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

J.P. Comstock, T.A. Cooper, and J.R. Ehleringer
Department of Biology, University of Utah, Salt Lake City, UT 84112, USA

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, Salixera 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

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 CO₂ (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 Bent., Chrysothamnus paniculatus (Gray) Hall, Encelia farinosa Gray, Encelia virginensis A. Nels., Gutierrezia microcephalum (D.C.) Gray, Gutierrezia sarothrae (Pursh) Rusby, Hymenoclea monogyra Torr. and Gray., Hymenoclea sal soda T. & G., Parophyllum gracile Bent., Psilostrophe cooperi (Gray) Greene, Salazarix 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:

$$A_tS_t = A_sS_s + A_I S_I$$

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

$$A_I = (A_s S_s - A_t S_t)/S_I$$

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 CO$_2$ 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 season's 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