthesis during drought under natural conditions, seasonal changes in leaf gas exchange were studied in plants of five species differing in life form and carbon fixation pathway growing in a thorn scrub in Venezuela. The species were: *Ipomoea carnea, Jatropha gossypifolia,* (C3 deciduous shrubs), *Alternanthera crucis* (C4 deciduous herb), and *Prosopis juliflora* and *Capparis odoratissima* (evergreen phreatophytic trees). Xylem water potential (Ψ) of all species followed very roughly the precipitation pattern, being more closely governed by soil water content in *I. carnea* and *A. crucis*. Maximum rate of photosynthesis, P_{max}, decreased with Ψ in *I. carnea, J. gossypifolia,* and *A. crucis*. In *I. carnea* and *J. gossypifolia* stomatal closure was responsible for a 90 % decline in net photosynthetic rate (P_N) as Ψ decreased from -0.3 to -2.0 MPa, since stomatal conductance (g_s) was sensitive to water stress, and stomatal limitation on P_N increased with drought. *In A. crucis,* P_N decreased by 90 % at a much lower Ψ (-9.3 MPa), and g_s was relatively less sensitive to Ψ. In *P. juliflora* and *C. odoratissima*, P_{max}, g_s, and intercellular CO_2 concentration (C_i) were independent of soil water content. In the C3 shrubs stomatal closure was apparently the main constraint on photosynthesis during drought, C_i declining with Ψ in *I. carnea*. In the C4 herb, C_i was constant along the range of Ψ values, which suggested a coordinated decrease in both g_s and mesophyll capacity. In *P. juliflora*

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Abbreviations: C_a = ambient CO_2 concentration; C_i = intercellular CO_2 concentration; g_s = stomatal conductance; L_m = relative mesophyll limitation; L_s = relative stomatal limitation of photosynthesis; P_{max} = maximal photosynthetic rate; P_N = net photosynthetic rate; Ψ = xylem water potential; PPFD = photosynthetic photon flux density.

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C_i showed a slow decrease with Ψ which may have been due to seasonal leaf developmental changes, rather than to soil water availability.

Additional key words: *Alternanthera crucis*; C3 and C4 plants; *Capparis odoratissima*; drought; intercellular CO_2 concentration; *Ipomoea carnea*; *Jatropha gossypifolia*; photosynthetic rate; *Prosopis juliflora*.

Introduction

Water is the major limiting factor of photosynthesis in most deserts. Water deficit can cause a decrease in P_N either by a direct effect on photosynthetic capacity of the mesophyll or by CO_2 limitation resulting from stomatal closure (Chaves and Pereira 1992, Pospíšilová and Šantrůček 1994). In many plant species, stomatal closure has been suggested as the main regulatory mechanism of photosynthesis under water stress (Farquhar and Sharkey 1982, Downton *et al.* 1988, Cornic 1994, Brestic *et al.* 1995, Ehleringer 1995). In response to a decrease in Ψ, a decrease in C_i and thereby a reduction in P_N may arise due to stomatal closure.

However, cases in which stomatal closure is not the sole factor in reducing CO_2 assimilation have been reported (Ehleringer 1983, Forseth and Ehleringer 1983, Tezara and Lawlor 1995). The reduction in P_N is caused by a decrease in the amount and/or activity of ribulose-1,5-bisphosphate carboxylase/oxygenase, at least in C3 plants (Caemmerer and Farquhar 1981, Woodrow and Mott 1989, Tezara and Lawlor 1995). Therefore, it becomes very important to evaluate the relationship between stomatal functioning and leaf metabolism and how their integration helps optimize water use, while only marginally limiting the photosynthetic process (Farquhar and Sharkey 1982).

Changes in g_s cause changes in Ψ by altering the transpiration rate (Farquhar and Sharkey 1982). The decline in P_N with decreasing Ψ is often linear, and stomata operate at such a g_s that C_i remains constant (Ehleringer 1983, Forseth and Ehleringer 1983, Comstock and Ehleringer 1984), which may result in a maximal water use efficiency (Caemmerer and Farquhar 1981, Farquhar and Sharkey 1982). Both stomatal and non-stomatal components are thought by some authors to be responsible for the decrease in P_N during drought (Farquhar and Sharkey 1982, Comstock and Ehleringer 1984, Sobrado 1996). The correlation between g_s and CO_2 assimilation apparently has great ecological significance; the relationship between g_s (at P_{max}) and P_{max} assumes that g_s is governed by P_{max} through changes in C_i (Schulze and Hall 1982). When this relationship is not linear the effects of long-term water stress would be largely on g_s and not on photosynthetic capacity; on the contrary, a linear relationship of zero intercept would imply that stomatal and non-stomatal limitations to photosynthesis change in a co-ordinate manner, *i.e.*, they co-limit photosynthetic rate (Schulze and Hall 1982). Simultaneous measurements of g_s (at P_{max}) and P_{max} have been done under controlled environmental conditions but few results are available for naturally varying field conditions (Schulze and Hall 1982).

In the present study, five species from the Venezuelan northwestern semiarid regions were selected on the basis of their carbon metabolism, life form, and leaf duration. Since annual rainfall is less than 400 mm, and the pattern is highly unpredictable, plants are often exposed to long droughts. The C3 shrubs, *I. carnea* and *J. gossypifolia*, have partly succulent stems. The C4 herb, *A. crucis*, keeps its leaves longer and at lower Ψ during drought than the shrubs (Urich 1978, Ríos 1993). The phreatophytes, *P. juliflora* and *C. odoratissima*, are evergreen C3 trees. All species of *Prosopis* are considered phreatophytic (Nilsen *et al.* 1981), roots of *P. juliflora* reaching down to 53 m (Canadell *et al.* 1996).

In the present study seasonal changes of g_s and photosynthesis of these five species were followed in order to determine whether changes in g_s may explain the ecological responses to drought of these species, that is, whether stomatal closure alone regulates photosynthesis and carbon gain during drought under natural conditions.

Materials and methods

The study was carried out under natural conditions in a thorn scrub located in the semiarid zones of northwestern Venezuela, at *ca.* 20 km from the city of Coro (11°25'N 69°36'W, 20 m). A total of seven daily courses done from June 1989 to January 1991 are reported. The majority of species which constitute this scrub are C3 and CAM; C4 metabolism is poorly represented. The species were: *Ipomoea carnea* Jacq. (*Convolvulaceae*), *Jatropha gossypifolia* L. (*Euphorbiaceae*), *Alternanthera crucis* (Moq.) Bondingh (*Amaranthaceae*), *Capparis odoratissima* Jacq. (*Capparidaceae*), and *Prosopis juliflora* DC. (*Leguminosae: Mimosoideae*). All measurements were made on adult individuals ($n \geq 3$).

The following microclimatic parameters were measured every hour: photosynthetic photon flux density (PPFD) with a *LI-170* quantum sensor connected to a *LI-185* meter (*LI-COR*, Nebraska, USA), air and leaf temperature with *YSI 400* thermistors connected to a telethermometer (*Yellow Springs Instruments*, Ohio, USA), and relative humidity with a hair strand hygrometer (*Abbeon* model *AB167B*, *Abbeon Cal.*, California, USA). Soil water content in the field (SWC, % DM) was determined in 4 samples taken at 30-50 cm depth, placed in airtight metal containers, weighed, dried at 100 °C for 72 h, and re-weighed.

Xylem water potential (Ψ) was measured in triplicate at 07:00-08:00 h on single leaves or short branches using a pressure chamber (*PMS*, Corvallis, OR, USA); in all these species maximal Ψ is found before dawn and values taken at 08:00-09:00 h are representative of water status. Gas exchange measurements were made with an *LCA 2* infrared gas analyzer connected to a *PLC(B)* assimilation chamber and an *ASU(MF)* air supply unit (*Analytical Development*, Hoddesdon, UK). Measurements were made in triplicate every two hours from 08:00 to 16:00 h on each species. Values were collected manually, and gas exchange parameters calculated with a custom-made programme according to Long and Hällgren (1985). Leaf temperature, incident PPFD, and leaf-air water vapour concentration gradient were those imposed by the environment during measurement. Ambient CO_2 concentration (C_a) was 367.7±13.6 µmol mol^{-1}. Integrated daily P_N was determined gravimetrically from paper copies of the area under the curves of its daily changes.

Response curves of P_N/C_i were determined on potted plants of *I. carnea, J. gossypifolia,* and *A. crucis* growing at the field site with controlled watering using a *CIRAS 1* IRGA connected to a *PLC(B)* assimilation chamber (*PPSystems*, Hitchin, UK) during 14 d of water deficit. The P_N/C_i curves were fitted to the empirical equation P_N = b + d e^{KC_i}, where b = theoretical maximal photosynthetic capacity (RuBP-limited rate) and (b + d) = y-intercept. Carboxylation efficiency was calculated as dP_N/dC_i on the linear portion of the curve. Measurements were done at a PPFD of 1800±200 µmol m^{-2} s^{-1}. Relative stomatal limitation of photosynthesis, L_s, was calculated as $L_s = 100\ (P_0 - P_N)/P_0$, where P_0 is the photosynthetic rate when C_i = 350 µmol mol^{-1} and P_N is the net photosynthetic rate at C_a = 350 µmol mol^{-1} (Farquhar and Sharkey 1982). Relative mesophyll limitation, L_m, was calculated as $L_m = 100\ (P_c - P_d)/P_c$, where P_c is the photosynthetic rate in control leaves at C_i = 1600 µmol mol^{-1} and P_d is the rate in droughted leaves at the same C_i (Jacob and Lawlor 1991).

Regression coefficients were considered significant at $p<0.05$. Statistical significance of other parameters was assessed through one-way analysis of variance at $p<0.05$. Curves were adjusted using the *Sigmaplot* package at $p<0.05$.

Results

Mean daily changes in microclimatic parameters during the period of study were: air temperature, 28.3±1.2 to 36.2±1.0 °C; relative humidity (RH), 56.4±2.9 to 80.6± 2.8 %; midday PPFD, 1200 to 2000 µmol m^{-2} s^{-1}, and leaf-air water vapour concentration gradient, 30 to 60 mmol mol^{-1}. A total of 240.4 mm of rainfall were recorded, with a maximum of 60 mm in June (Fig. 1*A*).

The relationship between rainfall and Ψ (Fig. 1) was low in any of the species. Changes in Ψ were well correlated with soil water content (Fig. 1) in *A. crucis* (r^2 = 0.74) and *I. carnea* (r^2 = 0.69), whereas poor relationships were observed in *J. gossypifolia* (r^2 = 0.008), *P. juliflora* (r^2 = 0.016), and *C. odoratissima* (r^2 = 0.005).

In *I. carnea,* P_{max} decreased exponentially from 14.5 to 1.3 µmol m^{-2} s^{-1} as Ψ declined from -0.5 to -1.8 MPa (Fig. 2). In *J. gossypifolia* a similar trend was observed, *i.e.*, a 90 % decrease in P_{max} within a narrow range of Ψ (-0.5 to -2.0 MPa). In *A. crucis*, a decrease in P_{max} of 90 % with Ψ also occurred, but for a range of Ψ four times as wide (-0.5 to -9.3 MPa) as that for the C3 avoiders; maximal rates were three times those of the C3 species (Fig. 2). No significant change in P_{max} with Ψ was observed in either *P. juliflora* (in the range of -1.0 to -4.2 MPa) or *C. odoratissima* (-2.5 to -4.6 MPa). The g_s showed the same trend as P_{max} with changing Ψ in all species (Fig. 2).

The relationship between g_s (at P_{max}) and P_{max} (Fig. 3) was curvilinear in *I. carnea* and *J. gossypifolia*, whereas in *A. crucis* it was characterised by a straight line of zero intercept which explained 84 % of the variation in g_s (at P_{max}). A lack of such response was found in *P. juliflora* and *C. odoratissima*.

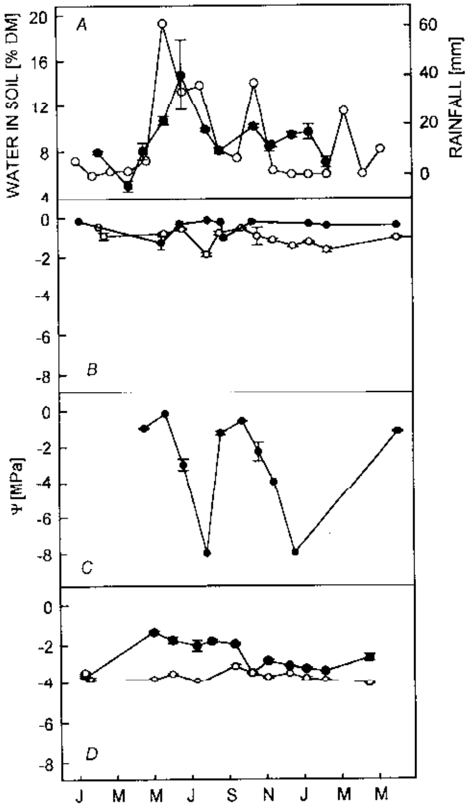

Fig. 1. Changes during the period of study in (*A*) total precipitation (○) and water in soil (●), and xylem water potential (Ψ) in plants of (*B*) *Ipomoea carnea* (○) and *Jatropha gossypifolia* (●), (*C*) *Alternanthera crucis*, and (*D*) *Prosopis juliflora* (●) and *Capparis odoratissima* (○). Values of Ψ are means±SE.

Values of C_i/C_a declined with Ψ in *I. carnea, P. juliflora* and *C. odoratissima*, whereas no change was observed in *J. gossypifolia* and *A. crucis* (Fig. 4). Both P_{max} under high C_i and carboxylation efficiency from P_N/C_i curves (Fig. 5, Table 1) declined over 14 d of drought in *I. carnea* and *J. gossypifolia*, but no changes were detected in *A. crucis*. Values of L_s and L_m were relatively high in watered plants of *I. carnea* and *J. gossypifolia* and increased approximately three times after 14 d of drought, while lower values were observed even in droughted plants of *A. crucis* (Table 1).

There was a strong linear relationship between the daily carbon gain (integrated daily P_N) and P_{max} for all the species studied. The relationship explained 86 % of the variation in integrated P_N with P_{max} (Fig 6). The highest values of this relationship were found in *A. crucis*.

Table 1. Effects of drought on carboxylation efficiency and relative stomatal and mesophyll limitations. Values are means. Different letters indicate statistically significant differences ($p<0.05$).

	Duration of drought [d]	Carboxylation efficiency [mol m^{-2} s^{-1}]	L_s [%]	L_m [%]
I. carnea	0	0.12 b	23.5 a	21.0 a
	7	0.19 b	35.0 b	32.5 b
	14	0.09 a	63.0 c	63.9 c
J. gossypifolia	0	0.07 b	35.2 b	24.5 a
	7	0.07 b	26.8 a	36.7 a
	14	0.03 a	26.8 a	60.5 b
A. crucis	0	0.08 a	0 a	2.2 a
	7	0.15 a	0 a	10.1 b
	14	0.09 a	9.5 b	24.2 c

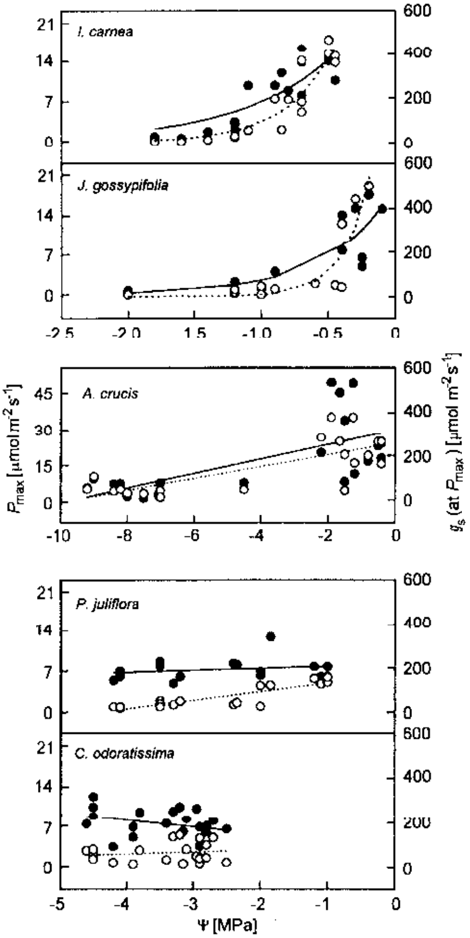

Fig. 2. Changes with xylem water potential (Ψ) in maximal photosynthetic rate, P_{max} (●, ——) and stomatal conductance, g_s at P_{max} (○, ...) in plants of *Ipomoea carnea* ($r^2 = 0.88$ and 0.93 for P_{max} and g_s, respectively), *Jatropha gossypifolia* ($r^2 = 0.65$ and 0.89), *Alternanthera crucis* ($r^2 =$ 0.43 and 0.56), *Prosopis juliflora* ($r^2 = 0.04$ and 0.73), and *Capparis odoratissima* ($r^2 = 0.09$ and 0.02). Results are measurements on individual leaves.

Discussion

Throughout the period of study, marked differences in Ψ occurred among the species, although a poor correlation was found between Ψ and precipitation. Changes in Ψ were evidently related to soil water availability in *I. carnea* and *A. crucis*, whereas in *C. odoratissima* they were the least conspicuous, highlighting the evergreen phreatophytic habit of this species. These observations suggest that changes in Ψ were apparently related to soil water availability, root depth, and the specific plant responses to drought. Air temperature and relative humidity may have exerted little influence on Ψ, since their monthly variations were smaller than daily changes (Urich 1978).

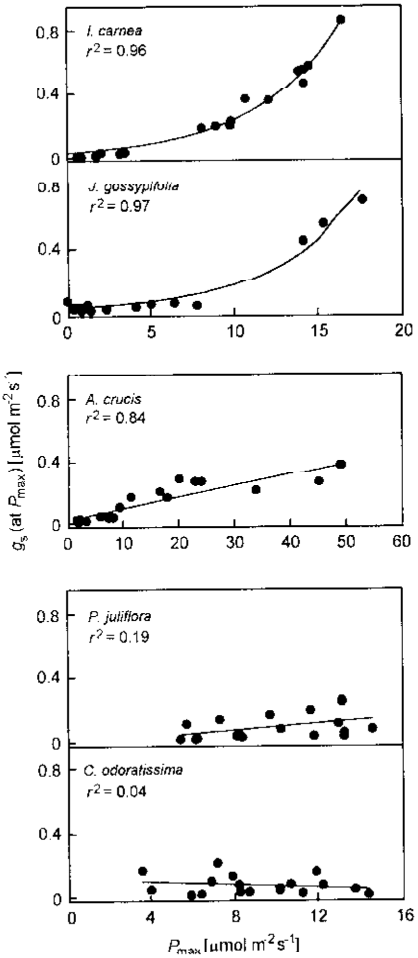

Fig. 3. Relationship between stomatal conductance, g_s (at maximal photosynthetic rate, P_{max}) and P_{max}. Results are measurements on individual leaves. Species and regression coefficients as indicated.

The expected decrease in P_{max} with Ψ was found in *I. carnea, J. gossypifolia,* and *A. crucis*. In plants of *I. carnea* growing in the greenhouse, a reduction of 98 % in

P_{max} was observed after 10 d of drought for a range of Ψ similar to this and a previous field study (Herrera *et al.* 1994). Although the decline in photosynthesis with decreasing Ψ is often linear (Ehleringer 1983, Forseth and Ehleringer 1983, Comstock and Ehleringer 1984), in *I. carnea* and *J. gossypifolia* the regression was exponential.

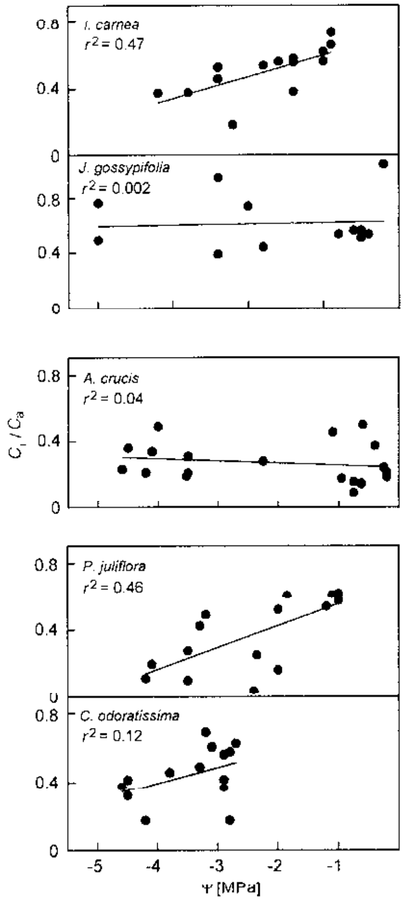

Fig. 4. Changes with xylem water potential (Ψ) in ratio of internal and ambient CO_2 concentration, C_i/C_a. Results are measurements on individual leaves. Species and regression coefficients as indicated.

Plants of *I. carnea* and *J. gossypifolia* exhibited a high sensitivity of g_s to Ψ (the initial slope of the relationship was almost asymptotic in *J. gossypifolia*). In *I. carnea* the decrease in P_{max} during drought was accompanied by a decrease in C_i/C_a and an increase in L_s. These results suggest that stomatal closure is the main limitation to P_N during drought in this species. In *A. crucis* g_s was less sensitive to decreasing Ψ.

Water stress markedly inhibited carboxylation efficiency in *I. carnea* and *J. gossypifolia*. In general, the decline in P_N with decreasing Ψ is correlated with a reduction in g_s and C_i (Farquhar and Sharkey 1982, Downton *et al.* 1988, Cornic 1994). In this study, a decrease in C_i/C_a during drought was associated with decreasing Ψ in *I. carnea*. Concurrent decreases in P_{max}, C_i, and g_s with Ψ are criteria necessary but not sufficient to prove the hypothesis that stomatal closure is the main limitation to photosynthesis under drought. It is also necessary to demonstrate that L_s increases with Ψ. In *J. gossypifolia*, C_i/C_a remained unchanged as Ψ declined but an increase with drought in L_s suggested that g_s is the main factor governing carbon gain. In *A. crucis* co-limitation of P_N by g_s and mesophyll factors was suggested by the maintenance of C_i/C_a with Ψ, low values of L_s and L_m in droughted plants, and the lack of a decrease in carboxylation efficiency.

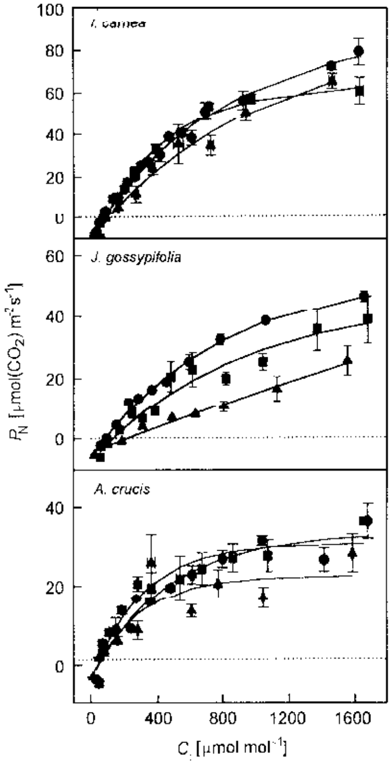

Fig. 5. Changes with drought in the response curves of net photosynthetic rate (P_N) to intercellular CO_2 concentration (C_i) of three plant species indicated after 0 (●), 7 (■), or 14 (▲) d of drought. Values are means±SE.

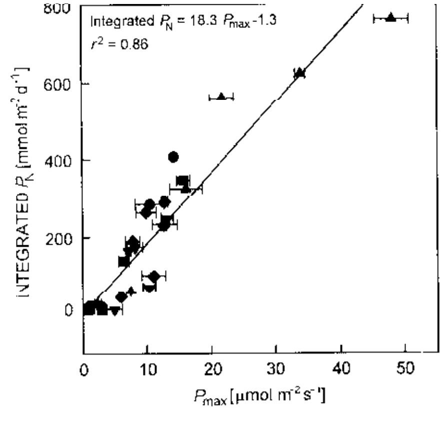

Fig. 6. Relationship between maximal photosynthetic rate, P_{max} and integrated daily net photosynthetic rate, P_N in plants of *Ipomoea carnea* (●), *Jatropha gossypifolia* (■), *Alternanthera crucis* (▲), *Prosopis juliflora* (▼), and *Capparis odoratissima* (◆). Values are means±SE. The equation of the regression and the regression coefficient are indicated.

Dependence curves of P_N on C_i done during water stress have proved a useful tool to evaluate the relative limitations of photosynthesis (Farquhar and Sharkey 1982). However, conclusions based on P_N/C_i curves may in some cases be incorrect due to errors in the calculation of C_i (Downton *et al.* 1988) and hence of L_s because of stomatal patchiness, *i.e.*, a non-uniform distribution of g_s (Terashima *et al.* 1988, Pospíšilová and Šantrůček 1994). Stomatal patches due to water deficit are probably not frequent under natural conditions (Ort *et al.* 1994); besides, leaves of the species in the present study may be classified as homobaric (Terashima *et al.* 1988) due to the absence of bundle sheath extensions which would create isolated mesophyll patches. The lack of a straightforward correlation in *J. gossypifolia* between changes in C_i/C_a and changes in L_s may be simply reflecting the difficulty in determining C_i precisely under uncontrolled microclimatic variables.

A slower decrease in P_{max} with Ψ occurred in *A. crucis* for a wider range of Ψ compared to *I. carnea* and *J. gossypifolia*. This could be related to the occurrence in this species of an osmotic adjustment of 0.8 MPa during drought (Ríos 1993). In addition, a change in leaf colour associated with drought may have increased reflectivity (Urich 1978). These characteristics could aid in a longer leaf duration and significant values of g_s at low Ψ. In the desert C4 ephemeral, *Amaranthus palmeri*, osmotic adjustment extended the range of Ψ for carbon gain for as much as 0.35 MPa (Ehleringer 1983). Paraheliotropic movements plus osmotic adjustment in *Malvastrum rotundifolium* (C3) were associated with a maintenance of C_i over the dry period and a lowering of L_S (Forseth and Ehleringer 1983).

In *P. juliflora* and *C. odoratissima* no relationship was found between either P_{max} or g_s and Ψ. Values of P_{max} measured in *P. juliflora* were very similar to those reported in *P. glandulosa* (Wang and Sosebee 1990). Plants of *P. juliflora* and *C. odoratissima* may have maintained a metabolic activity partly independent of water content in the first centimeters of the soil and, due to their phreatophytic character, may have counted on an sufficient water supply. Nevertheless, the observed decrease in Ψ does suggest stress, caused probably by a descent in the water table. A reduction in C_i in spite of a maintenance of P_{max} with Ψ may be reflecting seasonal changes in leaf development (leaves in September and December appeared younger).

The curvilinear relationship between g_s (at P_{max}) and P_{max} observed in *I. carnea* and *J. gossypifolia* suggests that drought affected stomatal aperture to a greater extent than it affected photosynthetic metabolism. Similar observations have been found in *Lupinus arizonicus* (Forseth and Ehleringer 1983). In the area of study, plants are often exposed to long dry spells. Plants of *I. carnea* and *J. gossypifolia* growing in the greenhouse close their stomata after a few days of water deficit (Herrera *et al.* 1994, M. Quijada and A. Herrera, unpublished). The demonstrated absence of osmotic adjustment in *I. carnea* (Herrera *et al.* 1994) would not allow a low Ψ to be reached and stomatal opening to be maintained.

The slope of the linear regression between g_s (at P_{max}) and P_{max} in *A. crucis* was lower than those observed in *I. carnea* and *J. gossypifolia*, thus indicating higher water-use efficiency and lower C_i values, as expected in a C4 species. This type of response has been reported in some C3 species from arid habitats (Schulze and Hall

1982, Forseth and Ehleringer 1983) and a C4 species (Ehleringer 1983) under controlled conditions. The possible occurrence of co-limitation and the ability for osmotic adjustment in *A. crucis* may allow leaves to keep C_i and carboxylation efficiency constant, therefore extending the period of carbon acquisition.

This study revealed a linear relationship between integrated P_N and P_{max}, similar to that reported in several C3 rain forest species (Zotz and Winter 1993). It may become difficult to define the most useful value of P_N during a day when trying to establish relationships with growth; the integrated daily P_N would provide this value but P_{max} can be for most purposes practical (Pereira 1995). In the present study, values of P_{max} were found mainly at 11:00 h. By using the relationship determined, it should be feasible to estimate the daily carbon balance of leaves of these species from measurements of P_N done at that time of day.

We were able to distinguish between three categories of responses of gas exchange to drought: (*1*) In the C3 shrubs, a reduction in P_N apparently due to stomatal closure at a fairly high Ψ (tolerance at a high water status); (*2*) the possible occurrence of co-limitation in the C4 species, allowing this species to extend the period of carbon acquisition (tolerance at a low water status), and (*3*) a relative independence of P_N and g_s from Ψ, and from each other in the phreatophytes (avoidance).

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