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Gas exchange of a desert shrub (*Zygophyllum dumosum* Boiss.) under different soil moisture regimes during summer drought

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Abstract

The effects of soil water potential on photosynthesis and transpiration of whole *Zygophyllum dumosum* Boiss. shrubs were examined with a field IRGA system during a rainless summer. Daily photosynthesis and transpiration activities were not notably different on a unit phyllode area basis among shrubs at naturally differing soil water potentials. Irrigation of shrubs caused phyllodes to increase significantly in water content and new leaflets to appear. Leaflets had three times as many stomata per unit area (23 000 stomata cm^{-2}) as phyllodes (7100 stomata cm^{-2}) but photosynthesis and transpiration rates were not measurably different between irrigated and non-irrigated shrubs on a unit area basis. This finding suggests that sufficient soil moisture will lead to increased carbon uptake of the entire shrub simply because the total area of photosynthesizing tissue increases. Gas exchange rates appear to be controlled solely by atmospheric conditions under the stresses of summer.

Introduction

In deserts, dominance in space and time of a plant species should be strongly influenced by characteristics that enhance survival during long, hot, extremely dry periods rather than fleeting moist, temperate periods. Slight topographical variations in soil moisture may affect the success of reproductive propagules (Beatty 1984; Beatty & Stone 1986) and are thought to be a particularly important influence on the growth rates of desert plants (Ehleringer 1985; Smith & Nowak 1990). Soil moisture contents following rain on extremely arid slopes are influenced as much by spatial differences in the physical characteristics of soil and rock as by the direct quantity of rainfall (Yair 1987; Yair & Berkowicz 1989).

In the Negev Desert, soil water contents after storms are often higher in the middle elevations of slopes with upper reaches of massive rock than on all portions of slopes covered by a thick mantle of permeable löess (Yair & Enzel 1987). The result of most storms on slopes with rocky upper reaches is as follows: (1) rainfall runs off the relatively impermeable upper elevation of a slope; (2) the shallow soils at mid-slope collect both rainfall and runoff but do not generate saturated flow; and (3) the lowest elevation receives rainfall alone. Yair & Lavee (1985) suggest that soils at mid-slope have the highest water potentials after most storms both because these regions receive the most water and because the water is distributed throughout the smallest volume. They hypothesize that these systematic differences in soil moisture distribution following storms affect the distribution and productivity of vegetation on slopes in the northern Negev Desert. Yair & Danin (1980) note that plant species of Irano-Turanian (steppe) origin dominate the mid-slope elevations of slopes with rocky upper reaches whereas lower elevations contain more species of Saharo-Arabian (very dry desert) origin (classification of Zohary 1966). Yair (1987) proposes that soils at mid-slope will be wettest not just following storms but throughout the year, thereby fostering local increases in plant productivity.

We address herein three hypotheses about soil moisture dynamics and plant productivity during a long, hot, dry period in the northern Negev Desert. The first hypothesis is that soil water potential varies down a slope with rocky upper reaches not only as described by Yair & Lavee (1987) following storms but for the duration of summer drought in the Negev Desert as well. The second hypothesis is that summer photosynthesis and transpiration activities of the widespread shrub, *Zygophyllum dumosum* Boiss. are related to natural positional differences in soil water potentials on slopes during rainless periods. The final hypothesis is that large, artificially imposed differences in soil water potential will influence the photosynthesis and transpiration activities of *Z. dumosum* during the hot, dry summer weather of the Negev. *Zygophyllum dumosum* is one of the most widespread species in the northern and central Negev. We examine the assumption that relationships between gas exchange and soil water status indicate how *Z. dumosum* occupies a wide range of microhabitats in the Negev.

Methods

Field site

The study was conducted on a northeast facing slope of 22° at the Sede Boker Research area of the Hebrew University of Jerusalem, approximately 40 km south of Beersheva (30° 53′ N 34° 46′ E, elevation 490–538 m, Fig. 1). The slope consists of exposed limestone bedrock above 515 m elevation. The soil mantle initiates at 515 m elevation and increases in thickness to approximately 2 m at 500 m elevation. Portions of the slope above 500 m are dominated by *Zygophyllum dumosum* in a vegetation mixture resembling the association *Zygophylletum dumosi* rupestre (of Zohary 1973). *Zygophyllum dumosum* is a clonal species with deciduous leaflets and evergreen petioles that function as photosynthesizing phyllodes even after the abscission of leaflets. The lowest portion of the slope extends at an angle of 3° into a wadi and has no *Zygophyllum dumosum*. Specific lithologic features of the study area have been described elsewhere (Yair 1983; 1987; Wieder et al. 1985; Yair & Lavee 1985; Yair & Enzel 1987; Yair & Shachak 1987; Yair & Berkowicz 1989).

This study spanned the summer of 1989. Rain did not fall during this period and had not fallen since 14 March 1989 (a storm of 3.8 mm). The total rainfall for the year preceding our study was 95.4 mm (from the site specific records of Aaron Yair).

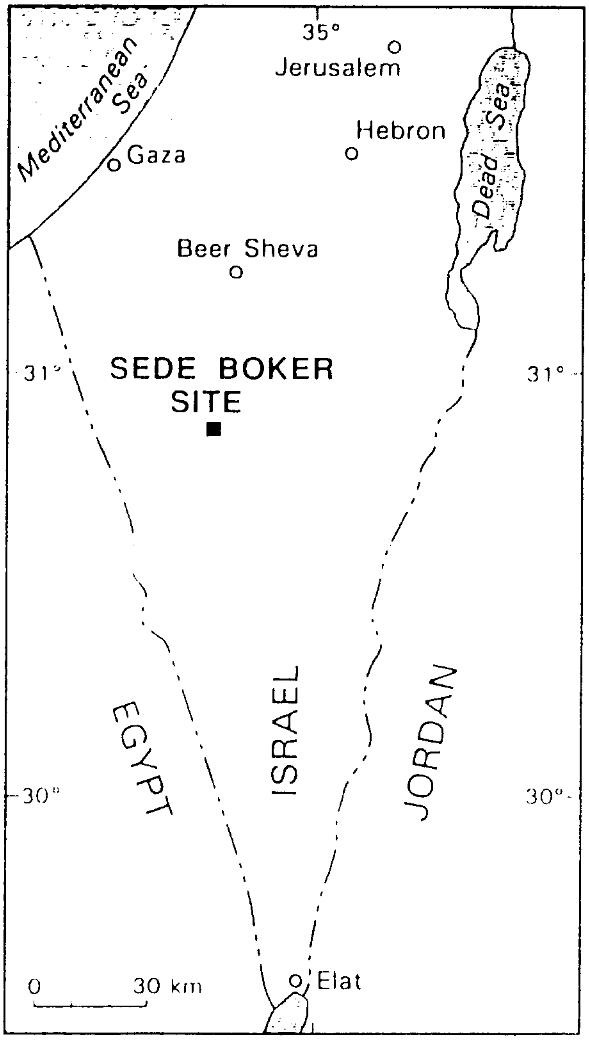

Fig. 1. Location of study slope.

Species distribution

We compared species distributions at the different slope positions as one indication of whether net photosynthesis productivity varied with elevation. Species composition was examined from twelve 10 × 4 m transects divided into four cells. Transects were arranged such that three were spaced at 100 m distances at the same elevation at each of four elevations. The suites of four transects occurring at the same cross slope position but different elevations are hereafter referred to as positions 1, 2, and 3 from West to East. Transect elevations began where the soil initiated and extended to the toe of the slope. Densities (numbers of ramets) of all plant species were recorded for each transect. Absolute dominance (total volume, where each shrub was assumed to be ellipsoidal) was determined for *Z. dumosum* in each transect.

Photosynthesis, conductance, and transpiration

Two *Zygophyllum dumosum* shrubs, one from an upper cell and one from a lower cell of each transect were randomly selected in each of the twelve transects for study of photosynthesis and transpiration rates. Although gas exchange measurements are most precise when done on no more than a few leaves of a plant at a time, our objective of examining spatial variation in gas exchange among individuals of a *Zygophyllum dumosum* population could not be met by measurements of parts of plants. We therefore designed a 1 m^3 chamber and fit it to a closed system Li-Cor 6000 infra-red gas analyzer (Li-Cor Corp., Lincoln, Nebraska, USA) for quick, non-destructive gas exchange measurements of whole shrubs. The chamber was constructed of 5 mm polycarbonate (Lexan). The polycarbonate was lined with 125 μm thick, clear high density polyethylene (HDPE) which is an effective water vapor barrier. The combination of polycarbonate and polyethylene reduced photosynthetic photon flux (PPF) by 710%. Air was mixed by two plastic fans positioned at different heights at opposite sides of the chamber. A metal frame was installed in a levelled, 1 m^2 area of ground around each study shrub. The ground space around the shrub and frame was covered with 125 μm HDPE before each photosynthesis measurement in order to prevent flow of respired CO_2 from the microorganisms and roots in the soil to the chamber. The chamber was then inserted into the frame to make a closed box containing the shrub alone. A tight seal at the chamber bottom was achieved by using a lubricant appropriate for high vacuum gas extractions.

Zygophyllum dumosum has multiple stems so that exposure of small areas of soil could not be prevented. We minimized this effect by measuring fluctuations of CO_2 and H_2O in control areas and subtracting the resulting computations for rates of 'photosynthesis' and 'transpiration' from rates obtained for corresponding shrubs. Control areas near study shrubs consisted of bare (but not root-free) sections of earth fitted with frames that were enclosed as the study shrubs had been enclosed during measurements.

Humidity and leaf temperature thermocouple sensors extended into the volume of a shrub but could not be clamped onto a leaf. Temperature readings from the leaf volume within the chamber were compared to measurements obtained by an infrared pyrometer and from measurements where a 1/4 l chamber of LiCor manufacture was used and contact between leaf and sensor were achieved. Leaf temperature values were not significantly different among the three methods of measurement.

Flow rates were adjusted so that relative humidity would remain constant throughout a measurement and the photosynthesis system was programmed to correct for water vapor variability. Relative humidities and temperatures near shrubs were checked frequently with a psychrometer and compared to relative humidity in the chamber in order to detect unacceptable accumulations of water in or overheating of the chamber. We cooled the chamber whenever interior temperatures became >3 °C warmer than those of open surrounding atmosphere. This was accomplished during cooler portions of the day by putting the chamber on its side, covering it with a white sheet, and allowing the fans within to run while the next shrub was prepared for measurement. Under cloudless conditions at mid-day, however, it was often necessary to move the chamber to a table in a nearby shaded hut in order to cool it to ambient temperature. Humidity control was occasionally a problem in pre-dawn and post-dusk fogs. This problem was also overcome by elevating the chamber and running the fans between measurements. Data were discarded when discrepancies existed of >3 °C or 5% humidity between the inside of the chamber and the open during measurements. Temperatures and humidities were constant to within a maximum of 1 °C and 2% respectively during all measurements.

As a final check of accuracy of the large chamber, one late morning and another afternoon were devoted to obtaining photosynthesis measurements using a standard 1/4 l chamber of LiCor manufacture on *Zygophyllum dumosum* shrubs that were not being used for repeated study. Photosynthesis and transpiration rates were not significantly different from those found for study shrubs measured with the large chamber. Boundary layer resistances were determined as suggested by the manufacturers, except that filter paper pieces were attached to a ring stand to achieve values for whole shrubs. Boundary layer resistances for 10 measurements in the large chamber were 2.3 times (0.35 s cm^{-1}) higher than boundary layer resistences in the standard 1/4 liter chamber (0.15 s cm^{-1}).

Photosynthesis and transpiration rates of *Z. dumosum* shrubs were assessed as frequently as possible at all times of day each week from late June through August 1989. The first shrub to be measured and the direction of travel to measure other shrubs was different each day. This procedure was followed in order to avoid mistaking variations in photosynthesis and transpiration rates caused by soil moisture availability to a shrub for variations in these rates caused by changes in PPF, relative humidity, and temperature. Each individual shrub was sampled a maximum of twice on any given day of measurements. Photosynthesis measurement times varied from 45 s to 135 s. Shorter measurement times were used when photosynthesis activity was readily detectable and measurement times increased as activity slowed.

Photosynthesis and transpiration rates were measured per unit leaf area. All calculations of photosynthesis and transpiration rates were done with the LiCor C6000 program. Total areas of the tiny, ellipsoid phyllodes and leaflets were estimated as follows. Leaf areas of shrubs were estimated with a Delta T leaf area meter (Delta Devices Ltd., Cambridge, U.K.) from photographs taken at the beginning, two weeks after irrigation, and five weeks after irrigation. To do this, a total of five black and white photographs were taken of each shrub, one from the top and one from each of four sides of a shrub. Photographs were taken against a black background and included a rectangle of known dimensions which was used to calibrate the leaf area meter. A green filter was used on the camera to eliminate error associated with shades of grey on resulting prints of leaves. Prints were blacked out to reveal only leaves. The leaf area of a shrub was the sum of leaf area measurements from the five photographs. This method yielded leaf area values that were consistent with spatial covers of the individual shrubs and was functional for the purpose of comparing gas exchange activity of one shrub to another.

Soil water potentials

We inserted 28 calibrated soil psychrometers (WESCOR PCT-55, WESCOR Inc., Logan, Utah USA) at 50 cm depth into the study slope. This was the depth of soil of the transects at highest elevation where moisture levels were hypothesized (Yair 1987) to remain highest throughout the year. Psychrometers were calibrated at water potentials of 0, −2.5, and −5.0 MPa at temperatures of 20 and 25 °C. A psychrometer was inserted under each study shrub and the remainder of the psychrometers were placed in bare soil 4 m from a shrub. Soil water potentials were measured weekly during July, August, and early September of 1989 with a WESCOR HR33 dew point microvoltmeter and corrected for soil temperatures that were obtained in 50 cm deep, 1 cm diameter holes.

Irrigation of shrubs

In order to compare the photosynthesis and transpiration responses of *Zygophyllum dumosum* to large differences in soil water potential under summer conditions, we irrigated study shrubs in transects at all elevations along position 3 from the third week in July until the end of the study in September. Wet soil conditions were sustained by digging a 0.5 m × 1.5 m × 0.6 m deep trench above each shrub, filling each trench with 120 l of water each week, and covering each trench with sheet polyethylene.

Results

Vegetation distribution

The densities, total areas, and total volumes of *Zygophyllum dumosum* per unit ground surface area were lowest at the bottom of the slope but did not vary significantly between other elevations (Table 1) (Mann Whitney U tests, $p \leq 0.05$). Ramets were moderately variable in volume at each elevation (based on Gini coefficients, Weiner & Solbrig 1984). Species richness was slightly higher at the bottom elevation of transects (number of species = 6) than at all other elevations (5 species per elevation) (Table 2). The total density of all vegetation was highest at the top and lowest at the bottom elevation of transects, however (Mann Whitney U tests, $p \leq 0.05$). The densities and frequencies of the much smaller *Artemisia herba-alba* Asso were higher than those of *Z. dumosum* at all but the bottom elevation.

Soil water potentials

No systematic differences in soil water potentials were observed between elevations under natural conditions, although there was a greater range in soil moisture across the higher two elevations than across the lower two elevations of the slope (Fig. 2). Soil water potentials were significantly higher in early summer than in late summer (KRUSKAL-WALLIS ANOVA, $p < 0.05$, Mann Whitney U tests, $p < 0.05$, treatment = 2 weeks of data). Irrigated plots were significantly wetter than

Table 1. Densities (no. ramets m^{-2}), areas (m^2 shrub m^{-2} ground), volumes (m^3 shrub $\mathrm{m}^{-}2$ ground), frequencies (% of cells containing *Z. dumosum*), and Gini coefficients of *Zygophyllum dumosum* volume distributions at each elevation of transects. A Gini coefficient of unity would occur if one shrub were extremely voluminous compared to others. A Gini coefficient of zero would occur if all shrubs were precisely the same size. Letters refer to slope elevations. H = highest (top) location. U = the upper middle elevation. L = the lower middle elevation, and B = the lowest elevation.

Elevation	Density ± S.E.	Area ± S.E.	Volume ± S.E	Frequency	Gini coeff.
H	0.13 (0.03)	0.06 (0.00)	0.01 (0.001)	58	0.42
U	0.28 (0.04)	0.10 (0.02)	0.02 (0.004)	92	0.50
L	0.13 (0.04)	0.07 (0.01)	0.02 (0.004)	58	0.54
B	0.05 (0.02)	0.02 (0.01)	0.04 (0.002)	42	0.48

Table 2. Densities (number of ramets m^{-2}) and frequencies (% of cells containing species) of herbs and smaller shrubs at each elevation of transects. Codes for elevations are explained in Table 1. A. h. = *Artemisia herba-alba* Asso; N. m. = *Noaea mucronata* (Forssk.) Aschers. et Schweinf.; R. h. = *Reamuria hirtella* Joub. et Sp.; S. i. = *Salsola inermis* Forssk.; H. s. = *Hammada scoparia* (Pomel) Botsch.

	Density				Frequency			
Species	H	U	L	B	H	U	L	B
A. h.	2.43	1.33	0.84	0.02	100	100	92	17
N. m.	0.08	0.00	0.08	0.03	50	0	33	25
R. h.	0.15	0.04	0.00	0.02	33	3	0	8
S. i.	0.01	0.03	0.10	0.05	8	17	33	17
H. s.	0.00	0.01	0.75	0.18	0	8	33	75

Table 3. Total leaflet and phyllode area (m^2) per shrub at the beginning, middle, and end of the study. Codes for elevations are given in Table 1. Shrubs in position 3 were irrigated after the July measurement, whereas shrubs in positions 1 and 2 were never irrigated.

	1			2			3		
Elevation	Jun	Jul	Aug	Jun	Jul	Aug	Jun	Jul	Aug
H	1.61	1.20	1.13	0.64	0.45	0.45	0.35	0.24	0.34
	1.12	0.79	0.78	0.35	0.25	0.24	1.20	0.83	1.19
U	0.15	0.11	0.10	0.72	0.51	0.50	0.41	0.28	0.40
	0.10	0.07	0.06	0.29	0.20	0.20	1.10	0.74	1.00
L	0.23	0.16	0.16	0.89	0.62	0.62	0.54	0.38	0.54
	0.26	0.19	0.18	1.19	0.84	0.83	0.46	0.33	0.47
B	0.45	0.32	0.31	0.26	0.19	0.18	0.98	0.70	1.01
	0.22	0.16	0.15	0.24	0.20	0.19	0.50	0.34	0.49

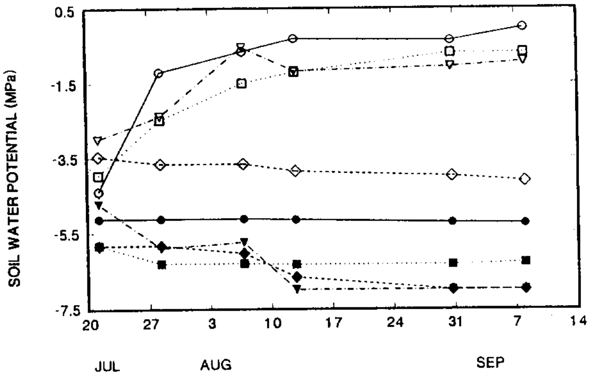

Fig. 2. Average soil water potentials (MPa) at each elevation under natural conditions. Vertical bars are standard errors (n = 4). Circles = highest elevation, squares = upper middle elevation, triangles = lower middle elevation, and diamonds = bottom elevation.

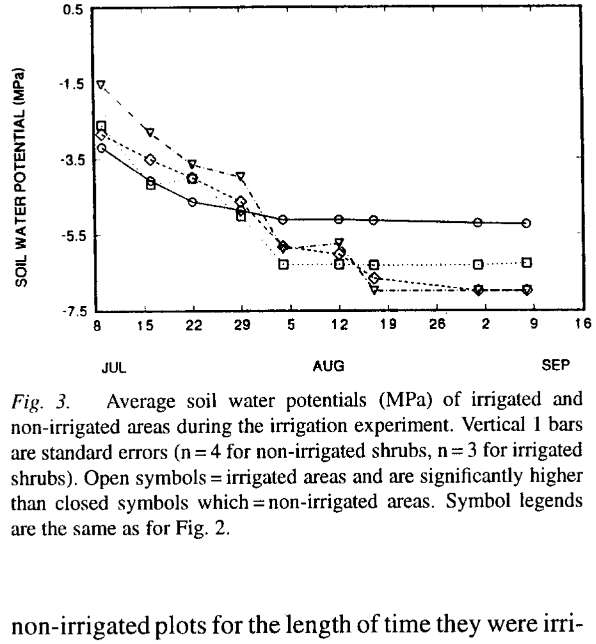

Fig. 3. Average soil water potentials (MPa) of irrigated and non-irrigated areas during the irrigation experiment. Vertical 1 bars are standard errors (n = 4 for non-irrigated shrubs, n = 3 for irrigated shrubs). Open symbols = irrigated areas and are significantly higher than closed symbols which = non-irrigated areas. Symbol legends are the same as for Fig. 2.

Table 4. Average water contents ([100 × g water]/g fresh tissue) of phyllodes of study shrubs (n = 2). Shrubs in position 3 had been irrigated for 3 weeks. (See Table 1 for explanation of elevation codes.)

Elevation	1	2	3
H	72	76	79
U	73	72	80
L	71	73	80
B	69	65	76

non-irrigated plots for the length of time they were irrigated (Mann Whitney U Test, $p \leq 0.01$) (Fig. 3). The bottom elevation transect of position 3, once irrigated, had significantly lower water potential than any of the higher elevation irrigated transects. Soil temperatures at 50 cm depth rarely differed from 29 °C during the entire study.

Net photosynthesis, stomatal conductance, and transpiration

Net photosynthesis occurred fleetingly, if at all in *Zygophyllum dumosum* shrubs on any given day. Maximum net photosynthetic activity tended to occur soon after dawn and was next most frequently detectable towards dusk. There was no linear relationship between net photosynthesis and any environmental parameter. Net photosynthesis activity appeared to be triggered by an interactive complex of ambient conditions, however. For instance, net carbon assimilation occurred at all observed relative humidities but was not detectable if photosynthetic photon flux was above 1300 μmol m^{-2} s^{-1} when relative humidity was low (Fig. 4). Some net carbon assimilation was observed at temperatures as high as 45 °C. Photosynthetic photon flux and relative humidity were moderate at that temperature (590 μmol m^{-2} s^{-1} and 25%).

Photosynthetic activity was higher during weeks 3–6 of the study than during any other three week period (Kolmogorov-Smirnoff two sample tests on diurnal distributions where time schedules were matched, $p \leq 0.05$). If measurements on one cloudy day during weeks 3–6 are excluded, then differences in photosynthetic activity did not appear over the study period. Photosynthesis rates did not vary systematically with elevation on the slope but were significantly greater at the lower middle elevation than at the uppermost and lowermost elevations (Kolmogorov-Smirnoff two sample test on distributions of matched time schedules until late July irrigation began, $p \leq 0.05$).

Measurements of carbon assimilation were sporadic from noon until 15:00 most days, in part because of the frequent need to cool the chamber. Measurements during the early afternoon were most frequent at the beginning of the study but never yielded any apparent photosynthetic activity. Throughout the study, all net photosynthetic activity ceased well before this hottest, driest portion of the day and did not begin again until well after it became cool enough to resume frequent measurements. Yellowing leaflets were still

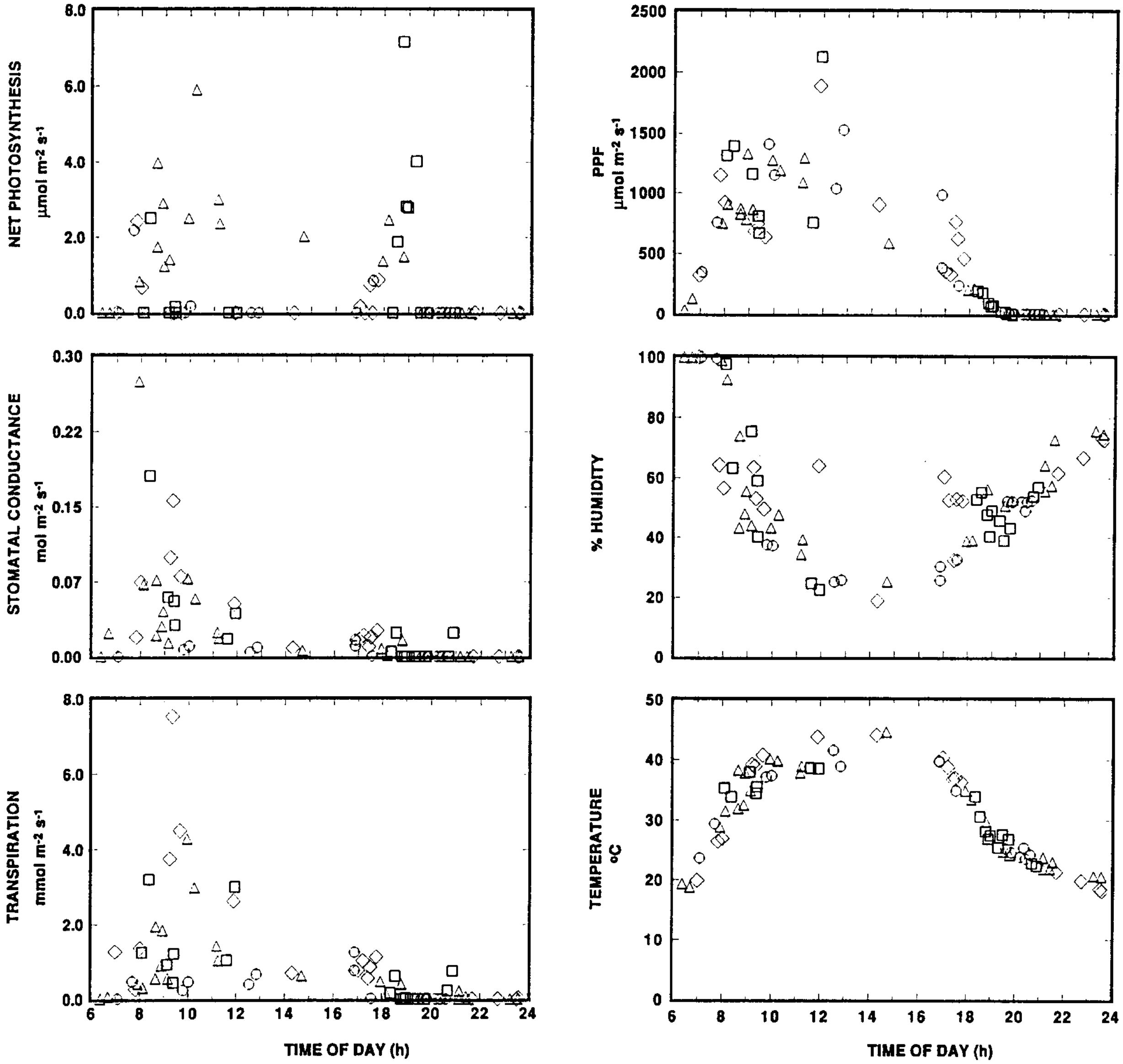

Fig. 4. Early to mid-summer net photosynthesis, stomatal conductance, and transpiration rates recorded during each hour interval of the day in *Zygophyllum dumosum* under natural soil moisture conditions. Symbol legends are the same as for Fig. 2. Corresponding environmental conditions shown for each photosynthesis and transpiration rate include photosynthetic photon flux (PPF), relative humidity, and chamber temperatures of *Zygophyllum dumosum* shrubs throughout the day under natural soil conditions in summer.

on shrubs when we began the gas exchange measurements but only phyllodes remained by the first week of July. Total photosynthetic area was reduced by an average of 30% by leaflet abscission (Table 3).

Transpiration activity was significantly greater during weeks 3–6 of the study than during any other three week period (Kolmogorov-Smirnoff two sample tests on matched time schedules, $p \leq 0.05$). Transpiration rates were significantly higher in *Z. dumosum* shrubs at the bottom of the slope than in *Z. dumosum* at the top of the slope (Kolmogorov-Smirnoff two sample tests on matched time schedules using all data obtained before the irrigation experiment began, $p \leq 0.05$). Transpiration rates were not otherwise systematically related to the elevation at which shrubs were located, however. Transpiration activity was greatest at the intermediate levels of radiation of mid-morning, regardless of whether concomitant net photosynthetic activity was detectable. Relative humidity tended to decrease during this period of maximum transpiration. Transpiration dropped to considerably lower rates at higher noon-time temperatures and radiation levels but remained detectable. Relative humidity was usually low but stable during this time. The highest rates of stomatal conductance were observed as the early morning humidity first began to drop although more frequently conductance and transpiration rates peaked simultaneously. Transpiration and stomatal conductance were usually not detectable at night, although there were instances of measurable transpiration and conductance at dusk.

Usually, no net carbon gain occurred in conjunction with the low transpiration rates of late morning to early afternoon (Fig. 4). Water use efficiency in the one instance where photosynthesis activity was detectable at mid-day was lower (2.3 mmol net CO_2 assimilation per mol H_2O transpired) than at comparable photosynthesis activity levels (2.4 μmol m^{-2} s^{-1}) in the early morning (9.2 mmol mol^{-1}, time = 7:40) and late afternoon (9.5 mmol mol^{-1}, time = 18:20). Water use efficiency of *Z. dumosum* did not vary systematically with elevation but was significantly higher at the lower middle portion than at any other elevation on the slope (Kolmogorov-Smirnoff two sample tests, $p \leq 0.05$).

Gas exchange in irrigated shrubs

New leaflets appeared on shrubs along position 3 within two weeks after irrigation, increasing the area of photosynthesizing tissue by an average of 30% per shrub (Table 3). Petioles (future phyllodes) of irrigated shrubs had significantly higher water contents than phyllodes of shrubs that hadn't been irrigated (Table 4) (Mann Whitney U tests, $p < 0.05$). Phyllodes and petioles at the bottom of the slope were drier than at any location above at the same vertical position. Stomata of leaflets and phyllodes were the same size (mean = 0.02 mm, S.E. = ±0.005 for leaflets and for phyllodes) but the density of stomata was far greater on leaflets (mean = 23 000 stomata cm^{-2}, S.E. = ±3823) than was the density of stomata on phyllodes (mean = 7100 stomata cm^{-2}, S.E. = ±2332). Leaflets persisted for an additional three weeks, then yellowed abruptly despite continued maintenance of high soil water potentials.

Net photosynthetic activity per unit area of photosynthesizing tissue did not change significantly as a result of leaflets growing (Fig. 5). As before, the majority of measurements showed little to no net carbon uptake. Rare instances of greater carbon assimilation occurred during the lower daytime temperatures, lower PPF, and higher relative humidities. Shrubs that had not been irrigated showed no differences in photosynthesis activity over the course of a day than shrubs that had been irrigated (Kolmogorov-Smirnoff twosample tests, $p \leq 0.05$).

Transpiration and stomatal conductance activity were detected at all daylight hours measured in both irrigated and non-irrigated shrubs. Transpiration was recorded at very low rates (0.6 mmol m^{-2} s^{-1}) shortly after leaflets appeared on irrigated shrubs. Transpiration was never observed in non-irrigated shrubs after sunset, however. No stomatal conductance was detectable at this time in any shrub. Water use efficiencies were similar between shrubs in irrigated and non-irrigated areas with two notable exceptions in the late afternoon when net photosynthesis rates alone increased in a non-irrigated shrub (Fig. 5).

Discussion

Soil water status and plant distribution

The distribution of soil water potentials under our irrigated shrubs (Fig. 3) mimicked the tendency of soil to contain less water after rainfall at the bottom of slopes with massive rocky upper reaches than above (Yair 1987). The prediction that topographic disparities in soil water potentials would be maintained throughout summer drought was not supported by our measurements, however. As the dry period progressed, soil water potentials in non-irrigated positions were occasionally higher at higher elevations than at any point measured at lower elevations. These differences were neither frequent nor great enough to conclude that soils were significantly wetter upslope than downslope, however. The possibility that cracks retain water in the bedrock beneath the soil mantle cannot be dismissed. A rhizotron in deep soil nearby, showed most roots of *Z. dumosum* to be shallow but a few, thin roots extended several meters in depth. Penetration of cracks by roots of shrubs at higher elevations may explain why water contents of phyllodes were lowest at the bottom elevation but so could storage of a greater water supply from previous storms.

In some regions, transpiration may cause soil to dry more rapidly than where vegetation is not present (Greenway 1987). Nonetheless, water potentials have been found to be equally low in shallow soils of veg-

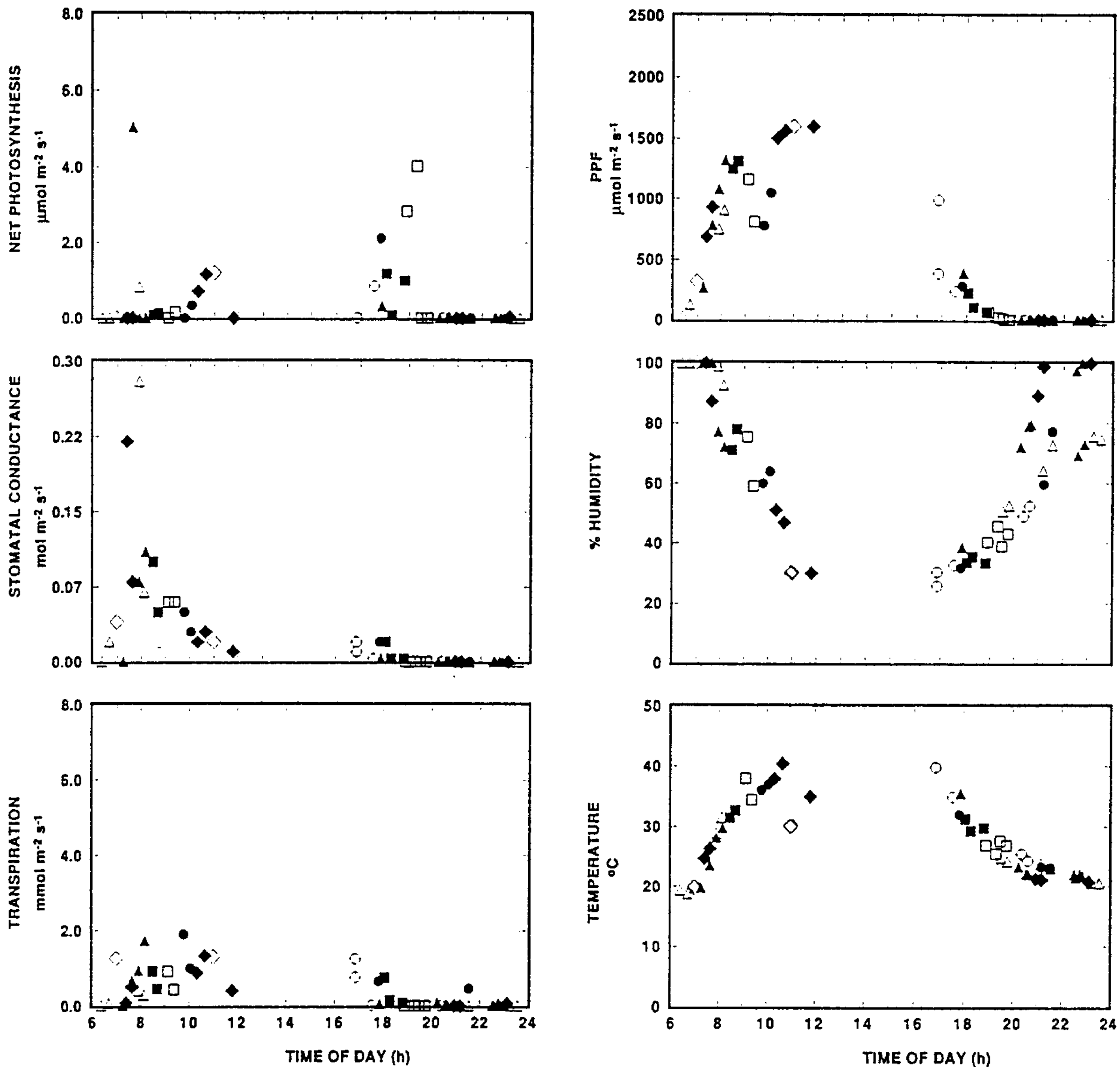

Fig. 5. Late summer net photosynthesis, stomatal conductance, and transpiration rates recorded during each hour interval of the day in *Zygophyllum dumosum* under natural (open symbols) and irrigated (closed symbols) soil moisture conditions. Symbol legends are the same as for Fig. 2. Corresponding environmental conditions shown for each photosynthesis and transpiration rate include photosynthetic photon flux (PPF), relative humidity, and chamber temperatures of *Zygophyllum dumosum* shrubs.

etated and bare areas during hot, dry periods in arid climates (Terwilliger 1990). It is, therefore, unlikely that higher transpiration activity of *Z. dumosum* at the lowest elevation transects accounts for the absence of variation in soil water potentials with elevation, however.

Evidence exists that soil moisture status is a key determinant of the geographical limits of species (e.g., Oberbauer & Billings 1981; Bliss 1985; DeLucia et al. 1989; Dawson 1990). The architecture of individuals throughout a species' areal may vary with soil water and concomitant available nutrient status, as well (Fitter 1986). A logical but inconclusively tested explanation for these phenomena has been that photosynthesis and transpiration dynamics vary among individuals according to associated soil water status (Oberbauer & Miller 1980; Oberbauer & Billings 1981). There were no indications that *Zygophyllum dumosum* capitalized spatially on soils at highest elevation that may have been wettest following storms. *Z. dumosum* was not more abundant, greater in total volume, nor were occasional individuals strikingly larger at the uppermost transects than elsewhere (Table 1).

Summer environment and gas exchange

New leaflets quickly emerged on our study shrubs when soil water potentials were raised. The average percentage of total photosynthesizing area attributable to the new leaflets was 30% (see Table 3), which conforms to measurements of optimal spring leaf set in *Z. dumosum* (Zohary & Orshan 1954). An adequate addition of water to the soil appears to be the condition that triggers rapid and maximum leaf set in *Z. dumosum*. The total area of photosynthesizing tissue in *Zygophyllum dumosum* can thus be increased by higher soil water potentials than would normally occur in summer.

Net photosynthesis seems to occur only during a narrow combination of ranges of weather conditions that were seldom present during the study (Fig. 4). Schultze et al. (1972) concluded that the stomatal apertures of both irrigated and non-irrigated *Zygophyllum dumosum* were greatest during periods of high ambient humidities in summer. We found no detectable net photosynthesis at the highest photosynthetic photon fluxes regardless of atmospheric relative humidity. In contrast, photosynthetic activity was usually highest during periods of high humidity at lower PPF levels. Apparently, an interactive relationship of PPF, temperatures, and humidities had the primary influence on net photosynthesis activity.

Our results suggest that net photosynthesis activity per unit area of photosynthesizing tissue is unaffected by a wide range of soil water potentials at the atmospheric conditions of summer (Figs 3 and 6) even though the density of stomata are far greater on leaflets (23 000 cm^{-2}) than on phyllodes (7100 cm^{-2}). This result departs only slightly from previous findings where another method of irrigation failed to evoke leaf development or any physiological activity in *Z. dumosum* in summer (Waisel et al. 1970). Lange & Meyer (1979) also found a bimodal photosynthesis activity pattern in apricot trees and grape vines that was insensitive to soil water status during summer in the desert. There does not appear to be a universal relationship between gas exchange of plants and soil water status, however (Schulze 1986).

Two more results support the conclusion that environmental conditions other than soil water status control unit photosynthesis rates of *Zygophyllum dumosum* in summer. First, phyllodes of *Z. dumosum* were higher in water content but not in photosynthetic productivity when irrigated. Second, net photosynthesis activity was somewhat higher at the lower middle elevation than elsewhere; a phenomenon unrelated to our or other measurements of lithologic water status (e.g., Yair & Berkowicz 1989). The precise atmospheric conditions surrounding an individual shrub may be affected by the shrub's position on a slope. Net photosynthesis activity may vary among shrubs due to small differences in their individual microclimates.

Transpiration rates tended to peak as morning relative humidity abated but diminished in association with high mid-day PPF levels at disparate relative humidities. Thus, at the lower temperatures and higher humidities of early to mid-morning, transpiration rates appear to be more affected by vapor pressure gradients than by variations in stomatal conductance. Low transpiration rates from late morning on can be best explained by reduced stomatal aperture and concomitant low conductance rates. Persistent stomatal conductance throughout the day suggests that lulls in net photosynthetic activity were not a consequence of complete stomatal closure. Where conductance of air into the leaf is low but not excessively restricted, O_2, and hence photorespiration, may be increasingly favored in dark reactions as CO_2 becomes depleted. Sufficiently high rates of photorespiration relative to photosynthesis can yield measurements of no apparent net carbon assimilation. High rates of photorespiration may explain the low transpiration rates but undetectable net photosynthesis observed at mid-day.

We found no striking differences in transpiration rates per unit area between irrigated shrubs bearing leaflets with high stomatal densities and non-irrigated shrubs with only phyllodes of low stomatal densities (Figs 5 and 7) during the portions of the day when atmospheric conditions were most conducive to these activities. We assume that the ubiquitously low levels of activity of late morning and middle afternoon are characteristic of early afternoon as well. These results do not reflect responses to long-term irrigation, however.

A plausible explanation for the lack of effect of irrigation on transpiration is that individual stomatal apertures are less in leaflets than in phyllodes during the day. If this is the case, then *Zygophyllum dumosum* drops the photosynthetic tissue that has greatest resistance to water loss per individual stomate during summer but maintains smaller phyllodes with weaker daytime stomatal closure. The yellowing of leaflets shortly after their irrigation-induced emergence further suggests that structural differences may have permitted phyllodes to endure prolonged limiting climate conditions that leaflets could not survive. A balance between water conservation and prevention of photoinhibition might best be met by phyllode structures.

In conclusion, the persistence of *Zygophyllum dumosum* in arid climatic extremes may be facilitated by the following mechanisms. A capacity to take up and react to ephemeral inputs of soil water is achieved with certain tradeoffs. Whole plant transpiration is reduced in summer by abscission of leaflets. Smaller phyllodes with fewer stomata are retained. Maintenance of this tissue is of dubious direct value to the annual growth of a shrub because photosynthesis is negligible most of the time. Sufficient soil moisture derived from rainfall is rapidly absorbed by the succulent phyllode and evokes rapid emergence of new leaflets. If these events occur when other environmental conditions favor greater photosynthesis activity, the plant is ready to exploit these conditions. When environmental conditions other than soil water do not favor growth, the leaflets abscise. The *Zygophyllum dumosum* shrub then returns to a mode where just enough physiological activity occurs to promote rapid exploitation of the next rainfall event.

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