

Seasonal patterns of canopy development and carbon gain in nineteen warm desert shrub species

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Summary. Canopy development and photosynthetic rate were measured at monthly intervals over a period of one year in 19 shrub and subshrub species of the Mojave and upper Sonoran Deserts. Thirteen of these species realized a substantial fraction of their total net carbon assimilation via twig photosynthesis. The twig contribution to whole plant yearly carbon gain reached a maximum of 83% in species such as *Thamnosma montana*, *Salizaria mexicana*, and *Baccharis brachyphylla*. This large contribution by twigs was due to both low levels of leaf production and the greater longevity of twig tissues. In some other species, however, leaf and twig organs had similar lifespans. During the year of this study (which had an unusually warm, mild winter), no species showed a pattern of winter deciduousness. The reduction in total photosynthetic area between maximal spring canopy development and mid August summer dormancy ranged from 32 to 94%. Some herbaceous perennial species died back to the ground, but none of the woody shrubs were totally without green canopy area at any time of the year. No species studied were capable of high rates of photosynthesis at low plant water potentials in July and August, but, in those species which maintained a substantial canopy area through the drought period, previously stressed tissues showed substantial recovery after fall rains. Photosynthetic rate was significantly correlated with both plant water potential and tissue nitrogen content over the entire year, but only weakly so. This is due in part to the winter months when plant water potentials and tissue nitrogen contents were high, but photosynthetic rates were often low.

Key words: Phenology – Leaf demography – Carbon balance – Water stress – Twig photosynthesis

Due to cyclic variations in water availability, seasonal changes in warm desert environments impose extreme contrasts in growing conditions for perennial plants. Furthermore, the timing of rainfall and drought is easily predicted only in long-term averages, and plants must show considerable flexibility in response in order to survive and flourish under such uncertain and periodically stressful climatic regimes. Photosynthetic assimilation of CO_2 for growth occurs, in many shallow-rooted desert shrubs, primarily during restricted rainy seasons (MacMahon and Schimpf 1981).

Rates of carbon assimilation and growth are often very high during the growing season, but community level productivity is still low to moderate due to the low standing crop of foliar biomass (Chew and Chew 1965; Whittaker and Niering 1975; Ehleringer and Mooney 1983). During the ensuing drought period, many of the shrubs shed most of their photosynthetic area in a drought-deciduous dormancy response (Orshan 1954; Orshan and Diskin 1968). Although desert shrubs respond to the alternating periods of water availability and drought with alterations in both seasonal canopy dynamics and the physiological activity of individual organs, physiological responses are generally much faster than changes in standing biomass (Wallace and Romney 1972; Comstock and Ehleringer 1986). The interactions of these two components of whole-plant carbon gain and the limitations imposed by time-lags in photosynthetic surface production during a short favorable growing season are important aspects of the autecology of desert plants (Comstock and Ehleringer 1984, 1986).

A salient feature distinguishing the canopy architecture of a great many warm desert shrubs is the utilization of current season twigs and, often, even the older stems, as primary organs of photosynthetic assimilation of CO_2 (Cannon 1908; Adams et al. 1967; Szarek and Woodhouse 1978; DePuit and Caldwell 1975; Gibson 1983; Comstock and Ehleringer 1988). Although the importance of stem photosynthesis in desert plant communities has long been recognized, little progress has been made in understanding its unique prominence in warm desert habitats (Gibson 1983). Neither the physiological tradeoffs nor the alteration of canopy structure implied by a qualitative shift from leaf to stem photosynthesis have been adequately studied to reach an ecological understanding of the distribution of species with photosynthetic stems. This study was initiated to collect baseline data on the phenology of carbon gain in a large number of warm desert species. Both physiological capacity for photosynthesis and the level of canopy development were followed throughout the seasons for slightly over one year. A special emphasis was placed on contrasting the performance of photosynthetic leaves and twigs. This was done both within the canopies of particular species, and between canopies of different species showing a wide range in percent contribution by photosynthetic twigs and stems to total plant carbon gain. Such data are important for understanding the canopy dynamics of desert shrubs, and may help to evaluate the special role of photosynthetic twigs and stems in warm desert environments.

Methods

This report is the first part of a larger study being conducted on the ecophysiology of green twig subshrubs. Green twig species and non-green twig species were sampled at two Mohave Desert sites in Western Arizona. Site one was approximately 9 km west of Oatman, Arizona (lat. 34°57' N, long. 114°25' W, 785 m elevation). The vegetation of this area is transitional between Mojave Desert southwestern portion and the Sonora Desert Lower Colorado valley portion (Shreve and Wiggins 1964). Site two was approximately 16 km north of Littlefield, Arizona (lat. 37°01' N, long. 113°50' W, 1028 m), within the Joshua Tree Natural Area. Data for species occurring at both sites were averaged between sites for this analysis. Between site analyses will be discussed in later reports. The species measured grew in gravelly or sandy washes and along side them or on adjacent slopes with shallow gravelly soils. Wash species measured included *Ambrosia dumosa* Gray, *Ambrosia eriocentra* Gray, *Baccharis brachyphylla* Gray, *Bebbia juncea* Benth., *Chrysothamnus paniculatus* (Gray) Hall, *Encelia farinosa* Gray, *Encelia virginensis* A. Nels., *Gutierrezia microcephala* (D.C.) Gray, *Gutierrezia sarothrae* (Pursh) Rusby, *Hymenoclea monogyra* Torr. and Gray., *Hymenoclea salsola* T. & G., *Porophyllum gracile* Benth., *Psilostrophe cooperi* (Gray) Greene, *Salazaria mexicana* Torr., *Salvia dorrii* (Kell.), *Senecio douglasii* D.C., *Sphaeralcea parvifolia* A. Nels., and *Stephanomeria pauciflora* (Torr.) Nutt. (Munz 1964). Observations were collected over a sixteen month period beginning in April, 1985. Gas exchange measurements were made on outer canopy leaves and green-twig tissues. Due to the small size of most leaves and internodal distance between leaves it was often difficult to measure leaf photosynthesis rates without the inclusion of at least some green-twig tissue. When leaf gas exchange measurements included twig tissue, the leaf rates were obtained indirectly from measurements on leafless twigs and whole shoots. Leaf photosynthetic rates were calculated using an area-weighted relationship between total shoot flux and the partial fluxes of the two component tissues:

$$A_s S_s = A_t S_t + A_l S_l$$

where A_s , A_t and A_l are the shoot, twig and leaf photosynthetic rates, respectively, and S_s , S_t and S_l are the shoot, twig and leaf projected areas, respectively. Upon rearrangement:

$$A_l = (A_s S_s - A_t S_t) / S_l$$

In order to measure the gas exchange rates of green twigs, it was necessary to first remove the leaves with a razor. Previous experiments to assess potential effects of wound respiration and/or water loss from leaf scars, demonstrated little appreciable effect on gas exchange calculations (Comstock and Ehleringer 1988). At each sampling interval, maximum daily photosynthetic rates (A_{max}) were measured for three different green-twig and leaf tissues of each species. A_{max} refers to maximum net photosynthetic rates measured under late morning conditions of irradiance (1.4–2.0 mmol m⁻² s⁻¹, 400–700 nm), ambient temperature, humidity, and CO₂ levels. Net photosynthesis was measured with a portable gas exchange system (LI-6000 LI-Cor, Inc., Lincoln, Nebraska).

Canopy development for each species was estimated by harvesting three representative shoots (one from each of

three individual shrubs) for each species on each sampling date and dividing them into green twig (non-green twigs were not measured) and leaf fractions. Individual "shoots" were usually (though not always) composed of just the current seasons growth which, depending on the species, may have been highly branched. Each shoot was cut just below the point of the oldest possible green tissue (for the majority of species this included only current year's growth), and included all age-classes of photosynthetic leaves and/or twigs present in the canopy. Projected area measurements of the leaf and twig fractions were made using a leaf area meter (Li-3100, Li-Cor Inc., Lincoln, Nebraska).

Most desert subshrubs have small canopies and do not have major distinctions between upper and lower (sun and shade) canopy shoots. Furthermore, most major shoots are initiated as an annual cohort (the timing varies with the phenology of each species but this event usually occurs in the winter or early spring) and later growth occurs as side-branching or other alterations of this recognizable shoot cohort. Consequently, although total canopy area was never measured, it was assumed to be proportional to the measured areas of individual component shoots. Values given for relative canopy area represent the shoot areas relative to the maximal shoot area measured for each species during the course of the study. In response to drought, some (usually quite limited) asynchronous mortality of whole shoots occurred as well as the partial defoliation or browning of individual living shoots as measured with the techniques described above. Consequently, the estimates of reduction of canopy area given are conservative and may tend to underestimate the total reduction of green tissues.

Amino nitrogen was analyzed on the same twig and leaf tissues used for gas exchange using standard Kjeldahl techniques. Tissues brought from the field were oven dried, ground to 40 mesh in a Wiley Mill, weighed and analyzed using an auto analyzer (Technicon, Tarrytown, NY).

Plant water potential was measured using a Scholander type pressure chamber. Measurements were made on individual leaves when leaves were sufficiently large, and on short terminal twigs (with leaves attached) when leaves were very small. Measurements were made one hour before sunrise and at midday.

Stomatal counts were made on twigs harvested from plants grown in the greenhouse at the University of Utah. Twig epidermis was coated with clear nail polish which was allowed to harden, removed from the specimen, and examined under the light microscope. When necessary, two successive impressions were made of the same specimen, the first serving to remove most of the trichomes and the second providing a clear impression of the epidermis with stomata.

Results

All of the species included in this study showed some degree of summer deciduousness and little or no winter deciduousness during 1985–1986 (Figs. 1–6d). In all cases, summer deciduousness appears to be associated with low plant water potentials, but the degree and length of dormancy, as well as the tissues most affected varied considerably between species. It was found that the 19 species studied could be subdivided into six useful groups based on 1) the percent contribution of green twigs to whole plant carbon gain, and 2) the percent reduction of photosynthetic area during

Table 1. Degree of summer-deciduousness and percent importance of twigs in the yearly integrated carbon assimilation of each study group of species. Percent canopy reduction represents the decrease in photosynthetic canopy projected area between spring maximal areas (whenever they occurred) and early August. Leaf and green twig reductions are based on the maximal seasonal values of each individual organ type, which may not have peaked simultaneously. Total dieback is based on the sums of leaf and twig areas for each sample date. Group 1: *Ambrosia dumosa*, *Encelia farinosa*, *E. virginensis*, Group 2: *Ambrosia eriocentra*, *Salvia dorrii*, *Hymenoclea monogyra*, Group 3: *Bebbia juncea*, *Porophyllum gracile*, *Stephanomeria pauciflora*, Group 4: *Psilostrophe cooperi*, *Senecio douglasii*, *Sphaeralcea parvifolia*, Group 5: *Chrysothamnus paniculatus*, *Gutierrezia microcephala*, *Gutierrezia sarothrae*, *Hymenoclea salsola*, Group 6: *Baccharis brachyphylla*, *Salazaria mexicana*, *Thamnosma montana*

	% leaf dieback	Green % twig reduction	% total reduction	Annual assimilation by twigs
Group 1	90	—	90	00
Group 2	32	—	32	00
Group 3	100	91	94	55
Group 4	99	72	92	16
Group 5	69	58	54	33
Group 6	100	38	55	83

drought periods (Table 1). In some cases these groupings were quite homogeneous with strongly convergent plant habits and phenologies among included species. In other cases the groupings were looser categories, but still facilitated a condensed summary of the seasonal activity patterns within the limits of a broad survey and limited data on any individual species.

Six species were considered, in the context of the present study, to have non-photosynthetic twigs. This does not mean that no functional chloroplasts were present in the cortical parenchyma or cambial layers of twigs in these species, but rather that the twigs never, or at least very rarely, achieved positive net assimilation of atmospheric CO₂. Many, perhaps most woody species have some functional chloroplasts in superficial tissues of twigs and stems (Schaefer 1975), and such tissues are nearly ubiquitous among desert shrubs (Cannon 1908). In some species, these twig and stem chlorenchyma tissues are well developed (though less so than in leaf tissues) and capable of substantial gross photosynthesis (Coe and McLaughlin 1980; Foote and Schaefer 1978; Keller 1973; Parker 1978; Wiebe et al. 1974). Most woody species, however, have a well developed periderm even in relatively young twigs restricting the diffusion of CO₂ between the chlorenchyma tissues and the ambient atmosphere. Only endogenously derived CO₂ is normally utilized in the stem chloroplasts of such species (Brayman and Schaefer 1982; Nedoff et al. 1985). In contrast, a sizable fraction of the desert shrub species have twigs with chlorenchyma development equivalent to that found in leaf tissues of the same species, and associated with these twigs are other anatomical specializations allowing positive net assimilation of atmospheric CO₂ (Cannon 1908; Gibson 1983). These include 1) delayed formation of periderm, 2) retention of functional stomata throughout the twigs lifespan, and 3) high stomatal densities (Gibson 1983). Stomatal density of photosynthetic twigs in this study averaged

Table 2. Stomatal density of twigs of co-occurring subshrub species. The striations referred to are longitudinal furrows on the twigs of many Asteraceae (usually those which have photosynthetic twigs). When it occurs, chlorenchyma tissue forms vertical stripes alternating with leaf traces and bundles of fibers. The stomata of photosynthetic twigs are commonly restricted to epidermal regions subtended by chlorenchyma. Total stomatal density is an average density of the entire surface which may or may not be divided into smaller regions of differing stomatal density as described above

	Total stomatal density mm ⁻²	Stomatal density on striations mm ⁻²
Photosynthetic twig species		
<i>Bebbia juncea</i>	65	120
<i>Gutierrezia sarothrae</i>	37	82
<i>Hymenoclea salsola</i>	70	108
<i>Porophyllum gracile</i>	42	140
<i>Senecio douglasii</i>	22	97
<i>Sphaeralcea parvifolia</i>	34	N/A*
$\bar{x} \pm \text{s.e.}$	45 \pm 7.8	109 \pm 10.1
Non-photosynthetic twig species		
<i>Ambrosia eriocentra</i>	2	
<i>Encelia farinosa</i>	6	
<i>Encelia virginensis</i>	4	
<i>Salvia dorrii</i>	1	
$\bar{x} \pm \text{s.e.}$	3 \pm 1.1	

N/A = not applicable (twig epidermis not striate)

15 times greater than that of young nonphotosynthetic twigs (Table 2). Chlorenchyma tissues in the photosynthetic twigs of members of the Asteraceae were always found in vertical striations alternating with leaf traces. Depending on species and, possibly, growth conditions, the chlorenchyma tissues may be found subtending the furrows (Gibson 1983) or the ridges (Comstock and Ehleringer 1988) of the striations. Stomata were found restricted entirely to the vertical stria subtended by chlorenchyma tissues (Gibson 1983; Comstock and Ehleringer 1988). The stomatal density calculated only for these photosynthetic regions of the twigs was much higher yet than that calculated on a total twig area basis. Striations were not often observed in the twig epidermis of members of the Asteraceae in which the twigs were not photosynthetic. In species where well developed twig chlorenchyma is associated with a high density of functional stomata, net carbon assimilation can be measured in the twigs over a prolonged growing season (Adams et al. 1967; Adams and Strain 1969; Depuit and Caldwell 1975; Szarek and Woodhouse 1978; Comstock and Ehleringer 1988).

On a few occasions during the early spring of 1985 (but not repeatable in 1986), very vigorous new growth on plants classified as having nonphotosynthetic twigs (*Ambrosia dumosa*, *Salvia dorrii*, and *Hymenoclea monogyra*) actually included twigs which briefly (one observation only) achieved low but positive net photosynthetic rates (0–2.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Because the total contribution of such twigs to whole plant carbon assimilation, if included for these species, would be at most a few percent of the leaf contribution on the single date when positive rates were observed, and would be a negative quantity on an annual basis, only the

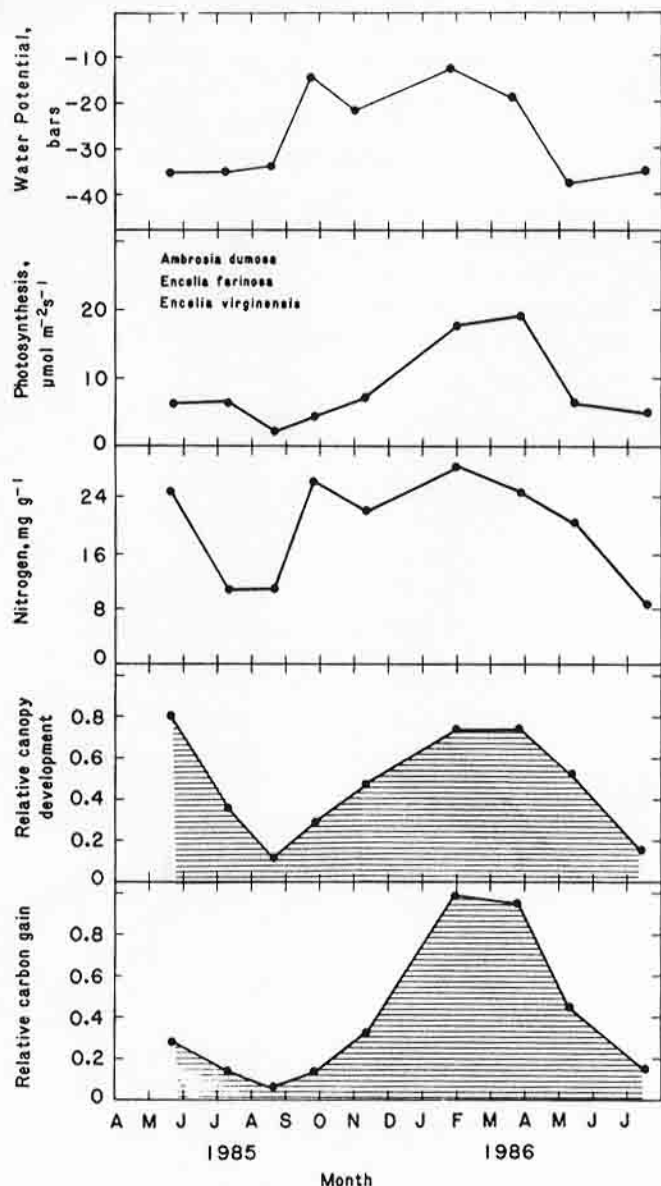


Fig. 1 A-E. Seasonality of photosynthesis and canopy development for species lacking photosynthetic twigs and showing extensive summer leaf fall (Group 1). A Predawn plant water potential, B Net photosynthetic rate measured in the field in late morning with irradiance levels of $1.4\text{--}2.0\text{ mmol m}^{-2}\text{s}^{-1}$. When more than one cohort of leaves and/or twigs were present the reported value represents an area weighted average of photosynthetic rates measured in the canopy for all cohorts, C Tissue Kjeldahl nitrogen content. Values were area weighted over all major age classes in canopy when necessary, D Relative canopy development. Each species had its seasonally changing photosynthetic canopy area relativized to the maximal canopy area observed for that species, and these relativized values were then averaged over included species. Canopy development does not ever reach a value of one because the included species did not reach their peak development simultaneously, E Relative carbon gain. This estimate was calculated as the product of the photosynthetic rates in B and the percent canopy areas in D above. Each species estimate of the seasonal pattern of carbon gain was relativized to its own maximum before averaging patterns between species

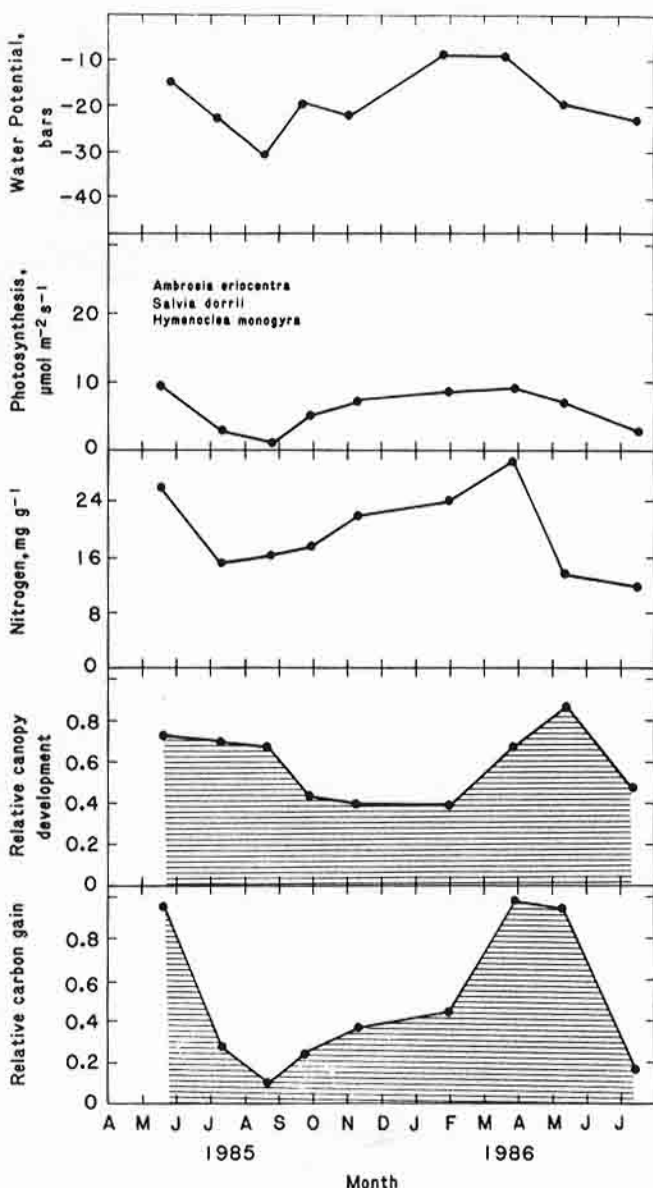


Fig. 2 A-E. Seasonality of photosynthesis and canopy development for species lacking photosynthetic twigs and maintaining a large fraction of the leaf area through the drought period. See Fig. 1 for definitions of A-E

seasonality of leaf photosynthesis and canopy area are reported here for species whose twigs showed such an ephemeral capacity for net uptake (Figs. 1 and 2).

The six species relying solely on leaf photosynthesis for net carbon assimilation form the most diverse groups of this study in terms of physiognomy and stature. Although none of these species are sclerophyllous, they can nonetheless be divided into two further groupings based on leaf longevity. *Encelia farinosa*, *E. virginensis*, and *Ambrosia dumosa* (Group 1) (Fig. 1) showed nearly complete summer deciduousness, while *A. eriocentra*, *Hymenoclea monogyra*, and *Salvia dorrii* (Group 2) (Fig. 2) maintained a large fraction of their leaf area through the drought period. None of these species maintained high photosynthetic rates during mid-summer drought conditions (Table 3).

Thirteen species were studied in which twigs contributed a substantial amount (16–83%) to estimated whole plant

Table 3. The ability of twigs to recover photosynthetic capacity after summer drought. Values for spring maximum, Summer drought, and spring growth under fall recovery represent a single cohort through time. Fall growth represents newly produced tissues. Mean plant water potentials (predawn) across species were -11.6 ± 4.4 , -29.5 ± 4.7 , and -12.7 ± 2.3 bars in spring, midsummer, and after fall rains, respectively

Net Photosynthesis $\mu\text{mol m}^{-2} \text{s}^{-1}$

Species	Spring maximum	Summer drought	Fall recovery	
			spring growth	fall growth
<i>Baccharis brachyphylla</i>	13.9	0.5	14.3	8.0
<i>Bebbia juncea</i>	13.2	0.1	5.0	7.8
<i>Gutierrezia sarothrae</i>	7.6	0.9	8.0	-0.01
<i>Hymenoclea salsola</i>	10.0	2.5	2.5	6.2
<i>Porophyllum gracile</i>	13.5	0.7	4.2	12.2
<i>Senecio douglasii</i>	7.2	0.4	4.0	6.3
<i>Sphaeralcea parvifolia</i>	8.2	0.4	8.1	2.3
$\bar{x} \pm \text{s.e.}$	10.5 ± 1.1	0.8 ± 0.3	6.6 ± 1.5	6.1 ± 1.5

carbon gain over an annual cycle (Table 1). These photosynthetic-twigged shrubs can also be divided into subgroups based on leaf and twig longevity. *Porophyllum gracile*, *Stephanomeria pauciflora*, and *Bebbia juncea* (Group 3) (Fig. 3) are all relatively herbaceous perennials whose canopies die back nearly to the ground during severe drought. These species had high photosynthetic rates in both leaf and twig tissues under conditions of high soil moisture. When low leaf water potentials developed, both photosynthetic rate and total canopy surface area declined. *B. juncea* and *S. pauciflora* appeared to favor the warmer conditions of late spring and had rather slow growth rates during the winter months. *P. gracile*, the smallest, most ephemeral of the three, had more winter activity and died back almost entirely by late May. Flowering occurred on current season shoots near the end of the spring growing season and again after fall growth for all three species.

Senecio douglasii, *Sphaeralcea parvifolia*, and *Psilostrophe cooperi* (Group 4) (Fig. 4), were also suffrutescent subshrubs with major summer dieback. They are distinguished from the previous group by 1) maintaining more of an above-ground woody caudex, 2) a coarser, more robust growth form with stout, virgate twigs and relatively large leaves, and 3) a much greater reliance on leaf rather than twig photosynthesis. These species also flowered in both the spring and fall. Considerable growth occurred during the winter months, and spring flowering peaked in April. Very high photosynthetic rates were measured in the leaves of these species, but twig photosynthetic rates, though consistently positive, were generally the lowest rates of any of the photosynthetic-twigged species. Although a distinct chlorenchyma layer could easily be seen on dissection, the twigs of *P. cooperi* and *S. parvifolia* were covered with a dense, reflective pubescence layer.

Chrysothamnus paniculatus, *Gutierrezia microcephala*, *G. sarothrae*, and *Hymenoclea salsola* (Group 5) (Fig. 5) maintained a considerable fraction of the green canopy through the drought period. As with non-photosynthetic twigged species with leaves enduring summer drought conditions, physiological stress and low photosynthetic rates reduced plant carbon gain to near zero during extreme

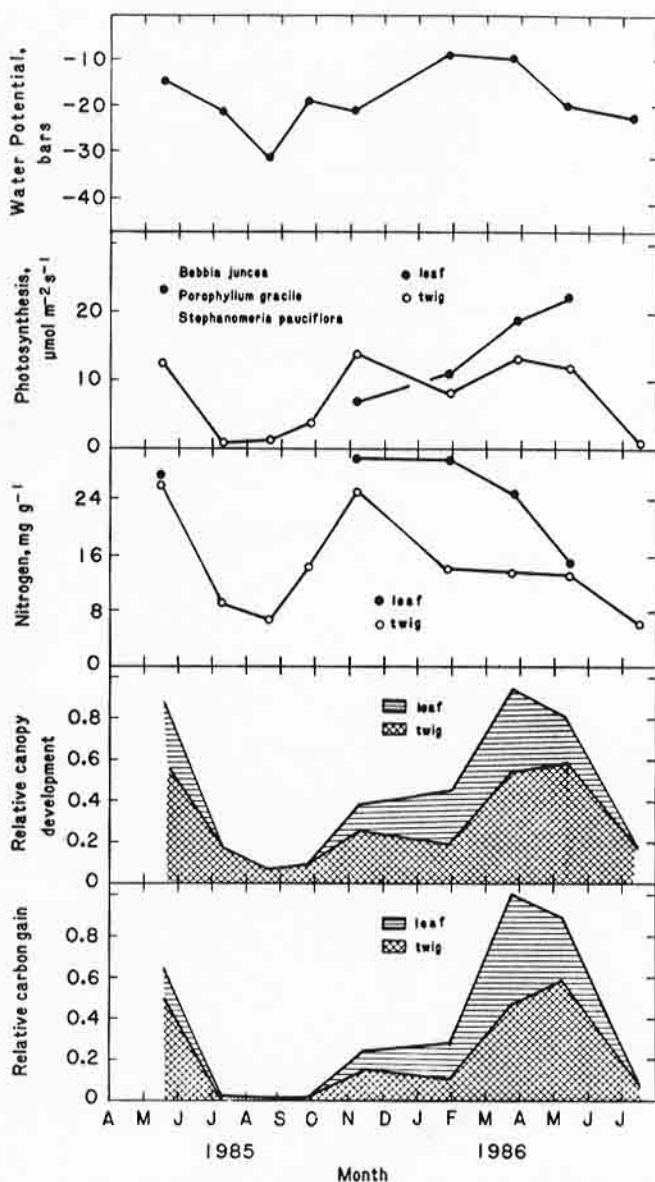


Fig. 3A-E. Seasonality of photosynthesis and canopy development for species with both photosynthetic leaves and twigs, and with a largely herbaceous-perennial habit (Group 3). See Fig. 1 for definitions of A-E.

drought conditions despite the maintenance of green tissues. Leaves almost always had higher photosynthetic rates than twigs, but this difference was most noticeable in mid-spring when the photosynthetic rates of both tissues were at their peak. The relative importance of twigs was greatest in the fall. This was due in part to greater leaf than twig mortality during the summer drought, and in part because leaves did not reach the same high photosynthetic rates in the fall that were observed at similar water potentials in late spring. The lower photosynthetic rates did not appear to be due to organ age or previous stress conditions experienced by specific organs since newly produced fall growth had similar rates to tissues which had endured the drought period (Table 3). All four of these species showed a pattern of delayed flowering relative to annual vegetative growth. *C. paniculatus* and the two *Gutierrezia* species flowered in the fall on vegetative shoots produced during spring and

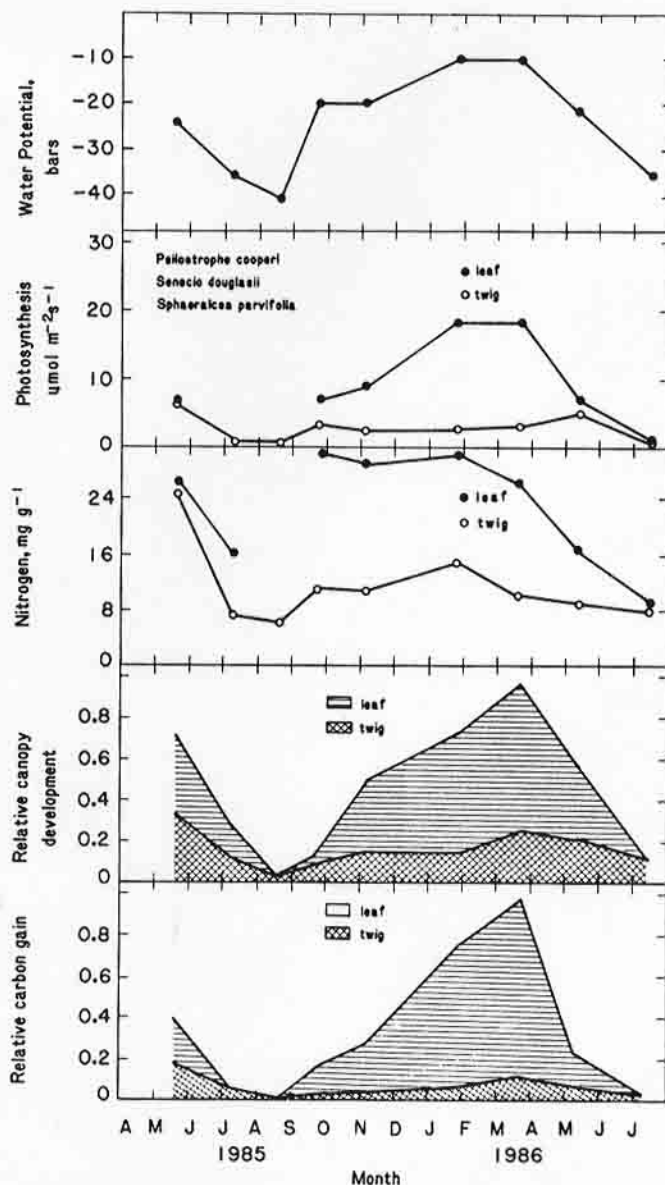


Fig. 4A-E. Seasonality of photosynthesis and canopy development for species with both photosynthetic leaves and twigs, and with a high level of summer deciduousness (especially the leaf fraction). These species (Group 4) were less herbaceous than those in Group 3, and had much greater emphasis of leaf photosynthesis due to the large leaf size and area. See Fig. 1 for definitions of A-E

winter of the same year. *H. salsola* flowered in the spring at the same time new vegetative shoots were being initiated, but the cohort of flowering shoots were then 10–12 months old being comprised of the surviving 'vegetative' growth initiated the previous spring (very short new sidebranches formed to bear the congested flowers during the second spring, but the main axis of the inflorescences were always one year old). After flowering, these one year old, often much branched, shoot systems died back to a more perennial woody axis. *Ambrosia eriocentra* (Fig. 2) and *Thamnosma montana* (Fig. 6) had this same flowering phenology and habit.

Baccharis brachyphylla, *Salizaria mexicana*, and *Thamnosma montana* (Group 6) (Fig. 6) had ephemeral leaves

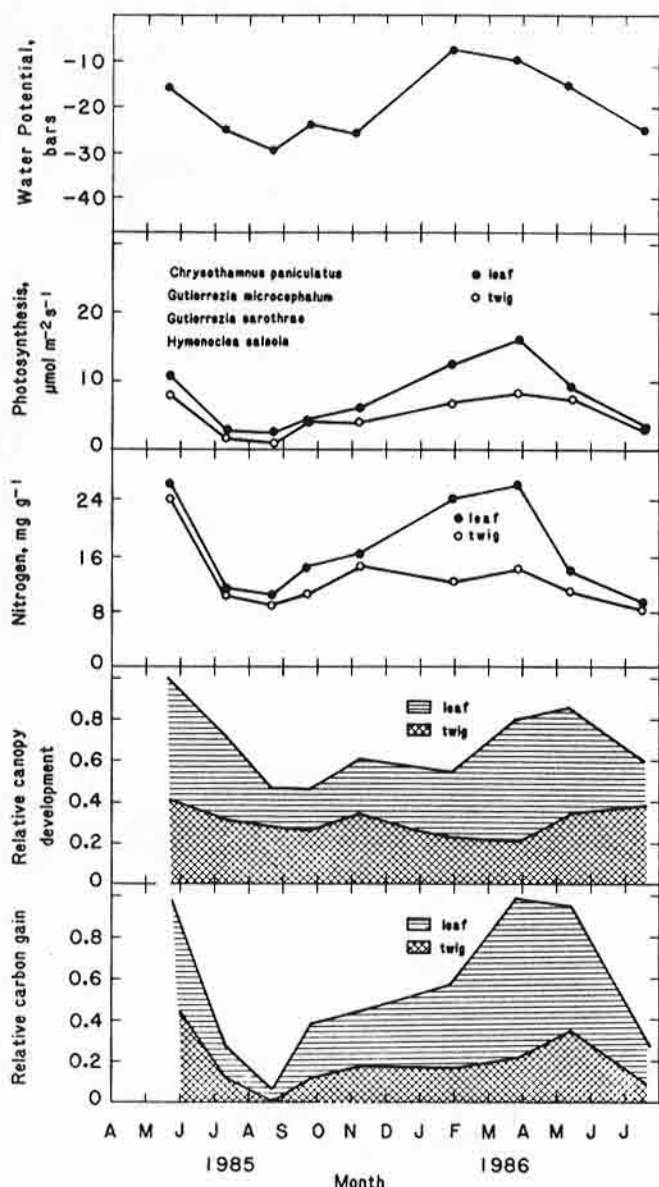


Fig. 5A-E. Seasonality of photosynthesis and canopy development for species with both photosynthetic leaves and twigs, and maintaining a large fraction of both the leaf and twig area through the drought period (Group 5). See Fig. 1 for definitions of A-E

which were completely drought-deciduous. These leaves usually had photosynthetic rates similar to or lower than their twigs. Leaves of *S. mexicana* did have high photosynthetic rates on at least one occasion (Leaf = 22 and twig = 11 $\mu\text{mol m}^{-2}\text{s}^{-1}$ in April 1985, not shown in Fig. 6 because measurements were not taken on the other two species), but did not appear to maintain such high rates under any but very favorable conditions. In sharp contrast to the leaves, twigs in this group were the most long-lived photosynthetic tissues studied. Although many green twigs in this group live longer than the study lasted, fairly accurate maximum ages could be reconstructed from a careful examination of the branching patterns. *S. mexicana* differed from the other two species of this group in being a rhizomatous perennial. Shoots originated from underground rhizomes and reached a height of 0.5–1.0 m in the first year. For the next two to five years whorls of short side branches

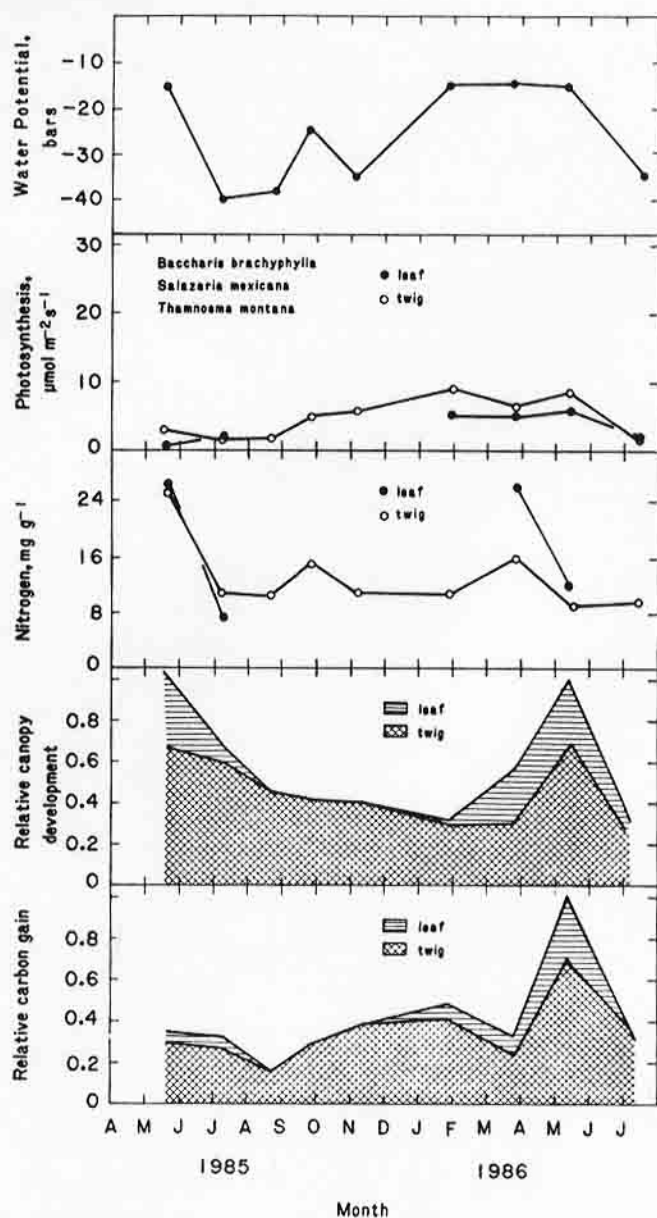


Fig. 6A-E. Seasonality of photosynthesis and canopy development for species with both photosynthetic leaves and twigs, and showing very little reduction of green twig area during drought (Group 6). Twigs of *S. mexicana* and *T. Thymosma* often remained green for three to five years, and thus represent the longest lived photosynthetic organ in this survey. The growth pattern and twig longevity of *B. brachyphylla* was in many respects more like the species of group 5 (which species, like *B. brachyphylla*, are all members of the Asteraceae), and *B. brachyphylla* is included here primarily because of the very low level of leaf production, and consequent low contribution of leaves to total carbon gain. See Fig. 1 for definitions of A-E.

originated repeatedly from the uppermost nodes forming short floral shoots and ever more tangled whorls of old twigs. Twig lifespans were variable with shoots originating from the rhizome lasting 3 to 5 years and the short floral sidebranches often dying back during their first drought. The mature plant forms a dense tangled clump of intertwined living and dead stems. Both *B. brachyphylla* and *T. montana* are typical 'broom' species with a very orderly array of long branches and twigs radiating outwards hem-

spherically from a central woody base. Some twigs on *T. montana* remained green for up to five years (though the majority lasted only 2 to 3 years), while twigs of *B. brachyphylla* remained green slightly over one year. In both these latter species, the entire twig cohort of the most recent springs growth survived the summer drought, though mortality of some of the older twigs and stems did occur at that time. Again, midsummer drought and low plant water potentials depressed the photosynthetic rate and caused low rates of whole plant carbon gain despite the retention of a large green canopy area. Substantial recovery occurred following fall rains.

Only the more herbaceous species (groups 3 and 4) and some of the strongly drought-deciduous sub-shrubs which lacked green twigs (Group 2) were ever observed to have no photosynthetic surface area at any time during the study. Most of the larger, woody shrubs all maintained at least a small (sometimes quite substantial) fraction of the canopy area even during the intense summer drought (Table 1). Greenstemmed species were more likely to go fully leafless than non-green-stemmed species. Some photosynthetic twigged species kept equally large areas of leaf and twig area during drought (Group 5), but none maintained green leaves while allowing the associated twigs to become permanently non-photosynthetic. Due primarily to reasons of technical difficulty more sampling was done following individual cohorts of twigs than of leaves through time. Older leaf cohorts were often diffusely scattered among other tissues and insufficient numbers of older leaves could be placed simultaneously in the cuvette to obtain a reliable measurement. In other species with most leaves in long-lived fascicles such as *S. dorrii*, it was not possible (using these survey techniques) to accurately assign leaves within a fascicle to specific cohorts. Finally, twigs of some species had greater lifespans, and were much more important during drought recovery stages. Although photosynthesis was invariably reduced to very low rates when plant water potential reached a minimum in midsummer, many species showed recovery of photosynthesis in old green twigs during the fall. The degree of recovery in such tissues was variable, but rates were often equivalent to those measured at similar plant water potentials in the spring or measured simultaneously on newly produced fall twigs (Table 3). Some photosynthetic twigged species such as *H. salsola* and *C. paniculatus* (Group 5) and some non-green stemmed species which maintained substantial canopy area through the drought (Group 2) produced leaves possessing similar maximum lifespans to the green twigs discussed above. Such longlived leaves may also be capable of substantial post-drought recovery.

Under laboratory conditions, strong linear relationships are often observed between plant water potential and photosynthetic rate, and similar relationships have also been observed under field conditions, especially when measurements are taken over a limited seasonal timespan. Significant relationships were found in this study between both leaf and twig photosynthetic rate and predawn plant water potential, but the explained variation was very low (Table 4). The low correlation is due primarily to three factors. In decreasing order of importance: 1) in winter and early spring plant water potential was very high, but growth rates and photosynthetic rates were often low, 2) many different species are combined in these regressions which have differing sensitivities to low plant water potential, and 3) the

Table 4. The relationship between the physiological parameters, relative photosynthetic rate and Kjeldahl nitrogen content, mg g^{-1} , and predawn plant water potential in bars. Each species on each sampling date was considered one data point. Photosynthetic rates were relativized within each species setting the highest rate for each species = 1.0 prior to entering the values into multi-species regressions

		Intercept	Slope	r^2	
Relative P.S. Rate vs. Water Potential					
All species	leaf	0.81	0.020	0.32	**
	twig	0.43	0.007	0.12	**
Group 1	leaf	0.76	0.012	0.22	*
Group 2	leaf	0.99	0.018	0.81	**
Group 3	leaf	0.45	0.007	0.13	NS
	twig	0.49	0.030	0.32	*
Group 4	leaf	1.3	0.051	0.86	**
	twig	0.32	0.006	0.13	*
Group 5	leaf	0.90	0.025	0.42	**
	twig	0.44	0.010	0.30	**
Group 6	leaf	0.78	0.020	0.55	**
	twig	0.84	0.011	0.34	**
Kjeldahl Nitrogen vs. Water Potential					
All species	leaf	29	0.44	0.21	**
	twig	14	0.12	0.09	**

*slope significant at $P \leq 0.05$; ** $P \leq 0.01$; NS = not significant

Table 5. Photosynthesis, $\mu\text{mol m}^{-2}\text{s}^{-1}$ vs. Kjeldahl Nitrogen, mg g^{-1}

		Intercept	Slope	r^2	
All species	leaf	3.2	0.31	0.16	**
	twig	1.4	0.22	0.09	**
Group 1	leaf	8.4	0.09	0.02	NS
Group 2	leaf	1.2	0.35	0.44	**
Group 3	leaf	36	-0.78	0.40	*
	twig	-1.1	0.75	0.34	**
Group 4	leaf	4.4	0.25	0.09	NS
	twig	0.80	0.20	0.11	*
Group 5	leaf	-1.7	0.58	0.38	**
	twig	1.6	0.24	0.08	NS
Group 6	leaf	4.4	0.05	0.02	NS
	twig	5.0	-0.03	0.001	NS

* = significant at $P \leq 0.05$; ** $P \leq 0.01$; NS = not significant

reported photosynthetic rates for each species represent a small number of instantaneous measurements and may be affected by factors of light intensity due to leaf orientation and other uncontrolled factors. The highest photosynthetic rates were commonly observed in mid-spring (March–April) when plant water potentials had already dropped slightly below their maxima.

Tissue Kjeldahl nitrogen contents were usually higher in leaves than in twigs when expressed on a mg g^{-1} basis, especially in species where the leaves had very high photosynthetic rates (Figs. 1–6). Because of the lower specific area (cm^2g^{-1}) of twigs, this relationship would be reversed in

all species studied if expressed in mmol N m^{-2} (projected area). Tissue nitrogen contents often underwent more seasonal variation in leaf than in twig tissues. Nitrogen contents were generally highest in young tissues in the winter and spring. Again, since photosynthetic rates were quite low in early winter, this contributed to a low correlation between nitrogen content and photosynthetic rate (Table 5). In many species (Figs. 1, 3 and 4) very high nitrogen contents were evident in fall and early winter in slow-growing new shoots which had not yet achieved high photosynthetic rates. As plant water potentials dropped during the summer drought, tissue nitrogen contents and photosynthetic rates both dropped, especially in leaf tissues. In twigs photosynthetic rates dropped during drought, but the nitrogen content of long-lived twigs did not show as great a percentage decline as did that of leaves. Similar results were obtained from greenhouse studies of *H. salsola* under controlled water-stress treatments (Comstock and Ehleringer 1988).

Discussion

Although the long-term rainfall patterns of the sites where this work was done are strongly bimodal, and the summer drought causes near total dormancy for most species between the two rainy periods, patterns of growth and development in spring versus late summer and fall are not usually independent events. In most subshrub species of arid regions, there is a high rate of twig turnover as well as leaf turnover (Orshan and Diskin 1968). This yearly dieback of most of the annually produced aboveground biomass is often a direct consequence of drought-stress as in the herbaceous perennial species of group 3, but in other species dieback is linked to other aspects of the life history making the probable relationship to drought more complex. In some of the fall flowering species, such as *G. microcephalum*, for instance, twig dieback occurs in the late fall after flowering, even though water stress at this time is not severe. In other species, such as *H. salsola* and *A. eriocentra*, extensive twig dieback occurs, again after flowering, towards the end of the second spring of the flowering twigs lifespan. Flowering is much heavier in some years than others, and this results in episodic stem dieback as well.

Typically, for species in groups 2, 4, 5, and 6, new shoots initiated in the winter and early spring originated from the lower regions of the canopy, and formed the true beginning of an annual growth cycle. In late spring these shoots often sidebranched and, depending on species, may have flowered. Fall growth tended to be comprised of a continuation of the branching pattern of shoot systems initiated in the winter and spring, and it occurred in the most distal portions of the canopy.

Figures 1–6 do not show the age structure of the photosynthetic canopy area, however, a few generalizations can be made. Relatively little mortality and hidden turnover of photosynthetic area occurred during the winter and spring growth periods. Some hidden turnover did occur in the early spring as surviving year-old green twigs formed bark, and any surviving leaves (rarely a large number) from the previous spring senesced after the new canopy growth was established. Older cohorts of green tissues were of major importance in the spring only in group six (*T. montana* and *S. mexicana*) where twigs and stems remained green and photosynthetically active for more than one year. Much more turnover occurred during the early fall following sum-

mer rains. At this time many shrubs had a complex age-structure to the canopy with substantial cohorts of winter, late spring, and fall leaves and twigs present simultaneously. After substantial new fall growth had occurred, there was generally an increased senescence of older cohorts.

In a previous study of the canopy dynamics and carbon gain of *E. frutescens*, Comstock and Ehleringer (1984) found that rates of leaf surface area production imposed the major limitation to whole plant carbon gain in the early portion of the season, while impaired physiological performance (water stress) was primarily responsible for the decline in whole canopy carbon gain during drought. The present data set, though lacking the resolution of the previous study, supports that interpretation on a broader scale. Photosynthetic rates and, consequently, whole plant carbon gain, were always severely depressed during July and August when plant water potentials reached a minimum. This was true regardless of whether the species lost most of the green canopy area during that period (Groups 1, 3, and 4) or not (Groups 2, 5, and 6), and also regardless of whether the major photosynthetic organs retained during drought were leaves (Group 2) or twigs (Groups 5 and 6). When high plant water potentials were restored in the fall, surface area limitations became an important component limiting whole-plant carbon assimilation. The degree of whole plant carbon gain was much higher in September and even in November for those species which had maintained a large canopy area through the drought period (Groups 1, 3 and 6). Periods of maximal whole canopy carbon gain almost always coincided with the time of maximal canopy development, and photosynthetic rates were usually near maximal at these times also. Photosynthetic rates, however, often reached near maximal values well in advance of maximal canopy development and maximal whole canopy assimilation rates (Groups 2, 4, 5, and 6).

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References

- Adams MS, Strain BR (1969) Seasonal photosynthetic rates in stems of *Cercidium floridum* Benth. *Photosynthetica* 3:55-62
- Adams MS, Strain BR, Ting IP (1967) Photosynthesis in chlorophyll stem tissues and leaves of *Cercidium floridum*: Accumulation and distribution of ^{14}C from $^{14}\text{CO}_2$. *Plant Phys* 42:1797-1799
- Brayman AA, Schaedle M (1982) Photosynthetic and respiratory rates of developing *Populus tremuloides* internodes. *Plant Phys* 69:911-915
- Cannon WA (1908) The topography of the chlorophyll apparatus in desert plants. *Pub Carnegie Inst Washington*, no 98
- Chew RM, Chew AE (1965) The primary productivity of a desert-shrub (*Larrea tridentata*) community. *Ecol Mon* 33:355-375
- Coe JM, McLaughlin SB (1980) Winter season cortical photosynthesis in *Cornus florida*, *Acer rubrum*, *Quercus alba*, and *Liriodendron tulipifera*. *For Sci* 26:561-566
- Comstock J, Ehleringer J (1984) Photosynthetic responses to slowly decreasing leaf water potentials in *Encelia frutescens*. *Oecologia* (Berlin) 61:241-248
- Comstock J, Ehleringer J (1986) Canopy dynamics and carbon gain in response to soil water availability in *Encelia frutescens* Gray, a drought-deciduous shrub. *Oecologia* (Berlin) 68:271-278
- Comstock J, Ehleringer J (1988) Contrasting photosynthetic behavior in leaves and twigs of *Hymenoclea salsola* a green-twigged warm desert shrub. *Am J Bot* (in press)
- De Puit EJ, Caldwell MM (1975) Stem and leaf gas exchange of two arid land shrubs. *Am J Bot* 62:954-961
- Ehleringer J, Mooney H (1983) Photosynthesis and productivity of desert and Mediterranean-climate plants. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) *Encyclopedia of plant physiology*, New Series, vol 12D. Springer Berlin Heidelberg New York
- Foot KC, Schaedle M (1978) The contribution of aspen bark to the energy balance of the stem. *For Sci* 24:369-373
- Gibson A (1983) Anatomy of photosynthetic old stems of nonsucculent dicotyledons from North American deserts. *Bot Gaz* 144:347-362
- Keller T (1973) CO_2 exchange of bark of deciduous species in winter. *Photosynthetica* 7:320-324
- MacMahon JA, Schimpf DJ (1981) Water as a factor in the biology of North American desert plants. In: Evans DD, Thames JL (eds) *Water in Desert Ecosystems*. Dowden Hutchinson Ross, Stroudsburg, Pennsylvania
- Munz PA (1968) *A California Flora*. Univ California Press, Los Angeles
- Nedoff JA, Ting IP, Lord EM (1985) Structure and function of the green stem tissue in *Ocotillo* (*Fouquieria splendens*). *Am J Bot* 72:143-151
- Orshan G (1954) Surface reduction and its significance as a hydro-ecological factor. *J Ecol* 42:442-444
- Orshan G, Diskin S (1968) Seasonal changes in productivity under desert conditions. In: Eckardt FE (ed) *Functioning of terrestrial ecosystems at the primary production level*. UNESCO, Paris
- Parker J (1978) Seasonal variation in photosynthesis in black oak twigs. *Photosynthetica* 12:423-427
- Schaedle M (1975) Tree photosynthesis. *Ann Rev Plant Phys* 26:101-105
- Shreve F, Wiggins IL (1964) *Vegetation and flora of the Sonoran desert*. Stanford University Press, Stanford, p 840
- Szarek SR, Woodhouse RM (1978) The daily course of photosynthesis for *Acacia greggii* and *Cercidium floridum*. *Oecologia* (Berlin) 35:221-229
- Wallace A, Romney EM (1972) Radioecology and ecophysiology of desert plants at the Nevada Test Site. *USAEC Report TID-25954*
- Weibe HH, Al-Saadi HA, Kimball SL (1974) Photosynthesis in the anomalous secondary wood of *atriplex confertifolia* stems. *Am J Bot* 61:444-448
- Whittaker RH, Niering WA (1975) Vegetation of the Santa Catalina mountains, Arizona. V. Biomass, production, and diversity along the elevation gradient. *Ecology* 56:771-790

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