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Photosynthetic characteristics of Sonoran Desert winter annuals

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Summary. Photosynthesis in Sonoran Desert winter annuals appeared to be similar to those observed in other C_3 photosynthetic pathway herbs, although photosynthetic capacities ranged from 18 to 65 μmol CO_2 m^{-2} s^{-1} under natural conditions. The higher photosynthetic capacities were associated with high leaf conductances to water vapor (up to 39 mm s^{-1}). Leaf Kjeldahl nitrogen contents were high, ranging up to 44.9 mg g^{-1}. We suggest that the high photosynthetic capacities in several species may be related to resource availability and enable successful exploitation of the short, unpredictable growth periods experienced by these annuals. Although photosynthetic rates in desert winter annuals spanned a wide range, the relationship between leaf conductance and maximum photosynthesis appeared similar to that of other C_3 vascular plants. It is possible that the resulting constant intercellular CO_2 concentrations were related to minimizing excessive water loss, while not severely imposing limitations to photosynthetic gains.

Introduction

Sonoran Desert annuals grow during the brief, infrequent periods of water availability within the desert. These short lived plants are ephemeral in nature, and normally complete their entire life cycle within several weeks to months following germination (Shreve and Wiggins 1964; Beatley 1974; Ehleringer 1983b). Annuals may comprise as much as half of the flora (Shreve and Wiggins 1964), and given sufficient precipitation, this diverse group of plants can achieve a high biomass over a brief period of time (Beatley 1969). Desert annuals appear to have specific characteristics which make them particularly suited to the warm desert environment. For instance, narrow germination requirements restrict germination to specific thermal periods. The amount of rainfall, the temperature following the rain, and the temperature during the dormant period all interact to control germination (Went 1949; Went and Westergaard 1949; Juhren et al. 1956). As a consequence, in the deserts of southwestern North America, the summer annuals flora is distinct from the winter annuals flora (Shreve and Wiggins 1964; Mulroy and Rundel 1977).

It has been noted that desert winter annuals may possess very high rates of photosynthesis (Mooney et al. 1976; Ehleringer et al. 1979; Seemann et al. 1980b; Forseth and Ehleringer 1983c). Although winter annuals possess the C_3 photosynthetic pathway and most summer annuals possess the C_4 photosynthetic pathway, both groups appear capable of achieving high photosynthetic capacities. A large percentage of both winter and summer desert annuals possess the ability to solar track, that is, for the leaves to move diurnally so that they remain perpendicular to the sun's direct rays (Ehleringer and Forseth 1980). The consequence of this is that individual leaves are exposed to high irradiances throughout the day. Selection for high photosynthetic capacities may be related to the shortness of the growing season or to the high irradiances which characterize these warm desert habitats.

In this study we address the question of whether the high photosynthetic capacities previously observed 1) are characteristic of all desert winter annuals and 2) are indications of inherent differences in the processes of photosynthesis and water loss between desert annuals and other C_3 plants, or alternatively, whether these differences in photosynthesis result from higher investment in biochemical and physiological components associated with photosynthesis.

Materials and methods

For laboratory measurements plants were grown from seed originally collected from several locations in the Death Valley National Monument, California. Plants were grown individually in pots and were watered daily and fertilized weekly. The plants were grown in either high light, environmental growth chambers or in an HID-lamp supplemented greenhouse. In both conditions, plants were exposed to a 14 h/10 h day/night cycle with a 25/10 C temperature cycle. Daily incident quantum flux in the 400–700 nm waveband averaged near 40 mol m^{-2}. The species used in these measurements were *Abronia villosa* Wats., *Geraea canescens* T. & G., *Lotus salsuginosus* Greene, *Lupinus arizonicus* Wats., *Malvastrum rotundifolium* Gray, *Mohavea breviflora* Cov., *Palafoxia linearis* (Cov.) Lag., *Phacelia crenulata* Torr., and *Salvia columbariae* Benth.

Simultaneous measurements of photosynthesis and transpiration were made with an open gas exchange system described previously by Ehleringer (1983a), in which irradiance, leaf temperature, ambient CO_2 concentrations, and vapor pressure deficit could be controlled. As a rule single

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attached leaves were initially exposed to an irradiance (400–700 nm) of 1.8 mmol m^{-2} s^{-1}, a leaf temperature of 30 C, an ambient CO_2 concentration of 330 µl l^{-1}, and a water vapor pressure deficit of 1.0 kPa. Three to five replicates were run for each species. In all cases representative individual response curves are presented.

Field measurements were obtained on populations in the Jubilee Pass area of the Death Valley National Monument, California during March and April, 1979. Midday photosynthetic rates of the youngest fully expanded leaf on intact plants were measured in situ using a CO_2 depletion technique described by Ehleringer and Cook (1980). This required enclosing a single leaf in a hand held chamber of known volume, immediately sub-sampling the air using a syringe, and then 20–30 s later again subsampling the air. The CO_2 concentration in the sampled air was then measured using an IRGA and photosynthetic rate calculated from the rate of CO_2 depletion (Ehleringer and Cook 1980). The CO_2 concentration was rarely allowed to decline below 300 µl l^{-1}. The youngest fully expanded leaf was chosen as representative since desert winter annuals tend to have few leaves and the photosynthetic rate declines only slightly from youngest to oldest (Mooney et al. 1981). In addition to the above mentioned species, field photosynthetic measurements were also made on *Atrichoseris platyphylla* Gray, *Camissonia brevipes* (Gray) Raven, *Chorizanthe rigida* (Torr.) T. & G., *Eriogonum deflexum* Torr., *E. inflatum* Torr. & Frem., *Phacelia calthafolia* Brand., and *P. fremontii* Torr. Leaf conductances to water vapor were measured using a null balance porometer (Forseth and Ehleringer 1982b). Specific leaf weights on a dry weight basis and Kjeldahl values (Lillevik 1970) were also determined on field collected material.

Results

Laboratory and field measurements were made on a number of winter desert annuals. Despite essentially common temperature and irradiance growth conditions, the maximum photosynthetic rates varied from a high of 65 µmol CO_2 m^{-2} s^{-1} in *Palafoxia linearis* to a low of 18 µmol CO_2 m^{-2} s^{-1} in *Abronia villosa*. The stomatal conductances to water vapor at these maximum photosynthetic rates were 39.0 and 6.6 mm s^{-1}, respectively. Over the wide range of photosynthetic rates in these C_3 plants, there was a strong linear relationship between the maximum photosynthetic rate at high irradiance and the leaf conductance to water vapor at that maximum photosynthetic rate (Fig. 1). The calculated intercellular CO_2 concentration was 261 ± 13 µl l^{-1} ($\bar{x} \pm$ S.D.) for all points. Thus, even though there was a large range of photosynthetic rates and leaf conductances to water vapor, intercellular CO_2 concentrations remained fairly constant over a diversity of species.

Midday photosynthetic measurements of maximum photosynthetic rate under ambient field conditions were lower than those measured in the laboratory grown plants (more luxuriant water and nutrient levels) (Table 1). None of the desert annuals measured in the field by us in April, 1979 had photosynthetic rates greater than 40 µmol CO_2 m^{-2} s^{-1}. Seemann et al. (1980b) reported similar results from field plants measured in March, 1980. Photosynthetic rates on these plants might have been substantially higher earlier in the growing season when leaf water deficits and vapor pressure deficits were lower. Alternatively, it is possible that extremely high photosynthetic rates occur under conditions of high nutrient and water availability, and thus are seen only occasionally in the field. Leaf conductance estimates were collected on field plants at the same time that the photosynthetic measurements were made. These photosynthesis-leaf conductance data are included in Fig. 1. For the most part these data were on the low activity end of the curve.

Individual photosynthesis-irradiance response curves were measured on laboratory grown plants. Maximum photosynthetic rates differed by approximately 3-fold among species (Fig. 2). Higher photosynthetic rates were the result of leaves not becoming light saturated at higher irradiances, not because of different photosynthetic efficiencies. The absorbed quantum yield (initial slope of the photosynthesis-irradiance curve), a common measure of photosynthetic ef-

Table 1. Photosynthetic rates of winter annuals measured in Death Valley National Monument in April 1979. Data were collected at midday on intact leaves using the CO_2 depletion technique (Ehleringer and Cook 1980). Data are averages; N is the sample size

Species	Photosynthesis, (µmol m^{-2} s^{-1})	N
Abronia villosa	19.2	2
Atrichoseris platyphylla	12.5	2
Camissonia brevipes	29.2	4
Chorizanthe rigida	25.2	2
Eriogonum defluxum	24.9	2
Eriogonum inflatum	33.9	4
Geraea canescens	30.0	2
Lotus salsuginosus	26.5	3
Lupinus arizonicus	29.9	5
Malvastrum rotundifolium	25.4	8
Mohavea breviflora	37.9	2
Phacelia calthafolia	27.3	2
Phacelia crenulata	23.0	6
Phacelia fremontii	24.3	4
Salvia columbariae	28.2	5

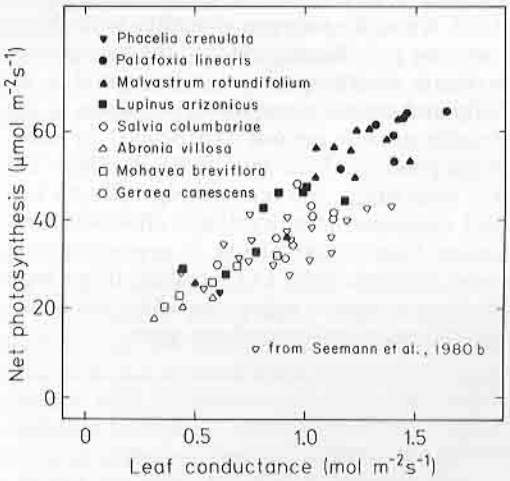

Fig. 1. The relationship between maximum photosynthetic rate and leaf conductance to water vapor for Sonoran Desert winter annuals. The correlation coefficient (r) is 0.87 for all data ($n = 64$). For laboratory grown plants, the measurement conditions were an incident quantum flux (400–700 nm) of 1.8 mmol m^{-2} s^{-1}, a leaf temperature of 30 C, an ambient CO_2 concentration of 330 µl l^{-1}, and a water vapor pressure deficit of 1.0 kPa

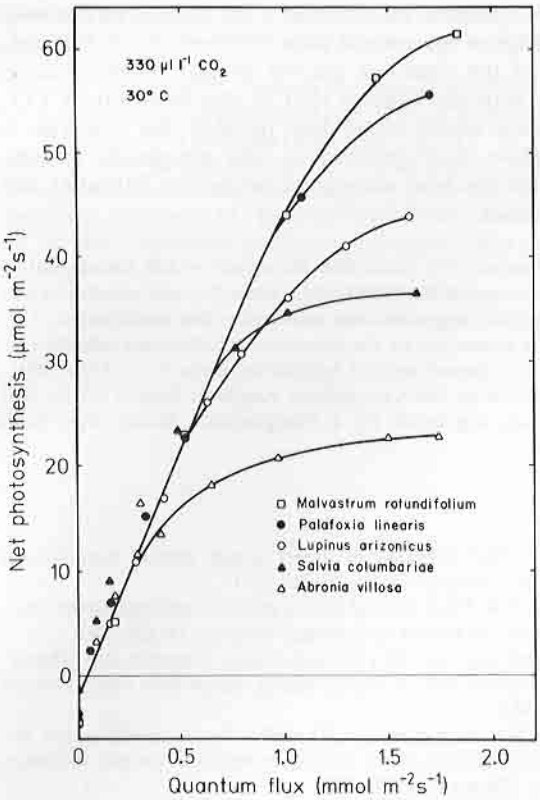

Fig. 2. The relationship between photosynthetic rate and quantum flux (400–700 nm) for the Sonoran Desert winter annuals *Abronia villosa, Lupinus arizonicus, Malvastrum rotundifolium, Palafoxia linearis, and Salvia columbariae*. Measurements were made with a leaf temperature of 30 C, an ambient CO_2 concentration of 330 µl l^{-1}, and a water vapor pressure deficit of 1.0 kPa

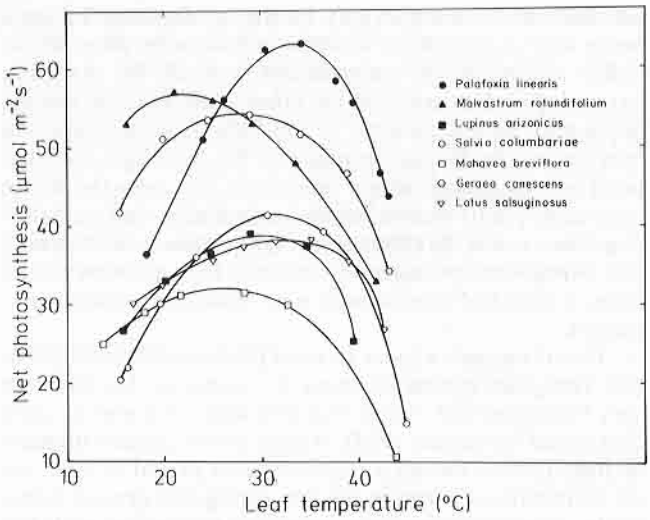

Fig. 3. The relationship between photosynthetic rate and leaf temperature for the Sonoran Desert winter annuals *Geraea canescens, Lotus salsuginosus, Lupinus arizonicus, Malvastrum rotundifolium, Mohavea breviflora, Palafoxia linearis,* and *Salvia columbariae*. Measurements were made with an incident quantum flux (400–700 nm) of 1.8 mmol m^{-2} s^{-1}, an ambient CO_2 concentration of 330 µl l^{-1}, and a water vapor pressure deficit of 1.0 kPa

ficiency, was approximately 0.053 for all species in Fig. 2. Plants with lower photosynthetic capacity, such as *A. villosa* were light saturated at approximately 1.0 mmol m^{-2} s^{-1} (400–700 nm). On the other hand, species such as *Ma. rotundifolium* and *P. linearis* which had very high photosynthetic capacities never became light saturated, even at irradiances equivalent to full noon sunlight ($\sim$1.8 mmol m^{-2} s^{-1} during the Spring in Death Valley).

The temperature dependence of net photosynthesis at high irradiances was determined on plants grown under the same laboratory growth conditions as before. Representative curves for each species generally indicated a very broad, flat temperature dependence of photosynthesis between 20–35 C, with a thermal optimum in the neighborhood of 30 C, which was about 5 C higher than the growth temperature (Fig. 3). Photosynthesis in all of the measured species became thermally unstable above 40 C.

Kjeldahl nitrogen contents of leaves collected in the field were generally high (Table 2). Nitrogen contents ranged from 24.6 mg g^{-1} in *Cryptantha utahensis* to 44.9 mg g^{-1} in *Lupinus arizonicus*. This corresponds to a range of 15–28% for crude leaf protein contents. The specific leaf weight was also determined on the same samples collected for nitrogen content in order to see if increased protein content (higher Kjeldahl value) was associated with thicker leaves (higher specific leaf weight). We found no significant relationship between Kjeldahl nitrogen content and leaf specific weight ($r = 0.10$, $P > 0.5$).

Table 2. Leaf Kjeldahl nitrogen contents and specific leaf weights of winter annuals collected in Death Valley National Monument in March, 1979

Species	Kjeldahl Nitrogen (mg g^{-1})	Specific Leaf Weight (g dry weight m^{-2})
Abronia villosa	39.6	0.87
Atrichoseris platyphylla	34.6	0.37
Calandrinia ambigua	32.3	0.83
Chorizanthe rigida	32.0	0.74
Cryptantha utahensis	24.6	0.77
Eriogonum inflatum	31.6	0.80
Geraea canescens	39.0	0.62
Lupinus arizonicus	44.9	0.74
Malvastrum rotundifolium	42.6	0.59
Mohavea breviflora	34.8	0.75
Plantago insularis	35.6	0.50
Polygonum aviculare	33.9	0.52
Salvia columbariae	37.7	0.48

Discussion

The data collected to date indicate that Sonoran Desert winter annuals appear to be fundamentally similar to other C_3 vascular plants. These annuals are, however, at the upper end of known ranges for leaf Kjeldahl nitrogen content, photosynthetic light saturation point, photosynthetic capacity, and leaf conductance to water vapor (Sestak et al. 1970). The level of these features may reflect a balance of resource availability (light, water, and nutrients), gains, and costs which has been successful in the brief growing period available in this desert environment.

The high leaf nitrogen contents (=protein levels) characteristic of many of these desert annuals probably represent a large investment in the enzymes used in photosynthe-

sis. Such an investment may be the consequence of there being only a short time window of favorable water availability and moderate temperatures in which the plant has to develop and set seed. On the other hand, the high protein levels may be independent of any time consideration and may instead be the consequence of the high light environment in this desert, where few plants (or even the leaves on a single plant) receive less than essentially "full sunlight" irradiance levels. In either case, high protein levels are only one component necessary to achieve high photosynthetic rates. A high leaf conductance is an equally important component.

Desert annuals appear to have photosynthetic-temperature responses typical of many C_3 plants in that they are very broad and flat over a relatively large temperature span (Berry and Björkman 1980). Winter desert annuals do most of their growth during a relatively cool period of year. As air temperatures warm in the late spring, the growth forms of the annuals change from prostrate to elevated with few or very small leaves. This tends to keep the plants away from the very hot surface microclimates (Mulroy and Rundel 1977). A few winter annuals have characteristics which extend their growth season into hotter, drier conditions (Clark and Burk 1980). Thermal acclimation of photosynthesis has been reported in *Malvastrum rotundifolium* and *Lupinus arizonicus* (Forseth and Ehleringer 1982a). A 5°–9° C upward shift in maximum temperature of membrane stability and thus photosynthesis has been reported in droughted, late season plants (Seemann et al. 1980a). These features are likely to maintain high rates of carbon gain later into the hot season.

As with the temperature dependences of photosynthesis, the photosynthetic responses to irradiance are basically similar to other C_3 plants. Desert annuals have the same photosynthetic efficiency or quantum yield as other C_3 plants (Ehleringer and Björkman 1977). Winter desert annuals which attain extremely high net photosynthetic rates do so by having very high light saturation requirements (Fig. 2). This point suggests that the high photosynthetic capacities do not represent a basically different photosynthetic mechanism, but are a result of an allocation pattern which results in short term, high level carbon gains.

Additional evidence supporting the similarity of winter desert annuals and other C_3 plants is seen in the relationship of leaf conductance to maximum photosynthetic rate. A strong correlation exists between leaf conductance and maximum photosynthetic rate (Fig. 1). This pattern is very similar to that reported by Körner et al. (1979) for 12 groups of C_3 vascular plants and by Wong et al. (1979). The datum reported by Körner et al. (1979) for herbs from open habitats fits on the curve of winter desert annuals. This underscores the similarity of gas exchange characteristics of desert annuals to other plants.

This relationship between leaf conductance and photosynthesis has interesting implications. When photosynthetic rate is reduced, leaf conductance decreased such that the intercellular CO_2 concentration remained fairly constant. Wong et al. (1979) interpret similar data as implying that leaf conductance is not severely limiting photosynthesis, but rather that the two parameters are balanced. Further observations suggest that plants are operating to maintain a more or less constant intercellular CO_2 concentration (von Caemmer and Farquhar 1981; Farquhar and Sharkey 1982). The tight linear relationship observed in Fig. 1 is indicative of a fairly constant intercellular CO_2 concentration over a broad range of species and photosynthetic rates. The consequence of the observed pattern of leaf conductance is consistent with the concept that at this intercellular CO_2 concentration excess water loss through the stomates is reduced while photosynthesis is only marginally limited. This concept has been elaborated further by Farquhar and Sharkey (1982).

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References

Beatley JC (1969) Biomass of desert winter annual populations in southern Nevada. Oikos 20:261–273

Beatley JC (1974) Phenological events and their environmental triggers in Mojave Desert ecosystems. Ecology 55:856–863

Berry J, Björkman O (1980) Photosynthetic response and adaptation to temperature in higher plants. Annu Rev Plant Physiol 31:491–543

Caemmerer S von, Farquhar GD (1981) Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153:376–387

Clark DD, Burk JH (1980) Resource allocation patterns of two California Sonoran Desert ephemerals. Oecologia (Berlin) 48:86–91

Ehleringer J (1983a) Ecophysiology of *Amaranthus palmeri*, a Sonoran Desert summer annual. Oecologia (Berlin) 57:107–112

Ehleringer J (1983b) Adaptations of annuals and perennials to warm deserts. In B Chabot and HA Mooney (eds), Physiological Ecology of North American Plant Communities. Chapman and Hall Ltd, London

Ehleringer J, Björkman O (1977) Quantum yields for CO_2 uptake in C_3 and C_4 plants: dependence on temperature, carbon dioxide, and oxygen concentration. Plant Physiol 59:86–90

Ehleringer J, Cook CS (1980) Measurements of photosynthesis in the field: utility of the CO_2 depletion technique. Plant, Cell and Environment 3:479–482

Ehleringer J, Forseth IN (1980) Solar tracking by plants. Science 210:1094–1098

Ehleringer J, Mooney HA, Berry JA (1979) Photosynthesis and microclimate of a desert winter annual. Ecology 60:280–286

Farquhar GD, Sharkey TD (1982) Stomatal conductance and photosynthesis. Ann Rev Plant Physiol 33:317–345

Forseth IN, Ehleringer J (1982a) Ecophysiology of two solar tracking desert winter annuals. I. Photosynthetic acclimation to growth temperature. Austr J Plant Physiol 9:321–332

Forseth IN, Ehleringer J (1982b) Ecophysiology of two solar tracking desert winter annuals. II. Leaf movements, water relations, and microclimate Oecologia (Berlin) 54:41–49

Forseth IN, Ehleringer J (1983) Ecophysiology of two solar tracking desert winter annuals. III. Gas exchange responses to light, CO_2, and VPD in relation to long-term drought. Oecologia (Berlin) 57:344–351

Juhren MF, Went FW, Phillips EH (1956) Ecology of desert plants. IV. Combined field and laboratory work on germination of annuals in the Joshua Tree National Monument, California. Ecology 37:318–330

Körner C, Scheel JA, Bauer H (1979) Maximum leaf diffusive conductance in vascular plants. Photosynthetica 13 (1):45–82

Lillevik HA (1970) The determination of total organic nitrogen, p 601–616. In: Joslyn MA (ed), Methods in Food Analysis. Academic Press, New York

Mooney HA, Ehleringer J, Berry JA (1976) High photosynthetic capacity of a winter annual in Death Valley. Science 194:322–324

Mooney HA, Field C, Gulmon SL, Bazzaz FA (1981) Photosynthetic capacity in relation to leaf position in desert versus old-field annuals. Oecologia (Berlin) 50:109–112

Mulroy TW, Rundel PW (1977) Annual plants: Adaptations to desert environments. Bioscience 27 (2):109–114

Seemann JR, Berry JA, Dowton WJS (1980a) Seasonal changes in high-temperature acclimation of desert winter annuals. Carnegie Inst Wash Yb 79:141–143

Seemann JR, Field C, Berry JA (1980b) Photosynthetic capacity of desert winter annuals measured in *situ*. Carnegie Inst Wash Yb. 79:146–147

Sestak Z, Catsky J, Jarvis PG (1971) *Plant Photosynthetic Production: Manual of Methods*. Junk The Hague

Shreve F, Wiggins IL (1964) Vegetation and Flora of the Sonoran Desert. Stanford Univ. Press, Stanford

Went FW (1949) Ecology of desert plants. II. The effect of rain and temperature on germination and growth. Ecology 30:1–13

Went FW, Westergaard M (1949) Ecology of desert plants. III. Development of plants in the Death Valley National Monument, California. Ecology 30:26–38

Wong SC, Cowan IR, Farquhar GD (1979) Stomatal conductance correlates with photosynthetic capacity. Nature 282:424–426

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