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Ecophysiological Studies of Sonoran Desert Plants

IV. Seasonal Photosynthetic Capacities of *Acacia greggii* and *Cercidium microphyllum*

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Summary. The gas exchange and water relations of two Sonoran Desert plants were measured throughout a 12 month period. Seasonal photosynthesis patterns of both species followed the seasonal variation in soil and plant water potential. *Acacia greggii*, a winter deciduous shrub, appears to be fall active since the day-long mean photosynthesis rate was maximum, i.e., 16 mg CO_2 dm^{-2} h^{-1}, at this time. *Cercidium microphyllum*, a drought deciduous and chlorophyllous-stemmed tree, also appears to be mainly fall active. For this species the day-long mean photosynthesis rate was not in excess of 14 mg CO_2 dm^{-2} h^{-1}. Both species initiate leaf production in the spring and neither experiences severe plant water stress. Seasonal minima of dawn plant water potential were −44 and −32 bars for the shrub and tree species, respectively. The two species differ slightly in their tolerance of heat and water stress, since foliated plants of *Acacia greggii* maintain summer gross photosynthesis.

All of the aboveground organs for plants of *C. microphyllum* are capable of exogenous $^{14}CO_2$ assimilation. This species appears to be unique in the magnitude of the photosynthetic production contributed by stems. Seasonal production by stems, leaves and flowers/fruits averaged 72, 24 and 4% of the total carbon gain per tree, respectively. Aboveground gross primary production was over 4.5-fold greater than aboveground net primary production. This difference between these two production estimates is likely due to the very small foliar biomass maintained throughout the year and the energy expenditure required to maintain the metabolically active cells of the chlorophyllous stems.

Introduction

In part III of this series of papers (Szarek and Woodhouse, in press) we reported the daily course of gas exchange and water relations for two Sonoran Desert plants during contrasting periods of water and temperature stress. The experi-

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mental species were *Acacia greggii* and *Cercidium microphyllum*. Although their daily carbon assimilation capacities were similar, plants of the shrub species *A. greggii* demonstrated both a greater overall stomatal conductance and a greater daytime decrease in plant water potential. Since the tree species, *C. microphyllum*, likely has a more extensive rooting system these two species may differ in their seasonal gas exchange and water relations.

Seasonal studies of *C. microphyllum* are additionally warranted because chlorophyllous-stemmed perennials, even excluding stem succulent cacti, are numerous in the Sonoran Desert. Moreover, this species is drought deciduous and normally maintains a very small foliar biomass for less than 6 months of the year (e.g., Turner, 1963). Thames (1975) has reported the peak seasonal foliar biomass is only 0.5% of the total aboveground biomass. This suggests leaf photosynthesis may not contribute a major portion of the year-round production. Previous photosynthetic production studies conducted with the ecologically related *Cercidium floridum* also emphasized the relative importance of corticular or stem photosynthesis (Adams and Strain, 1969). Thus, our field studies were extended to determine if stem photosynthesis was as relatively important for plants of *C. microphyllum*.

Our objective here is to assess seasonal variations in photosynthetic capacities for both the shrub and tree species. Also the contribution of all aboveground organs to the gross primary productivity of *C. microphyllum* will be compared with estimates of net primary production to further understand the carbon balance of desert perennials.

Materials and Methods

Climatic characteristics of the study site (Szarek and Woodhouse, 1976) and the two plant species (Szarek and Woodhouse, 1978) have been described previously. The precipitation during the 1976 period of study totalled 235, which was 35 mm greater than the 30 year average for this site. The primary production (harvest method) studies were conducted at Silverbell, the Tucson Basin Validation Site of the U.S./I.B.P. Desert Biome (Thames, 1973). The latter site is located approximately 120 km south of our study site, and both sites are similar in terms of community species composition and physiognomy.

The techniques employed for the measurements of environmental conditions, leaf gas exchange, plant water potential (ψ), seasonal photosynthesis rate of plant organs, aboveground net primary production (ANPP) and aboveground gross primary production (AGPP) have been described in detail elsewhere (Szarek and Woodhouse, 1977; 1978)

Specifically, ANPP was measured during 1972 by the harvest method as the biomass increment for terminal branches (less than 2.5 cm diam.) of *C. microphyllum* occurring at Silverbell. The ANPP of branches larger than this size was estimated from the studies of Turner (1963), as described previously (Szarek and Woodhouse, 1977). The gas exchange estimate of AGPP employed the results of the density and biomass studies conducted at Silverbell during 1973 and 1974 (Thames, 1974, 1975). These years were selected because the annual precipitation totalled 213 and 248 mm, respectively: being most like the annual precipitation during the subsequent gas exchange studies. Aboveground biomass values were determined from the combined ratios leaf to branch (less than 2.5 cm diam.) and branch to tree biomass. Similar formulations were used to estimate seasonal variations in flower and fruit biomass on a per tree basis. Peak foliar biomass and the ratio of leaf to branch biomass was verified during 1978 using plants of *C. microphyllum* from our study site. Leaf biomass per branch and leaf density were determined by oven-drying leaves for 48 h at 100° C. Mean biomass parameters used in the computation of AGPP are as follows:

Tree biomass	38.2 kg dry wt
Branch biomass tree^{-1} (less than 2.5 cm diam.)	10.2 kg dry wt
Foliar biomass tree^{-1} (peak value)	0.22 kg dry wt
Flower biomass tree^{-1} (peak value)	0.14 kg dry wt
Fruit biomass tree^{-1} (peak value)	0.55 kg dry wt
Basal diam.	18 cm
Cover	10 m^2

Similar production studies using plants of *A. greggii* were not conducted due to the lack of complementary biomass and gas exchange studies.

Chlorophyll was extracted and assayed according to Arnon (1949). Leaf or stem material was collected from the sunexposed side of the tree and stored on ice in polyethylene bags until returned to the laboratory. The tissue was ground by hand after the addition of quartz sand.

Results

a) Seasonal Patterns of Water Potential and Photosynthesis

The seasonal patterns of precipitation, soil and plant ψ, and photosynthesis throughout the study period are shown in Figure 1. Precipitation events and total rainfall at the study site were characteristic of the long-term climatic patterns (Fig. 1A). A spring drought normally occurs from April through June and a fall drought in the months of October and November. Prior to the termination of the spring rains in late April soil ψ at both depths was normally greater than -20 bars, which decreased rapidly to minimum measurable levels (-80 bars) by July. Throughout the drought period soil ψ was normally less than -60 bars, and soil water stress persisted until the September rains. As expected the seasonal patterns of dawn plant ψ tended to parallel the change in soil water status (Fig. 1B). Maxima and minima observed values throughout the year were -6 and -32 bars for the tree species *C. microphyllum* and -5 and -44 bars for the shrub species *A. greggii.* Noteworthy is the difference in time of occurrence of the minimal plant water stress, as measured by dawn plant ψ. Plant ψ maxima occurred in February for the tree species and in October for the shrub species. Also, both species were either deciduous or partially defoliated during the more mild winter and early spring months (LV horizontal bar, Fig. 1C and D). This occurred despite soil and plant ψ at levels capable of supporting gross leaf photosynthesis. Following the termination of the April rains plant ψ decreased for both species, although decreasing at a greater rate for the shrub species. After plant ψ of *C. microphyllum* had decreased to below -20 bars by early June, new leaf production was initiated. New leaf production by plants of *A. greggii* had initiated more than two months earlier when dawn plant ψ was near -15 bars. Both species bore leaves throughout the summer drought period, with some leaf loss occurring in July for the tree species. Throughout the remainder of the year plant ψ of both species continued to parallel the changes in soil ψ. The total foliar biomass

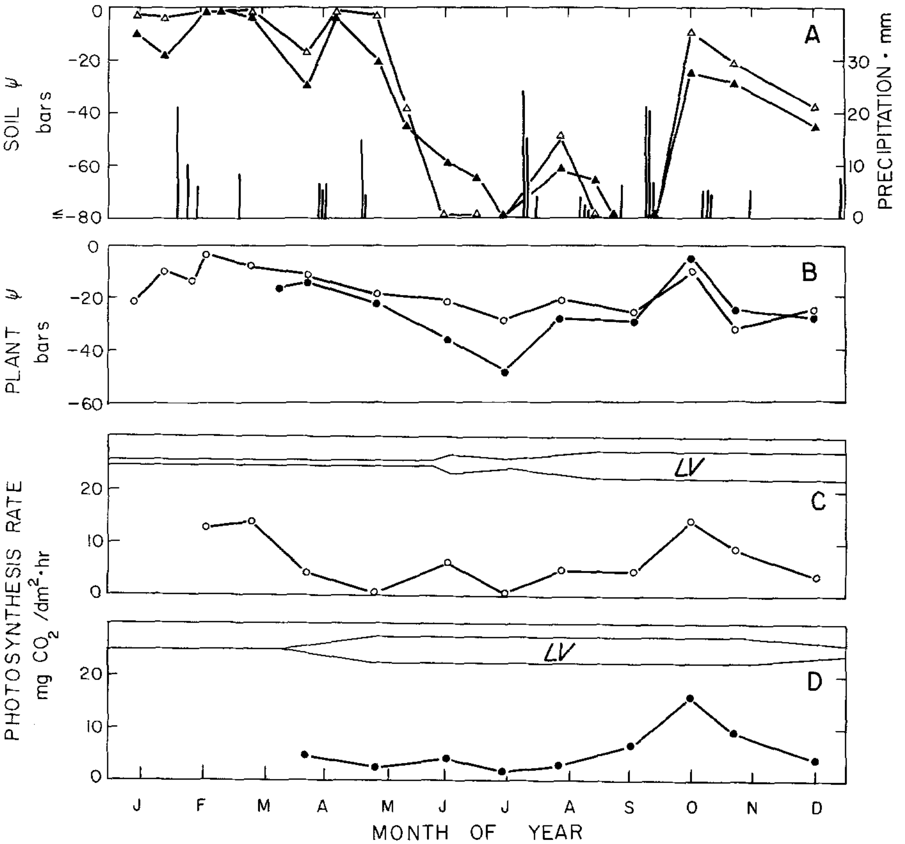

Fig. 1A–D. The seasonal patterns of precipitation, water relations, duration of foliage and photosynthesis for *Acacia greggii* and *Cercidium microphyllum*. **A** Predawn soil water potentials at 30 cm (*open triangles*) and 60 cm (*closed triangles*). **B** Predawn plant water potentials for *A. greggii* (closed circles) and *C. microphyllum* (*open circles*). **C** Day-long mean leaf photosynthesis rate for *C. microphyllum*. **D** Day-long mean photosynthesis for *A. greggii*. The day-long mean leaf photosynthesis rates (**C** and **D**) were determined from hourly measurements of $^{14}CO_2$ assimilation, with 5 replicates sampled per hour throughout the day. The duration of foliage (**C** and **D**) indicated by LV *horizontal bar*, and periods of deciduousness indicated by *horizontal line*

of *C. microphyllum* remained bear 0.200 kg dry wt during this period, while the winter deciduousness of *A. greggii* initiated in November.

The seasonal pattern of leaf photosynthesis for *C. microphyllum* followed the seasonal variation in plant ψ (Fig. 1 C). The only exception to this conformity was during the month of June, when the CO_2 assimilation capacity increased while plant ψ continued its steady decrease. Noteworthy is the initiation of new leaf production at this time and the termination of flowering which had initiated in May. Photosynthesis rates were comparatively low throughout much of the year, with day-long mean values seldom in excess of 14 mg CO_2 dm^{-2} h^{-1}. The photosynthetic capacity fell to near zero on two occasions in spring and summer, when dawn plant ψ was −19 and −29 bars, respectively. The first

Table 1. Seasonal photosynthesis rates and duration of occurrence for the aboveground plant organs of *C. microphyllum*. The photosynthesis rates represent mean values determined throughout the year

Organ	Photosynthesis rate (nCi per g dry wt per h)	Duration (mo)
Leaf	1,074	6
Stem (1°)[a]	278	12
Stem (2°)[b]	228	12
Flower	32	1.5
Fruit	380	2

Less than 0.2 cm diam. or rachis
0.2 to 0.6 cm diam

period of a low photosynthetic capacity was probably due more to the occurrence of flowering, than to high temperature stress. During May the mean monthly air temperature was 24° C, with absolute maxima less than 35° C. The second period of a low photosynthetic capacity was likely due to the combined effects of high temperature and water stress. During July the mean monthly air temperature was 31° C, with absolute maxima in excess of 46° C. It is apparent that plant ψ is not the sole factor regulation leaf photosynthesis. This is underscored by a day-long mean photosynthesis rate of 9 mg CO_2 dm^{-2} h^{-1} occurring during the November sampling period when dawn plant ψ was -32 bars. At this time mean monthly air temperature was 15° C, with absolute maxima less than 30° C.

The seasonal pattern of leaf photosynthesis for plants of *A. greggii* was virtually identical (Fig. 1D). The main difference between these two species was the maintenance of gross photosynthesis by the shrub species despite the extremes of temperature and water stress. Day-long mean photosynthesis was in excess 2 mg CO_2 dm^{-2} h^{-1} during May and July, when the CO_2 assimilation capacity of the tree species was virtually zero. A dramatic increase in photosynthesis rates occurred after the September rains, rising to a maximal day-long mean value of 16 mg CO_2 dm^{-2} h^{-1} during October when dawn plant ψ was also maximal.

b) Photosynthesis of the Plant Organs of Cercidium microphyllum

Seasonal photosynthesis rates of the different aboveground plant organs of *C. microphyllum* are presented in Table 1. The foliage is normally present for approximately 6 months of the year (Thames, 1973, 1974, 1975, 1976; Turner, 1963) and during a study period like 1976 would contribute 24% of the total seasonal carbon gain. Flowers and fruits are present for a shorter duration of time, with their combined contribution averaging slightly more than 4%. The fruit pods of this leguminous tree are 4 to 8 cm long, almost 1 cm wide and remain photosynthetically active for approximately 1.5 months. Noteworthy is the large contribution of stems to the seasonal carbon gain, which averaged 72% of the total for all size classes. Photosynthesis rates are reported for only two size classes of stems (stem diam. less than 0.6 cm) since they were studied most extensively, although larger sized stems were also investigated.

Table 2. Chlorophyll concentrations and relative photosynthetic capacities for various sized stems of *C. microphyllum*

Stem diam. (cm)	Total Chlorophyll (μg per cm^2)	Photosynthetic capacity[a] (%)
Less than 0.6	30.77	100
0.6 to 1.25	26.93	79
1.25 to 2.5	27.56	65
2.5 to 5.0	31.05	58
5.0 to 7.5	27.09	55
Greater than 7.5	29.44	51

[a] Computed relative to the photosynthetic capacity of stems less than 0.6 cm, equivalent to 1.5 mg CO_2 per dm^2 per h

Table 3. Estimates of aboveground net and gross primary production at Silverbell (Tucson Basin Validation Site) in the Sonoran Desert

Parameter	Units	*C. microphyllum*	
		per plant	per ha
Density	No.	–	27
Percent of perennial primary productivity[a]	Percent	0.04	1.2
Aboveground net primary production[b]	kg dry wt per yr	0.71	19.2
Aboveground gross primary production[c]	kg dry wt per yr	3.23	87.3

[a] Measured during 1972 at Silverbell (Thames, 1973)

[b] Calculated for 1976 from the relationship of ANPP and actual evapotranspiration (Webb et al., in press)

[c] Calculated for 1976 from the $^{14}CO_2$ assimilation studies

Stems of all size classes appear capable of gross CO_2 assimilation (Table 2), excluding basal trunks with a diameter of 12 cm or larger. As stem size increases the photosynthetic capacity decreases, although never less than 50% of the capacity of the smallest diameter stems (less than 0.6 cm diam. or stem 1° and 2° of Table 1). Total stem chlorophyll concentrations were not statistically different between the sizes classes, averaging 29.1 ± 5.8 μg cm^{-2}. Since foliar chlorophyll concentrations averaged 28.5 μg cm^{-2} some physical limitation to $^{14}CO_2$ assimilation likely accounts for the lower stem photosynthesis rates. Despite these differences in photosynthetic capacity large stems (greater than 5 cm diam.) and small stems (less than 5 cm diam.) contribute 22 and 50% of the total seasonal carbon gain, respectively.

c) Primary Production of *Cercidium microphyllum*

Primary production, expressed as ANPP and AGPP, was determined for *C. microphyllum* growing at the Silverbell site (Table 3). Although this species has a community importance value (Kershaw, 1964) of 54 (Szarek, unpublished results), its percent of the perennial net production is very low. During 1976 ANPP was calculated to be 538 kg dry wt ha^{-1} for all perennials, with this tree species contributing 19.2 kg dry wt ha^{-1} of the total. Aboveground gross primary production was determined to be more than 4.5-fold greater than ANPP, based upon the photosynthetic potential for all aboveground plant organs.

Discussion

The results of this study document the seasonal relationship between gross photosynthetic capacity and water potential for plants of *A. greggii* and *C. microphyllum*. While plant ψ is not to be the sole factor regulating CO_2 assimilation (Szarek and Woodhouse, 1978) the similarity of their seasonal courses is indicative of a causal relationship. Both species bore leaves throughout the summer, but seasonal photosynthesis rates were near minimal levels at this time. The highest day-long CO_2 assimilation rates occurred prior to year's end, indicating both species are mainly fall active. Although photosynthesis rates may also be elevated during the spring, this time corresponds to the occurrence of seasonally low foliar biomasses which affect a lower total photosynthetic capacity on a per plant basis. The two species appear only to differ in the magnitude of day-long gross photosynthesis during periods of water and temperature stress. The shrub species appears to be more tolerant of both environmental extremes and plant water stress. This comparison is not unexpected since: 1) *Cercidium* species are drought-deciduous (e.g., Turner, 1963); 2) other *Acacia* species do not show visible damage when exposed to temperatures of 47 to 52° C (Lange, 1959); and 3) absolute net photosynthesis rates of two *Acacia* species have even been reported to seasonally increase during periods of heat stress (Strain, 1969; Hellmuth, 1971).

Maximum seasonal photosynthesis for *A. greggii* and *C. microphyllum* occurs at both a different time of the year and magnitude than that for other life forms from the Sonoran Desert. Plants of *Ambrosia deltoidea*, a winter-active, drought deciduous shrub, had a maximum day-long photosynthetic capacity of 38 mg CO_2 dm^{-2} h^{-1} (Szarek and Woodhouse, 1977). Plants of *A. greggii* and *C. microphyllum* had a maximum photosynthetic capacity of 16 and 14 mg CO_2 dm^{-2} h^{-1}, respectively. These values are not significantly different than the photosynthetic capacities of an evergreen species. Plants of *Olneya tesota*, a virtual evergreen, microphyllous tree, demonstrated maximum day-long photosynthesis during the summer, averaging 12 mg CO_2 dm^{-2} h^{-1} (Szarek and Woodhouse, 1977).

Secondly, for plants of *C. microphyllum* all of the aboveground plant organs are capable of gross $^{14}CO_2$ assimilation and contributing exogenous CO_2 for the carbohydrate requirements of the entire tree. Photosynthesis by all size classes of stems occurs because of relative high chlorophyll concentrations, which slightly exceed foliar chlorophyll concentrations. This relationship is in agreement with previous studies of *Cercidium floridum*, a species with stem chlorophyll concentrations 22% greater than foliar chlorophyll concentrations (Adams et al., 1967). However, the amounts of total chlorophyll, expressed on a stem surface area basis, for the latter species are 40% greater than those of *C. microphyllum*. The fact that seasonal mean stem photosynthesis rates are at least 4-fold lower than foliar rates is not unexpected because stomatal densities on stems are comparatively low (e.g., Foote and Schaedle, 1976) and is in agreement with most previous studies of stem gas exchange (e.g., De Puit and Caldwell, 1975).

This species appears to be unique in the magnitude of the total seasonal carbon gain contributed by stems. Previously, Adams and Strain (1969) reported that stems of *C. floridum* contributed 40% of the total photosynthetic production for foliated trees. The greater relative contribution by stems of *C. microphyllum* is likely due to either a smaller foliar biomass throughout all times of the year or a lower net photosynthetic potential, since the foliar duration is longer in the Sonoran Desert for *C. microphyllum* than for *C. floridum* (Turner, 1963). The importance of stem photosynthetic production is underscored by two previous studies with plants of *C. microphyllum*: 1) flowering occurs prior to new leaf production in the spring (Turner, 1963); and 2) the water use efficiency for long-term dry matter production is 2-fold greater than other trees and shrubs from the Sonoran Desert (McGinnies and Arnold, 1939). Stem photosynthesis reduces respiratory CO_2 efflux from a plant, which can be a significant saving in carbohydrate resources of the stem (Schaedle, 1975) and affect a more favorable water use efficiency.

Finally, $^{14}CO_2$ assimilation estimates of AGPP for plants of *C. microphyllum* are over 4.5-fold greater than ANPP. This estimate was based upon the exogenous CO_2 contribution by all aboveground plant organs. Previously we had reported the AGPP/ANPP ratio to be approximately 3 for a winter-active shrub and an evergreen tree (Szarek and Woodhouse, 1977), these estimates being based solely upon the carbon contributions of leaves. Correcting for the carbon contributions of the other organs, the AGPP/ANPP ratios are 3.5 and 3.4, respectively. The difference in our current and earlier estimates of this ratio are likely due to difference in: 1) belowground carbon allocation; or 2) greater carbon requirements to maintain metabolically active chlorophyllous stems. The first alternative seems less likely since *Olneya tesota*, the evergreen tree with an AGPP/ANPP ratio of 3.4, is physiognomically similar to and coexists with *C. microphyllum* throughout the Sonoran Desert. Their microhabitats are "dry" washes and it is not intuitively obvious why the drought deciduous *C. microphyllum* would develop a proportionately larger rooting system. The second alternative is based upon the occurrence and magnitude of stem photosynthesis demonstrated by *Cercidium* species. Not only does stem photosynthesis reduce the rate of endogenous CO_2 efflux, as is characteristic of the gas exchange of most other chlorophyllous-stemmed species (e.g., Foote and Schaedle, 1976), but net exogenous CO_2 assimilation occurs (Adams and Strain, 1968). Since endogenous CO_2 may be produced by a variety of biochemical pathways occurring throughout a plant (e.g., Raven, 1972), its complete reassimilation as well as the supplemental assimilation of exogenous CO_2 must involve an efficient photosynthetic system. It is our interpretation that the year-round maintenance of stem photosynthesis affects a greater metabolic consumption of carbon, reducing that amount available for allocation to structural components of the entire plant and raising the AGPP/ANPP ratio.

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