

Canopy dynamics and carbon gain in response to soil water availability in *Encelia frutescens* gray, a drought-deciduous shrub

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Summary. The production and longevity of leaves of *Encelia frutescens* Gray, a drought-deciduous subshrub of the Mohave and Sonoran Deserts, were followed during the summer and fall of 1983 in an experimental field garden. The relationships between seasonally changing plant water status, extent of canopy development, and photosynthetic capacity per unit leaf area were determined. Maximum leaf life spans during a summer activity period were, between 3 and 4 months, with the great majority living between 1 and 3 months. Leaf production occurred synchronously in well defined cohorts triggered by precipitation events. Extensive leaf turnover occurred during the summer period even though the plants remained in continuous leaf. Turnover was most pronounced when precipitation triggered the production of new leaf cohorts.

Five weeks were required for plants to reach maximum canopy development when renewed soil-water availability followed a prolonged drought. Photosynthetic capacity per unit leaf area recovered much sooner than total leaf area, and submaximal leaf area development was the major factor limiting whole-plant carbon gain during a leaf-flushing period lasting several weeks. As the soil began to dry out, physiological capacity declined more rapidly than leaf area, and became the primary limiting factor to whole plant carbon gain.

Precipitation in arid regions can be highly variable in both total annual amount and its seasonal distribution (Bailey 1981; Ehleringer and Mooney 1983). Although limited periods which are highly favorable to plant growth may occur in such regions, they are interspersed with prolonged periods of drought. In regions of high aridity, a substantial fraction of the flora is composed of plants with the drought-deciduous leaf habit (Orshan 1954; Harrison et al. 1971; Mooney and Kummerow 1971). This leaf habit is thought to facilitate survival during prolonged drought by eliminating transpiring surface area, and by reducing whole plant respiration rates during periods of potentially negative carbon balance (Orshan 1954; Kozlowski 1976; Chabot and Hicks 1982). While leaf lifespans may be short, peak photosynthetic rates per unit leaf area are quite high in drought-deciduous shrubs when compared to evergreen shrubs of the same or adjacent habitats (Bamberg et al. 1975; Szarek and Woodhouse 1977; Ehleringer and Mooney 1983).

Greatly reduced leaf water potentials eventually lead to major reductions in the leaf photosynthetic capacity even for desert shrubs (Hsiao and Acevedo 1974; Odening et al. 1974; Mooney 1980; Schulze et al. 1980; Comstock and Ehleringer 1984). In evergreen plants, this impaired physiological capacity is sometimes the major limitation to carbon gain during drought periods (Oechel et al. 1972; Bamberg et al. 1975; Mooney et al. 1975). In drought-deciduous leaved shrubs, however, changes in physiological capacities may be superimposed on a dynamically changing total-canopy leaf area. The impact of variation in these two components of whole-plant carbon gain undergoes extensive and continuous change under the intermittent precipitation patterns typical of the growing season in arid and semi-arid regions. A thorough description of these changing relationships is essential to a full understanding of the productivity of drought-deciduous leaved shrubs. *Encelia frutescens* Gray is a drought-deciduous subshrub common in the washes of the Mohave and Sonoran Deserts. Under highly favorable plants water status and ambient midday conditions, net photosynthetic rates exceeding $40 \mu\text{mol m}^{-2} \text{s}^{-1}$ are observed in this species (Comstock and Ehleringer 1984). During prolonged drought, net photosynthetic rates and midday leaf water potential decrease in response to decreased soil water potentials, net photosynthetic rates approach zero as midday leaf water potential reach approximately -4.0 MPa . During a typical growing season, *E. frutescens* shrubs would experience repeated cycles of soil water availability, which would be manifested in cyclic variations in leaf water potential. Photosynthetic capacity per unit leaf area as described above, therefore, would not be constant through the season, but would undergo substantial fluctuations with each major precipitation event. This study was undertaken to compare the relative responses of total-canopy leaf area and photosynthetic capacity to fluctuations in leaf water potential, and thereby gain a better understanding of the limitations to whole-plant carbon gain for a drought-deciduous shrub under natural conditions of fluctuating soil water availability.

Methods

Canopy development was followed and concurrent measurements of photosynthesis and leaf conductance were made on individuals in a large, monospecific, experimental planting of *Encelia frutescens* Gray during the summer and fall of 1983. The experimental plot was located within the

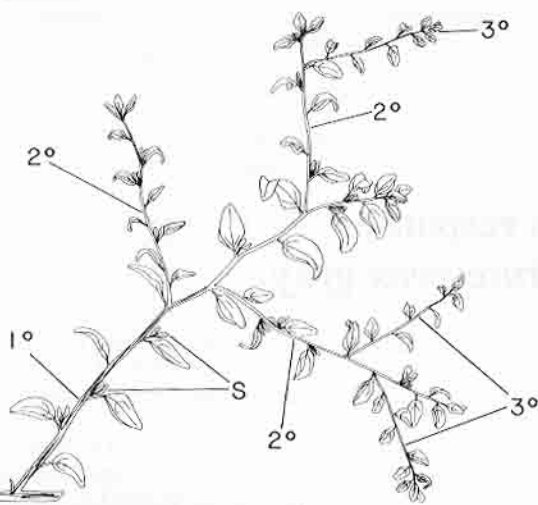


Fig. 1. Branching patterns of *Encelia frutescens* indicating the primary (1°) secondary (2°), and tertiary branches (3°) as well as the short shoots (S)

natural geographic range of the species at the Desert Botanical Garden in Phoenix, Arizona, USA (lat. 33°26' N, long. 112°01' W, 335 m elev.). Precipitation in this region is bimodal (Sellers and Hill 1974), and the observations were timed to coincide with the normal monsoon rainy season. Following a prolonged, natural drought period, which resulted in severe plant water stress, a new growth cycle was artificially initiated by a single, deep watering (equivalent of 75–100 mm precipitation) on July 27. This was similar to the soil water charge that would be expected in a wash microhabitat. During the rest of the observation period, the plants received no further supplemental watering.

Three plants were chosen for canopy dynamics measurements, and other plants of equivalent age and size were used for measurements of photosynthesis, leaf conductance, and leaf temperature. All plants had been transplanted to the experimental garden as seedlings, and were one year old when canopy measurements began. The mean height of the plants used for canopy measurements increased during the monitored growth period from 0.23 ± 0.02 m (mean ± 1 SE) to 0.41 ± 0.03 m, while mean shrub diameter increased from 0.29 ± 0.03 m to 0.58 ± 0.05 m, an increase of approximately 300% in ground area covered.

E. frutescens grows exclusively by repeated branching from axillary buds. Individual apical meristems were observed to have active lifespans of only a few weeks. Consequently, any sudden renewal of growth by the canopy results in the initiation of a distinct cohort of twigs. After a period of elongation and maturation, these twigs may give rise to yet another cohort of twigs, again by branching from axillary buds. Such synchronous twig cohorts are also natural divisions of leaf cohorts and were used as such in presenting data of canopy dynamics. In addition to distinguishing between temporal twig cohorts and their associated leaves, a qualitative distinction was made between longshoots exhibiting internodal stem elongation, and short-shoots producing axillary clusters of leaves.

Leaves produced in the spring and present at the beginning of the observation period had endured the early summer drought, and were designated Cohort O. The longshoots produced immediately after watering on July 27th were the 'primary twigs' (Fig. 1) and bore leaf cohort 1.

Subsequent leaf cohorts were borne on twigs of corresponding branch order. Leaf cohort 2 was thus borne on the secondary twigs, which were sidebranches of the primary twigs, and leaf cohort 3 was borne on tertiary twigs, the sidebranches of the secondary twigs. There was a minor fraction of twigs which was produced in synchrony with one of the above twig cohorts, but which arose from older, previously dormant axillary buds (i.e., a twig which was produced in synchrony with the tertiary twigs but was actually a secondary twig according to position). These twigs were very easily placed in the right age class based on clear differences in the degree of stem lignification.

In addition to the various categories of long-shoots, the shrubs produce numerous short-shoots. These bore two to four small leaves and lacked visible stem elongation. Although numerous, short-shoot leaves constituted, on average, approximately 10% of the total canopy leaf area. They were produced at the same time as the much larger long-shoot leaves (described previously), and did not have a longer lifespan. Thus, they do not represent the form of seasonal leaf dimorphism described by Orshan and Diskin (1968). For clarity, all short-shoot leaves produced in the summer were placed in a single cohort (Cohort 1 + 2s). Those short-shoot leaves produced when growth was reinitiated in the fall after a brief cessation of growth in late September were designated leaf cohort 3s.

Separate estimates were made of the number of twigs in each distinct age class on each sampling date, and also of the mean leaf area born by twigs of each age class. The product of these two canopy parameters gives the whole-shrub leaf area of a given leaf cohort, and when summed over all twig age classes yields the total canopy leaf area on a given date.

Total counts were made of the number of primary twigs on each bush on each of the eight sampling dates, and of the number of twigs in all age categories on two of the sampling dates. For the six sampling dates on which complete counts of all twig categories were not made, the shrubs were subsampled by choosing 2–3 major branches which arose from the ground level on each shrub. The number of twigs in each age category was counted on these branches, and a ratio was calculated between the number of primary twigs and the number of twigs in each higher branch category. These ratios were then multiplied by the total number of primary twigs on the bushes to obtain estimates of the total number of twigs of higher branches orders.

Mean leaf area per twig was followed for each twig category using repeated measurement of width and length of all leaves on a carefully chosen subsample of twigs. Leaf measurements were recorded under unique leaf-position codes, thus providing life table data of individual leaves as well as changing leaf areas per twig. At the beginning of the observation period each of the young shrubs consisted of 10–15 branches originating at a caudex near ground level. When growth was initiated, the primary twig cohort arose from axillary buds on these parental branches. On three such parental branches on each shrub, the primary twig cohort was subsampled for leaf demography by choosing the primary twig arising nearest to the plant caudex and every fourth primary twig moving distally along the parental branch. This gave 10–12 primary twigs per shrub for calculating leaf longevities and mean leaf area per primary twig. When the secondary twig cohort formed by side-

branching of the primary twigs, primary twigs from the above subsample were, in their turn, chosen as parental branches, and all side-branches arising on them were censused for leaf demography. This approach of choosing a small number of twigs from the previous cohort for parental branches and then sampling all side branches arising on them was repeated with each successive cohort. Total sample sizes were 30–40 long-shoots per cohort for a total of 146 long-shoots and 210 short-shoots bearing a total of over 2,000 leaves over the entire observation period.

To convert leaf width and length measurements into leaf areas, a multiple regression was determined for leaf area (cm^2) as a function of leaf width (mm), and length (mm). The regression was $\text{leaf area} = 0.04144 \times \text{leaf width} - 0.00503 \times \text{leaf length} + 0.00608 \times \text{leaf width} \times \text{leaf length} - 0.06735$ ($r^2 = 0.97$, $n = 204$).

There was generally a decrease in size of leaves with increasing branch order within a period of continuous growth. Since we were primarily interested in the dynamics of whole-plant photosynthetic capacity, leaf demographic data are presented in terms of leaf area rather than leaf number.

Net photosynthetic rates (A) in the field were determined using a clamp on CO_2 depletion technique described by Ehleringer and Cook (1980). The depletion time was 30 s for plants experiencing high water potentials and 40 s for plants experiencing low water potentials. Twigs with four or five attached leaves were placed in the chamber for each measurement. Previous laboratory work with this species had shown that twigs contributed little to gas exchange measurements when compared to their attached leaves, and, therefore, twigs were ignored in all calculations. Total projected leaf areas used for each measurement ranged from 4 to 10 cm^2 , and maximum chamber CO_2 differentials with the CO_2 depletion technique were about $30 \mu\text{l l}^{-1}$. Leaf conductance to water vapor was measured with a null balance porometer described by Forseth and Ehleringer (1980).

Plant water status was monitored by measuring xylem pressure potentials (assumed to be equal to leaf water potential) with a Scholander-type pressure chamber.

Leaf and air temperatures were measured using 36 gage copper-constantan thermocouples attached to a datalogger. These data were collected every minute and averaged over 30 min intervals. Reported leaf temperatures are averages of 3–9 leaves. Air temperature was measured with a shaded thermocouple located at mean canopy height.

Rainfall data were obtained from the records of the Desert Botanical Garden and represent the average of five rain gages located throughout the garden grounds.

Results

Prior to the beginning of canopy measurements on *Encelia frutescens* Gray in late July, no rainfall had been recorded during the months of May or June, and a single rainfall event of only 5 mm occurred on July 6th. This meant that foliage present at the beginning of this experiment had been produced during the previous spring, and had experienced a prolonged period of water stress. Most of the leaves which had been produced that spring (cohort 0) had already died (*E. frutescens* leaves are marcescent, withering without abscission), and the leaf area index was very low.

Within five days of the watering administered to study

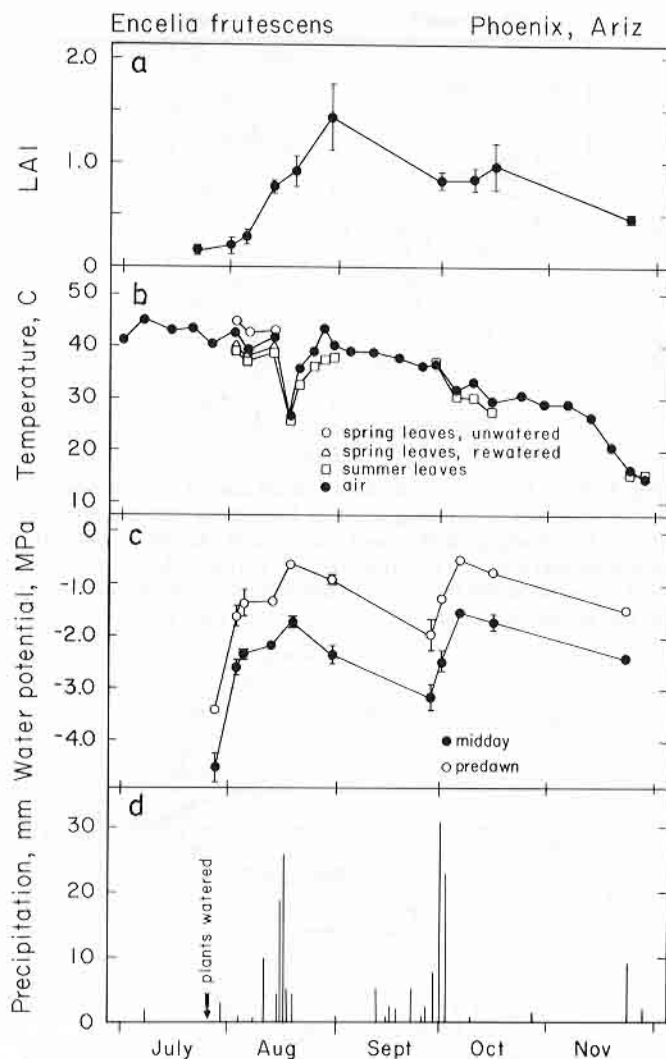


Fig. 2. a Leaf area index ($\text{m}^2 \text{ m}^{-2}$) based on ground area immediately under shrub canopy only. $n = 3$ shrubs for each point. b Maximum daily air and leaf temperatures during observation period. Unwatered spring leaves are measurements taken on plants which were not included in the supplemental watering on July 27th, and had water potentials similar to those shown prior to the July 27th watering in c below. Rewatered spring leaves and the newly produced summer leaves were measured on the same plant. $n = 3$ leaves in early August when three leaf types were measured, and 6–9 leaves on days when only summer leaves were measured. c Predawn and midday leaf water potentials for the plants observed for canopy dynamics. $n = 3$ twigs total, one each on three shrubs for each point. d Precipitation measured at the Phoenix Desert Botanical Garden. The supplemental watering which initiated growth in experimental plants on July 27 is indicated by an arrow. Error bars in A and B indicate one standard error of the mean. When one standard error was less than the radius of a point, the error bars have been omitted.

plants on July 27th, predawn leaf water potentials increased from -3.35 ± 0.07 to -1.6 ± 0.26 MPa (mean ± 1 SE, $n = 3$ shrubs), and midday values increased from -4.5 ± 0.2 to -2.5 ± 0.03 MPa. Leaf production also began almost immediately, but the first leaves produced were small even at maturity (Fig. 4b), and there was a lag period of about eight days before rapid production of new leaf area commenced (Figs. 2a, 3). Canopy development continued for

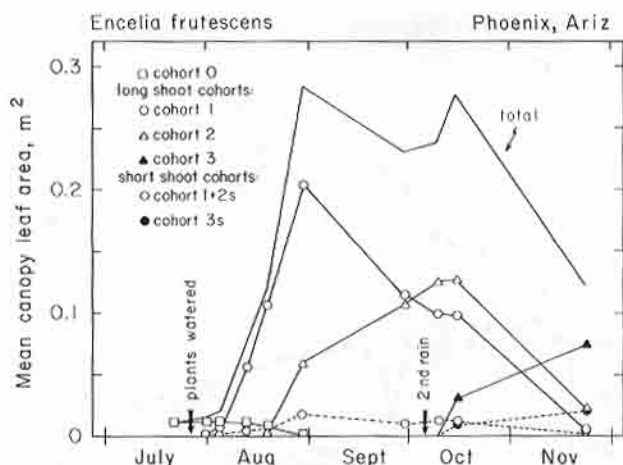


Fig. 3. Total leaf area of the entire shrub and of contributing cohorts of leaves. Solid lines indicate long-shoot leaf cohorts and dotted lines indicate short-shoot leaf cohorts. Arrows indicate the supplemental watering initiating the first period of leaf production, and the major storm (see Fig. 1d) which initiated the second period of leaf production observed. $n=3$ shrubs for each point.

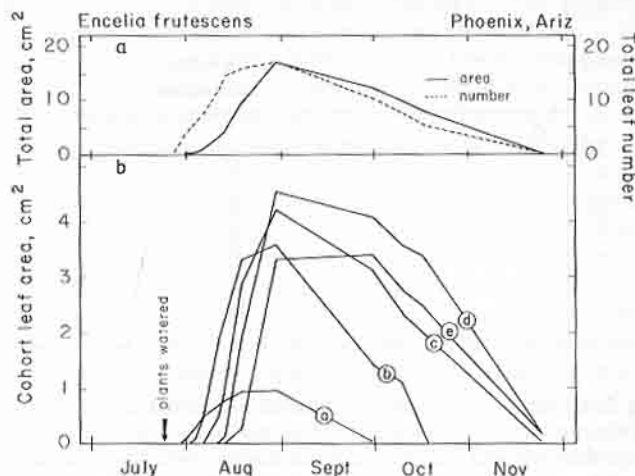


Fig. 4. a The average number of leaves and total leaf area present on each primary twig (leaf cohort 1). $n=10-12$ twigs on each of three shrubs bearing a seasonal total of 530 leaves. b The same leaves as in a, but subdivided by nodal position into five subcohorts on each primary twig. There was an average of 3.4 leaves per subcohort per twig. Total sample size was 31 twigs bearing a seasonal total of approximately 106 leaves per subcohort.

several weeks and did not reach maximum values until early September.

Changes in leaf water potential in response to meteorological events were often more rapid than the associated increases in canopy growth (following rain) or canopy reduction (following drought). There is a clear correspondence, however, between precipitation, leaf water potential, and leaf area index throughout the observation period (Fig. 2). A similar opportunistic response of leaf production to precipitation has been shown for *Encelia farinosa* Gray and *Encelia californica* Nutt (Ehleringer 1984a, 1984b), and for drought-deciduous shrubs in general (Bamberg et al. 1975; Szarek and Woodhouse 1977; Chabot and Hicks 1982).

The intricately branched shoot system of *E. frutescens*

formed a densely interwoven, hemispherical canopy 0.3–1.5 m high. The leaf-bearing twigs were numerous and slender, and reached lengths of 10–25 cm. The great density of twigs resulted in the many small leaves ($0.3-1.5 \text{ cm}^2$) being highly dispersed in the outer layers of the hemispherical canopy. The production of a new canopy after a period of drought stress was achieved by the production of a large number of new lateral twigs from previously dormant axillary buds. The buds were generally not visible during the period of drought stress, and were mostly located on the youngest twigs surviving the dormant period. New twigs were produced prolifically following rewetting, but many had short life expectancies. Only $53 \pm 9\%$ (mean $\pm 1 \text{ SE}$, $n=3$ shrubs with a total of 121 primary twigs) of the twigs initiated on July 27 (primary twigs) survived until early October. Presumably, such short-lived twigs serve to disperse the many small leaves for more efficient light capture at maximum leaf area index. Efficient display of leaf surface will be quite important for a species such as *E. frutescens* since the photosynthetic rate of individual leaves can be unsaturated even at full noon irradiances (unpublished data).

The apical meristems of vigorously growing twigs had short life expectancies, and were active in leaf production for only a few weeks. At the end of the leaf production phase, an apical meristem would either produce a terminal flower head or die. The main exception to this pattern was in the short-shoots produced during the first growth period. Many of these short-shoots produced additional leaves following the late September storms, and a small fraction even developed into elongated shoots at that time. Continued vegetative growth during a long, favorable growing period was achieved by the activation of lateral buds, in the same manner as the resumption of growth after a drought period. These lateral buds may or may not have undergone a prior dormancy period, depending on shrub water status and existing canopy development.

In addition to the initial, supplemental soil watering, there was greater than average precipitation during the summer of these observations, and the plants were not severely water stressed nor did they ever approach a fully leafless condition between July and December. The canopy was characterized by extensive leaf turnover, however, even within this continuously in-leaf period. Very few leaves survived from the first growth flush in early August to the final census at the end of November (Figs. 3 and 4).

Two distinct cycles of leaf production occurred during the experimental period. The first was initiated by watering on July 27th, and includes leaf cohorts 1, 2, and 1+2s (Fig. 3). Leaf production was complete in cohort 1 by the end of August and in cohort 2 by mid September. The small increase in leaf area in cohort 2 in early October was due entirely to further expansion of existing leaves. A second cycle of renewed leaf production was initiated by a major storm system at the end of September, and resulted in leaf cohorts 3 and 3s.

Even in the absence of severe water stress, many leaves had a lifespan of little more than thirty days. This is evident in the partial replacement of the newly produced primary twig leaf cohort by a secondary twig leaf cohort during the month of September (Fig. 3). In response to renewed soil water supply in late September, *E. frutescens* shrubs initiated renewed growth and leaf production, but did not appear to extend the lifespans of existing leaf cohorts. Thus,

there was considerable new leaf production in the fall even though total canopy leaf area declined.

The primary twigs and their leaves (leaf cohort 1) were produced in early August when leaf water potentials first recovered after prolonged water stress, and represented the most vigorous phase of leaf production observed. A more detailed analysis was made on the demography of the leaf cohort 1 than for leaf cohorts initiated later in the observation period. A population of 530 leaves produced by 31 primary twigs on three shrubs were censused throughout the leaf lifespans. Based on the final number of leaves produced in the season, the leaves of each twig were divided into five roughly equal groups by order of production (subcohorts a-e) (Fig. 4).

The activity of primary twig apical meristems in leaf production lasted for just over three weeks with a mean total of 17 ± 0.52 leaves produced per twig. The maturation of an individual leaf from first visibility (about 0.5 mm in length) to full size (10–20 mm in length) required about 14 days. The pattern of individual leaf initiation was very similar to that of leaf area development but preceded it (Fig. 4a). Leaf production within cohort 1 was completed just before the oldest leaves of cohort 1 began to senesce, and so there was no hidden turnover in Fig. 4 of leaf number and very little of leaf area. The maximum instantaneous mean leaf area per primary twig was reached on August 29th at 17.5 ± 2.1 cm² which was just slightly less than the integrated total of mature leaf area per twig of 18.4 ± 2.18 cm². Since 1) the younger leaves were also the larger ones (within a given long-shoot, but not across twig age categories) and 2) mortality followed a rough age progression up the stems, leaf number declined faster than did leaf area.

Leaf size at maturity increased from the first up to the fourth subcohort, and then decreased in the fifth. The most conspicuous size difference, however, was found when comparing the first sub-cohort, which had very small mature leaf sizes, with the other four sub-cohorts. This effect of first node positions on leaf size was far less conspicuous in the secondary twigs, and it may have been a result of prior water stress on the dormant axillary buds. Leaf life expectancy increased with node position on each twig until the terminal node position, which was often included in tip die-back, especially when a terminal flower head had been produced.

These field-grown plants maintained slightly higher photosynthetic rates at low leaf water potentials than predicted by previous laboratory work with potted plants (7 vs $2 \mu\text{mol m}^{-2} \text{s}^{-1}$ at -4.0 MPa) (Comstock and Ehleringer 1984), but were otherwise very similar (Fig. 5a). The very high leaf conductance to water vapor measured on watered plants resulted in a high latent heat flux and effectively lowered leaf temperature to 3–5°C below air temperature throughout the day. In contrast, water stressed leaves had a much lower leaf conductance to water vapor and leaf temperatures 1–2°C above air temperature (Fig. 5c). The higher leaf conductances to water vapor resulting in reduced leaf temperatures may have been important allowing the plants to maintain moderate-high net photosynthetic rates in the field, since temperatures of water stressed leaves were high enough to cause an inhibition of photosynthesis (Comstock and Ehleringer 1984).

As the first new leaves approached full expansion, moderate-high leaf photosynthetic rates were achieved rapidly.

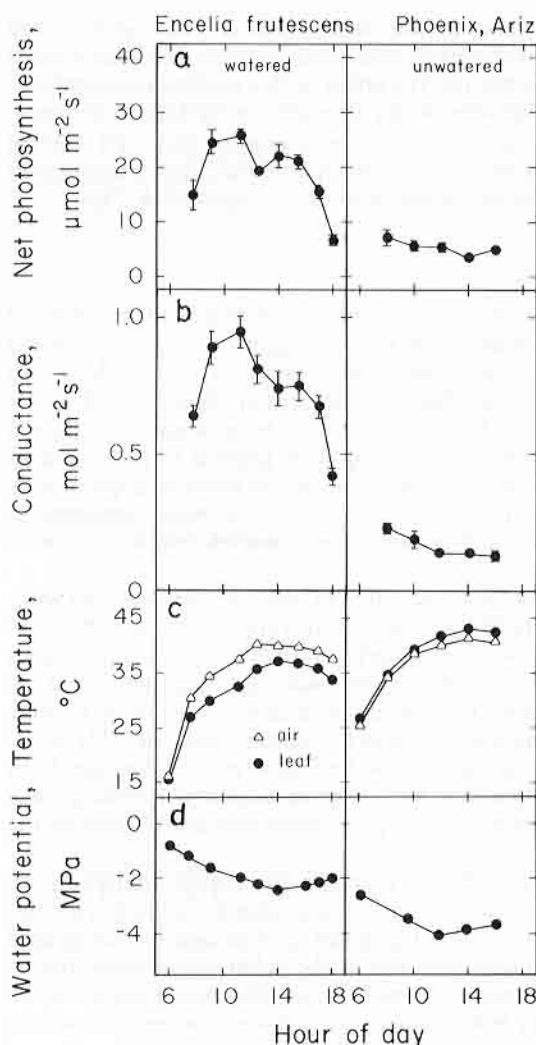


Fig. 5a–d. Diurnal courses of a net photosynthetic rates, b leaf conductances to water vapor, c leaf and air temperatures, and d leaf water potential. Watered leaves are summer leaves measured on August 30th, and unwatered leaves are spring leaves measured on August 15th. On both days the leaf to air water vapor concentrations varied from 18 mbar bar⁻¹ in the early morning to 72 mbar bar⁻¹ at midday. Error bars indicate one standard error of the mean, and were omitted when this was less than the radius of a point. The maximum air temperature was one degree warmer on August 15th. $n=9$ twigs for watered leaves and $n=4$ twigs for unwatered leaves during measurements of photosynthesis and leaf conductance, $n=6$ leaves for leaf temperature and $n=2$ twigs for leaf water potentials.

Mean midday rates (daily maxima) between 25 and $35 \mu\text{mol m}^{-2} \text{s}^{-1}$ were measured repeatedly between August 10 and August 30 (Fig. 5). This was consistent with the observation that development of leaf photosynthetic capacity does not lag behind leaf expansion (Chabot and Hicks 1982; Thomas and Stoddart 1980). Since maximal photosynthetic rate per unit leaf area was reached long before maximum total leaf area, the rate of increase in total leaf area at high leaf water potential was a close measure of increasing whole-plant photosynthetic capacity.

When watered in late July, the previously stressed spring leaves (cohort 0) increased in size by 20–30%, a phenomenon sometimes associated with regreening after stress (Thomas and Stoddart 1980). Both net photosynthesis and

leaf conductance greatly increased after watering, although not quite to the levels measured in newly produced foliage on the same plants. The effect of this intermediate leaf conductance (between water stressed spring leaves on unwatered plants and newly produced summer leaves on watered plants) can be seen in the intermediate leaf temperatures of rewatered spring leaves in early August (Fig. 2b).

Discussion

Threshold leaf water potentials triggering sudden, rapid leaf loss were not observed. Instead, canopy reductions occurred continuously with decreasing predawn and midday leaf water potentials. Such a relationship between leaf water potential and leaf area has also been shown for *Encelia farinosa* (Ehleringer 1984b). This gradual leaf area reduction results in a full 'evasion' by the active canopy of only the most extreme levels of water stress, while considerable leaf area was still present at intermediate leaf water potentials.

Photosynthetic capacity per unit leaf area was also without a threshold response to leaf water potential in this species (Comstock and Ehleringer 1984). Osmotic adjustment in response to decreasing leaf water potential permitted net photosynthesis to decrease in a linear fashion as midday leaf water potential decreased to less than -4.0 MPa. Although changes in soil and leaf water potential caused both total leaf area and physiological capacity to change in a similar direction, these parameters did not change at the same relative rates.

It was possible to estimate the relative limitations to whole-plant seasonal carbon gain due to 1) the physiological impairment of existing leaf area caused by suboptimal leaf water potentials, and 2) the submaximal development of total canopy leaf area (Fig. 6). This was done using the total canopy leaf area (Fig. 3), leaf water potential observed in the field through time (Fig. 2c), and the relationship of net photosynthesis to leaf water potential from Comstock and Ehleringer (1984). Light-saturated, instantaneous photosynthetic rates rather than integrated daily totals were used to scale the carbon-gaining efficiency of existing leaf area, and so whole plant carbon gain is presented as a relative value. The small amount of self-shading within the canopy did not generate substantial errors in these analyses, because the maximum mean leaf area index never exceeded 1.5, and prolific twig production prevented any leaf area clumping. Skies were predominantly clear with some late-afternoon thundershower activity throughout the study period.

The estimate of realized carbon gain can be compared to the simulated carbon gain for plants with continuously maximal canopy development. The relatively long period (up to five weeks) required for full canopy regrowth after prolonged drought caused a calculated 27% decrease in potential, whole-plant carbon gain between July 26 and October 15. It is instructive to compare this cost of the drought-deciduous leaved habit to the construction costs of canopy replacement. The specific leaf weight of *E. frutescens* is 90.7 ± 6.4 g dry wt m^{-2} . If the biomass of the leaf-bearing twigs is included, there is an investment of 154 g plant dry wt m^{-2} leaf area. Using a median literature value of 1.5 g glucose required to build 1 g of deciduous leaf (Penning de Vries et al. 1974; Miller and Stoner 1979; Merino et al. 1982) and a daily carbon gain measured for *E. frutes-*

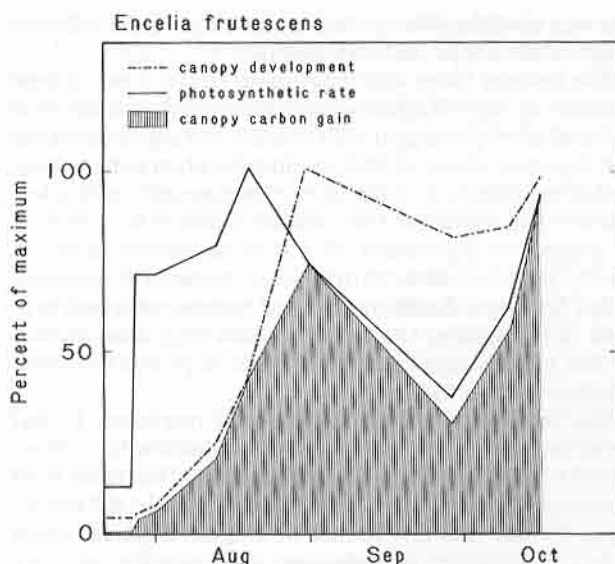


Fig. 6. Canopy development (total canopy leaf area) and light-saturated photosynthetic rate (predicted from midday leaf water potentials using the equation from Comstock and Ehleringer (1984), are shown as a percentage of their maximal values throughout the study period. These relativised curves can also be taken as the hypothetical pattern of whole plant carbon gain if first photosynthesis and then canopy development are held constant. The shaded region is an estimate of the actual pattern of whole plant carbon gain through the season, and represents the product of the two relativised parameters.

ens in August of 35.4 ± 1.6 g glucose m^{-2} day $^{-1}$ (mean ± 1 SE, $n=6$ diurnal courses of photosynthesis using 4–6 twigs each day), we calculate that under high leaf water potentials, a unit of canopy foliage could pay for itself in as little as 7 days. In contrast, the observed rate of canopy regrowth resulted in a calculated carbon loss of 22 full-canopy-days of photosynthesis. Total construction costs include the woody thickening of major branches and increased root growth which may double or triple the construction costs explicitly considered above.

The quantitative estimate of surface area limitations to whole-plant carbon gain during the leaf-flushing period is sensitive to assumptions concerning the dynamics of soil moisture availability, and possible tradeoffs between early and late season use of a finite soil water pool. Considerable evidence exists, however, to support the notion that a leaf-flushing delay in whole-canopy photosynthetic capacity can result in the loss of nonrecoverable soil water resources. For example, soil surface evaporation has been shown to extensively deplete soil water reserves in several desert systems (Evans et al. 1981). Although deep soil water (below 0.3 m) left by major storms may be less prone to surface evaporation (Noy-Meir 1973), even these pools may be utilized by neighboring competitors. Competition for soil water has been shown to effect the water status and productivity of several desert species (Fonteyn and Mahall 1981; Robberecht et al. 1983; Ehleringer 1984b).

In contrast to the surface-area limitation to whole-plant carbon gain which occurred during the period of leaf flushing, decreased photosynthetic capacity was the major limitation during the early phases of drought (Fig. 6). This indicates that seasonal carbon gain in *E. frutescens* was not curtailed by early leaf death. Total surface area was not

substantially reduced until the soil water which could be utilized within the physiological tolerances of photosynthesis had been thoroughly exploited. A relatively small amount of water is actually left in a sandy soil at water potentials equal to the predawn leaf water potentials (-2.0 to -3.0 MPa) at which extensive reductions in total leaf area occurred (Campbell and Harris 1981). Although many evergreen desert shrubs can endure much lower water potentials than *E. frutescens* while remaining active, their photosynthetic rates at such low water potentials are generally very low (MacMahon and Schimpf 1981; Ehleringer and Mooney 1983).

Physiological tolerance to low water potentials may have more to do with a maintenance of a partial canopy leaf area through times of stress than it does with making substantial contributions to net growth increments under stress conditions. Differences in a plant's physiological tolerance to leaf water potential among different drought-deciduous species may therefore be related to the minimum leaf water potentials which are likely to develop within a growing season. Canopy leaf area maintenance through temporary drought periods within the growing season would permit higher rates of canopy carbon gain following soil water recharge than would occur with a renewed leaf-flushing from a fully dormant state.

The nearly complete recovery of photosynthesis in mid-October (Fig. 6) assumes a full recovery of photosynthetic capacity in aging leaves with recovery of leaf water potential to high values. This is not an unreasonable assumption as the leaves of several desert plants have been shown to suffer little decline in photosynthetic rate with age (Syvertsen and Cunningham 1977; Mooney et al. 1981). This contrasts with the response of plants from many other communities, and may be related to the predictably high light environment and low leaf area indices of desert ecosystems. The limited field data available for *E. frutescens* indicated that major recoveries do take place in previously stressed leaves when recovery of high leaf water potential takes place, but not to the full capacity expected of newly produced leaves at the same leaf water potential.

This study has shown that the seasonal carbon gain of a drought-deciduous leaved shrub was not curtailed by leaf-area reduction in the early stages of drought stress, but by soil-water depletion and declining physiological capacity. In habitats with ephemeral soil moisture availability, the speed at which renewed soil-water resources can be utilized will be important. Canopy growth responses of *E. frutescens* during a summer growing season were sufficiently slow that major reductions in seasonal carbon gain were incurred. It is likely that considerable variation exists among drought-deciduous leaved species in the time required for canopy renewal. Morphological and physiological traits which permit rapid leaf flushing, and constraints which limit the rate of canopy renewal are important aspects of the drought-deciduous habit which deserve future study.

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