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Effect of variations in leaf size on morphology and photosynthetic rate of twigs

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Abstract. CO_2-exchange rates were measured in the dark and at high irradiance on the current season's twigs (the leaf-bearing portion of the stem) of 10 desert species with twigs capable of positive net assimilation of atmospheric CO_2, and for 28 species (some from warm desert communities and others from moderate elevation riparian communities bordering the deserts) whose twigs never exhibited positive net assimilation rates. Dark respiration rate of twigs was found to be strongly correlated with leaf size. Some of the causes of this correlation were revealed by harvest data on the current season's shoots of the same 28 species. As leaf size increased, total mass shoot^{-1} increased and twig diameter increased. This resulted in a decrease in twig surface volume^{-1} and an increase in twig respiration rate on a surface area basis. Regardless of the magnitude of the respiration rate in the dark, however, the rate of CO_2 efflux from twigs which did not achieve positive net photosynthesis was reduced to near zero in the light. This was attributed to photosynthetic recycling of the respired CO_2. By recycling endogenous CO_2 derived from mitochondrial respiration, the twigs of large-leaved species could achieve rates of twig gross photosynthesis comparable to those of desert species specialized for positive net uptake by the twigs. These observations suggest that scaling relationships between leaf and twig dimensions may have a strong influence on the kind of photosynthetic activity developed in twig tissues. Positive net assimilation of atmospheric CO_2 by twigs may generally be restricted to species with small leaves, small twig diameters and low rates of endogenous CO_2 production. Since leaf size varies systematically along aridity gradients, some of the observed distribution patterns of species with positive net assimilation in twigs (they are largely restricted to arid and semi-arid environments) may be caused indirectly through allometric relationships between leaves and twigs.

Key-words: Allometries, CO_2, desert recycling, diameter, leaf, photosynthesis, twig respiration

Introduction

Several studies have reported that the twigs and stems of many desert species are capable of high rates of positive net photosynthesis (Adams & Strain, 1968; DePuit & Caldwell, 1975; Szarek & Woodhouse, 1978; Osmond *et al.*, 1987; Comstock, Cooper & Ehleringer, 1988; Comstock, 1989). Although this appears to be a common feature in floras of arid and semi-arid regions, it has not been reported from more mesic communities and this association with aridity has not yet been adequately explained. We hypothesized that some of the factors favouring positive net photosynthesis in twigs of arid-land shrubs are related to selective pressures acting initially on leaf size in different environments. Selection for leaf size may indirectly influence twig photosynthetic physiology because: (1) twig photosynthesis may be influenced by twig surface volume^{-1}; (2) twig surface volume^{-1} is a direct function of twig diameter; and (3) twig diameter may be linked to leaf size by strong allometric relationships.

The twigs of most woody species contain chloroplasts in the cortical layers (Scott, 1907; Cannon, 1908; Schaedle, 1975) and these chloroplasts have proven to be capable of photosynthetic electron transport (Schaedle, Iannaccone & Foote, 1968; Nedoff, Ting & Lord, 1985) and starch synthesis (Pearson & Lawrence, 1958; Strain & Johnson, 1963). Positive net assimilation of atmospheric CO_2 does not usually occur, but the apparent respiration rate measured in the light is much lower than that measured in the dark (Strain & Johnson, 1963; Mooney & Strain, 1964; Kreidemann & Buttrose, 1971; Keller, 1973; Schaedle, 1975; Foote & Schaedle, 1978; Parker, 1978; Coe & McLaughlin, 1980). ^{14}C labelling studies have supported the interpretation that the reductions in CO_2 efflux are due to light-dependent increases in carboxylation rates (Zelawski, Riech & Stanley, 1970; Wiebe, Al-Saadi & Kimball, 1974; Shepard, 1975).

The positive net photosynthesis by the twigs of many desert shrubs contrasts strongly with the exclusive recycling of respiratory CO_2 reported in mesic shrubs and trees. The superficial tissues of twigs which achieve positive net photosynthesis are, in some respects, anatomically similar to leaf tissues. The specializations include (1) a high stomatal density in the epidermis; (2) highly developed intercellular airspaces in the outermost regions of the cortex which may develop as a palisade parenchyma; and (3) a delay of periderm formation (Cannon, 1908; Gibson, 1983). All these features facilitate diffusional uptake of atmospheric CO_2.

The rate of assimilation of atmospheric CO_2 varies with stomatal conductance and the biochemical capacity for carboxylation. Photosynthetic recycling, on the other hand, may often be limited by the endogenous rate of CO_2 production in mitochondrial respiration. Since uptake of atmospheric CO_2 as well as light interception is inherently a surface area phenomenon, it facilitates comparisons of the two CO_2 sources if the rate of respiratory CO_2 production is considered on a surface area basis also. An important difference between twigs (the leaf-bearing portion of the stem) and leaves is that while the latter is a planar organ in which surface to volume relationships are often independent of leaf length and width, twigs are cylindrical organs and the surface volume^{-1} is inversely proportional to twig diameter. Twig respiration rate on a surface area basis, therefore, can increase with either an increase in the respiration rate unit^{-1} mass of twig tissue at a constant twig diameter, or with an increase in twig diameter and a constant respiration rate unit^{-1} mass. The effect of twig diameter on respiration rate and hence the potential importance of photosynthetic recycling, is also of ecological interest because there are large differences in twig diameter among different species and different ranges of twig diameters might be found in different plant communities.

Leaf size is a morphological trait known to vary substantially between mesic communities (large leaves) where instances of positive net photosynthetic activity in woody twigs have not been reported, and arid communities (small leaves) where positive net twig photosynthesis is a common feature (Daubenmire, 1959; Whittaker & Niering, 1975; Givnish, 1984). The reasons for this gradient in leaf size may be complex, but one commonly accepted advantage of small leaves in arid environments is that they will tend to remain near air temperature and are less likely to overheat when water availability is limiting (Gates, Aldefer & Taylor, 1968; Parkhurst & Loucks, 1972; Smith, 1978). In more mesic sites, transpirational cooling can reliably moderate leaf temperatures on hot, bright days.

To investigate the relationships between leaf size, twig size, and twig photosynthetic behaviour, harvest data were collected and CO_2-exchange rates were measured in the dark and under high irradiance in 38 species of semi-arid and adjacent riparian communities. It was our aim to determine: (1) if variation in leaf size among species was a good predictor of twig diameter and surface volume^{-1}; (2) if this resulted in a strong relationship between leaf size and twig respiration rates; and (3) whether species whose twigs are capable of positive net assimilation of atmospheric CO_2 are also characterized by very low twig dark respiration rates per unit surface area.

Materials and methods

To obtain a wide range in leaf size among species, four arid-land sites were chosen that differed substantially in annual moisture availability. Two of the sites were located in warm desert plant communities. The first (Oatman site), was in Silvercreek Wash 9 km west of Oatman, Arizona (latitude 34° 57′N; longitude 114° 25′W, elevation 785 m). The vegetation was transitional between the Mohave Desert and the Lower Colorado Valley portion of the Sonoran Desert (Shreve & Wiggins, 1964). The second study area (JTNA site), was in the Joshua Tree Natural Area 16 km north of Littlefield, Arizona (latitude 37° 01′N; longitude 113° 50°W, elevation 1028 m) and was typical of south-eastern Mohave Desert vegetation. A third site (Cove Wash site), 8 km east of Enterprise Reservoir, Utah (latitude 37° 30′N; longitude 113° 45′W, elevation 1676 m), was in a semi-arid (Pinyon-Juniper) woodland. The fourth site (Red Butte Canyon site) was located in Red Butte Canyon Natural Area 4 km east of the University of Utah, Salt Lake City, Utah (latitude 40° 50′N; longitude 111° 45′W, elevation 1650 m). This site supported a wide riparian belt of broad-leaf deciduous trees dominated by *Acer negundo* L. All four sites were situated in large drainages, but the desert drainages ran only briefly, following major storms, while the Cove Wash and Red Butte Canyon sites had water flowing above ground all year. The species sampled at each site are listed in Table 1 along with the average leaf size on current season shoots.

All plants sampled were growing in direct sunlight. Unless otherwise stated, all measurements were taken on current season's long shoots (leaves plus twigs) in the spring and summer of 1988. The four sites differed in the severity and longevity of winter temperatures and thus reached full canopy development at different times during the summer. An effort was made to sample only mature tissues, defined as any region of the current season shoot in which internodal elongation and leaf expansion were complete. Measurements were taken in the desert sites in late April and early May as the shrubs approached full canopy development, and before summer drought initiated any leaf senescence. Cove Wash was sampled in late May and June and Red Butte Canyon in June and July.

The photosynthetic behaviour of the twigs of

Table 1. All 38 species sampled listed for each study site. Whether the twigs of each species were capable of positive net assimilation (A) incorporating atmospheric CO_2 during photosynthesis is also indicated. Nomenclature follows Munz (1968) and Welsh *et al.* (1987). Leaf mass refers to dry weight.

+Net A		Mean leaf size	
yes/no	Species	cm^2	mg
Site 1			
No	*Ambrosia eriocentra* (Gray) Payne	3·80	33·9
Yes	*Baccharis sergiloides* Gray	1·86	12·2
Yes	*Bebbia juncea* (Benth.) Greene	1·21	10·4
No	*Brickelia californica* (Gray)	3·89	10·7
No	*Chilopsis linearis* (Cav.) Sweet	4·42	52·4
No	*Hymenoclea monogyra* (Torr.) Nutt.	0·77	10·5
Yes	*Hymenoclea salsola* (Torr.) Nutt.	0·60	8·6
Yes	*Menodora scabra* Gray	0·56	5·9
Yes	*Stillingia linearifolia* Wats.	0·52	4·7
Yes	*Stephanomeria pauciflora* (Torr.) Nutt.	1·09	9·0
Site 2			
No	*Ambrosia dumosa* (Gray) Payne	0·45	4·5
No	*Encelia virginensis* A. Nels.	1·57	13·3
Yes	*Hymenoclea salsola* (Torr.) Nutt.	0·42	5·2
Yes	*Gutierrezia microcephalum* (DC.) Gray	0·46	5·8
No	*Prunus fasciculata* (Torr.) Gray	0·17	1·9
No	*Salvia dorrii* (Kell.) Abrams	0·59	5·8
Yes	*Senecio douglasii* DC.	1·81	15·3
Site 3			
No	*Amelanchier utahensis* Koehne	2·49	26·6
Yes	*Arenaria macrodenia* Wats.	0·22	3·7
No	*Artemisia tridentata* Nutt.	0·48	4·2
Yes	*Chrysothamnus nauseosus* (Pallis) Britt.	1·14	10·4
No	*Fraxinus anamola* Torr. ex Wats.	12·33	112·7
No	*Fraxinus velutina* Torr.	50·49	374·0
No	*Quercus gambellii* Nutt.	30·26	251·3
No	*Quercus turbinella* Greene	7·84	98·1
No	*Rhus trilobata* (Nutt.) Gray	7·08	49·8
No	*Ribes velutinum* Greene	0·80	12·0
No	*Rosa woodsii* Lindl.	23·81	161·4
No	*Salix* sp.	8·66	70·9
Site 4			
No	*Acer grandidentatum* Nutt.	30·22	186·0
No	*Acer negundo* L.	72·39	329·4
No	*Betula occidentalis* Hook	9·71	60·1
No	*Ceanothus velutinus* Dougl.	25·99	292·1
No	*Cornus sericea* L.	23·67	183·8
No	*Physocarpus malvaceus* (Greene) Kuntz	14·42	86·8
No	*Populus fremontii* Wats.	72·55	732·1
No	*Populus tremuloides* Michx.	12·81	78·1
No	*Prunus virginiana* L.	30·03	184·6
No	*Sambucus caerulea* Raf.	59·75	355·0
No	*Sorbus scopulina* Greene	48·12	343·6

each species was studied in the field with a portable gas-exchange system (model LI-6200, LI-COR Instruments, Lincoln, Nebraska, USA). Measurements were depletion based and null balance for CO_2 and water vapour exchange, respectively. For each species, three twig replicates were prepared for gas-exchange measurements by excising all the leaves and any immature terminal twig portions with a razor. Each twig replicate consisted of one to four twigs depending on twig size such that total twig area in the measurement cuvette was held constant across species. High-irradiance CO_2-exchange rates were first measured after a 30-min period (following leaf removal) during which the twigs were left in full, direct sunlight. Irradiance during this first measurement was $\geq$ 1·0 mmol photons (400–700 nm) m^{-2} s^{-1} from natural sunlight. Following this high-irradiance measurement, the twigs were loosely wrapped in aluminium foil to reduce illumination to near darkness. After a 30-min period the foil was removed and the dark CO_2-exchange rate (dark respiration) was measured. Twigs were shaded continuously while being placed in the cuvette and during the measurement the cuvette was wrapped in a heavy cloth. Gross photosynthesis was calculated as the difference between high-irradiance and dark CO_2-exchange rates.

Some wound respiration may have been generated by the excision of leaves. Comstock & Ehleringer (1988) did not find any increase in respiration rate during a 24-h period following similar treatments of leaf removal in *Hymenoclea salsola* (Torr) Nutt. Other authors, however, have reported that increased respiration can occur (Brayman & Schaedle, 1982). Although it was not practical to attempt repeated 24-h controls of dark respiration under field conditions for the many species involved in this study, the light and dark measurements were, on several occasions, repeated during the initial 3 or 4 h following leaf excision. Both dark respiration rate and the difference between respiration rate in dark and light were stable during this period provided that the tissues measured were past the stage of rapid expansion. It was concluded that wound respiration was a small quantity relative to the fluxes measured. It may nonetheless have been a small source of unexplained variance in the results.

Twig and leaf biomass, projected area and dimensions were measured for all species. Three current season's shoots from the same individuals used for gas-exchange measurements were harvested for each species and separated into leaf and twig components. Projected areas of both leaves and twigs were measured in The Mobile-Mouse field lab with a leaf area meter (model LI-3200, LI-COR Instruments, Lincoln, Nebraska, USA). Leaf number and stem length were recorded. Dry weights of all samples were determined after 3 days in a drying oven at 80 °C.

When the width of a sample object decreases below 2–3 mm, accurate measurement of projected area becomes progressively more difficult because of edge effects and the limit to resolution of most available instruments. It was found that greatly improved accuracy of the leaf area meter could be obtained by the use of appropriate calibration standards. Combs were made from paper of known area per mass (m^2 kg^{-1}). Each comb had teeth of a specific width which could be matched to the width of the leaves that were to be measured. The paper standards were sprayed with photomount adhesive and sandwiched between two layers of mylar to hold them flat while passing through the area meter. Although the mylar itself does not register at all passing through the meter, it does filter the light detected by the sensor and alter the calibration. The leaf samples, therefore, had to be placed in similar mylar sandwiches as the standards during measurement, a convenient technique when measuring many small leaves. Use of these realistic calibration standards allowed accurate measurement of leaves with mean widths as narrow as 0·7 mm. The measurements were checked by comparing the LiCor 3200 readings of very narrow leaves (*Porophyllum gracile* Benth., mean leaf width = 0·8 mm, and *Gutierrezia microcephalum* (DC.) Gray, mean leaf width = 0·7 mm) with area estimates made using a dissecting microscope with an ocular micrometer to determine mean leaf width. Area estimates with the two techniques agreed within 5%. As the calibration combs approached 0·5 mm mean width, unacceptable deviation from linearity was observed. No leaves encountered during this study were out of range of accurate measurement using the above calibration technique. No difference in the calibration of the instrument for projected area was found using planar *vs* cylindrical standards.

Twig mass per volume (kg m^{-3}) was calculated from measurements of total twig mass, twig length and total twig projected area. The mean diameter of the twig was calculated as the projected area divided by twig length. Twig volume was then calculated assuming a right circular cylinder equal in length to the twig and with a uniform diameter equal to the mean twig diameter. Since the actual twigs tapered from base to tip, the assumption of uniform diameter causes a slight underestimate of volume and a consequent overestimate of mass volume^{-1}. Integrating the expected volume of cylinders with different rates of taper, it was calculated that the error in volume estimates caused by assuming a uniform mean diameter is less than 4% even with a 50% decrease in diameter between the base and tip of the cylinder.

Results

It was our intent to examine allometric relationships between leaves and twigs that might influence the development of net photosynthetic activity in twigs. The analyses of morphology were inititally limited to those species that lacked positive net photosynthetic activity in the twigs. This was done because most species with positive net photosynthetic capacity in twigs were already known to have small leaves. We wished to take a conservative approach to analysing the effect of allometries on twig physiology and exclude consideration of the possible effects of specialized twig anatomies.

Among the 28 species whose twigs did not exhibit net assimilation of atmospheric CO_2, variation in leaf size, whether expressed as leaf mass or projected area, was strongly, positively correlated with the total leaf mass (Fig. 1a) and total mass (leaf plus twig) (Table 2) of the current season's shoots. The total leaf mass, which represents the minimum load to be borne by the twigs, can be expressed as the product of three factors: leaf size; leaf number per twig length (leaf frequency); and total twig length. Among the studied species, leaf size varied more than 100-fold while leaf frequency varied only 10-fold and twig length by a factor of 7. Due to the much greater range in values for leaf size than leaf frequency or twig length, variation in leaf size was the most important factor determining total leaf mass. The strong negative correlation between leaf frequency and leaf size (and, less importantly, between leaf frequency and twig length), results in the observed negative correlation between leaf number cm^{-1} and total leaf mass ($r = -0{\cdot}73$; Table 2).

A linear regression of twig diameter on total leaf mass explained a large fraction of the variance in twig diameter ($r^2 = 0{\cdot}78$). Addition of any one or two of the component factors of total leaf mass (leaf size, leaf frequency and twig length) into a multiple regression model already containing total leaf mass did not significantly improve the model's explanation of twig diameter and only the partial regression coefficient for total leaf mass on twig diameter was ever significant.

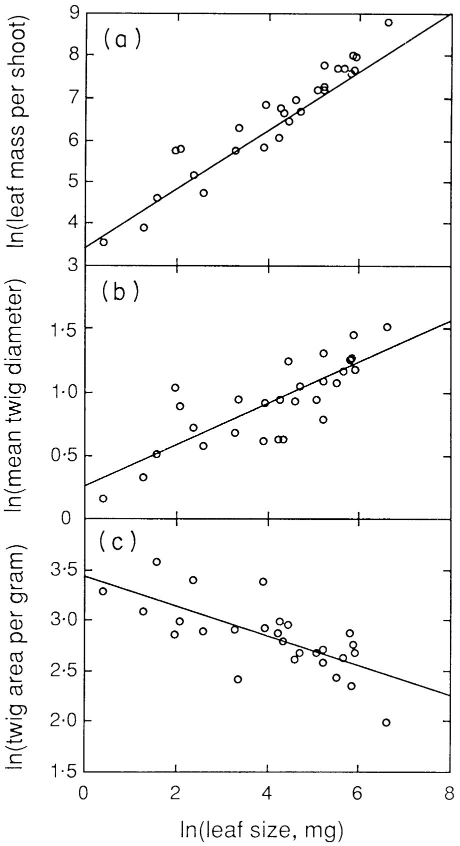

Fig. 1. Morphological relationships between total leaf mass, individual leaf size, twig diameter and twig surface volume^{-1}. Only the 28 species that did not exhibit net assimilation of atmospheric CO_2 are included in the analyses. (a) The relationship among species between the average mass (mg dry weight) of an individual leaf and the total leaf mass (mg dry weight) per shoot. The line is the least-squares best fit to the data: $\ln(y) = 3{\cdot}39 + 0{\cdot}76 \times \ln(x)$ ($r^2 = 0{\cdot}92$; $P < 0{\cdot}001$). (b) The relationship among species between the average mass (mg dry weight) of an individual leaf and the mean twig diameter (mm) of the current season shoots. The line is the least-squares best fit to the data: $\ln(y) = 0{\cdot}25 + 0{\cdot}16 \times \ln(x)$ ($r^2 = 0{\cdot}65$; $P < 0{\cdot}001$). (c) The relationship among species between the average mass (mg dry weight) of an individual leaf and the twig projected area per dry mass, cm^2 g^{-1} of the current season's shoots. The line is the least-squares best fit to the data: $\ln(y) = 3{\cdot}42 - 0{\cdot}15 \times \ln(x)$ ($r^2 = 0{\cdot}51$; $P < 0{\cdot}001$).

One additional variable was found, twig mass volume^{-1}, which significantly improved the explanation of twig diameter ($r^2 = 0{\cdot}86$) when included in a multiple regression with total leaf mass as the other independent variable. A given load could be borne by twigs composed of low density materials and possessing larger than expected (from purely mass loading considerations) diameters, or by twigs composed of high density materials and possessing smaller than expected diameters. Since twig mass volume^{-1} had a very low correlation with total leaf mass ($r = -0{\cdot}08$; NS) or leaf size ($r = -0{\cdot}06$; NS; Table 2), the main result of this effect, which was small compared to the effects of leaf size and number, was to add to the unexplained variance in the relationships between leaf size, twig diameter and twig physiology.

Leaf size alone, since it largely determined total leaf mass and was even highly correlated with the other contributing factors (leaf frequency and twig length), was also a very accurate predictor of twig diameter (Fig. 1b) and mean twig diameter increased four-fold with increasing leaf size in this dataset. From geometry, the surface volume^{-1} for a cylinder is inversely proportional to its diameter and, as expected, twig projected area mass^{-1} decreased significantly as leaf size and twig diameter increased (Fig. 1c).

The relationship between twig diameter and twig respiration rate was statistically significant only when respiration was expressed on a surface area basis (Table 3, Fig. 2a). When twig diameters increased from 1·2 to 4·5 mm (ln [twig diameter, mm] = 0·2 to 1·5) the observed increase in twig respiration using the regression equation from Fig. 2a was three-fold. This observed increase was only 8% greater than the increase which would be predicted based on changing surface:volume relationships over that range of twig diameters when holding respiration rate unit^{-1} volume constant. When twig respiration rates were regressed against twig diameter (Fig. 2a), twigs which achieved positive net assimilation tended to fall below the line, especially at larger twig diameters. All species appeared to fall on the same regression line, however, when twig respiration was plotted against leaf size (Fig. 2b). Twig diameters in these specialized species were relatively large for the associated low levels of leaf area development. It is possible that low levels of leaf area development

Table 2. Correlation matrix of selected morphological parameters of the shoots. The analyses include only the 28 species whose twigs did not achieve positive net assimilation of atmospheric CO_2 in the light. All masses refer to dry weight. All 28 species are used throughout the matrix. *Brickelia californica*, however, with a leaf area mass^{-1} (L a/m) of 364·4 cm^2 g^{-1}, differed from the mean leaf area mass^{-1} (132·5 cm^2 g^{-1}) by more than four standard deviations, and it was excluded from a second analysis, which is also shown. With the exclusion of *B. californica*, several significant relationships exist between leaf area mass^{-1} and other morphological traits. Exclusion of *B. californica* had little effect on the correlation coefficient (maximum effect = 0·04) of any cell in which leaf area mass^{-1} was not one of the variables (data not shown), and did not alter the significance of any cell not including leaf area mass^{-1} as a variable at the $P < 0{\cdot}05$ level. Critical value of the correlation coefficient ($P < 0{\cdot}05$) = 0·37.

	T m/S	L m/S	Ln/Tl	L mg	L cm^2	T len	T dia	T m/l	L a/m	T a/m	T m/v
T m/S	1·00	0·99	−0·74	0·93	0·90	0·64	0·91	0·93	0·17	0·80	−0·08
L m/S	0·99	1·00	−0·73	0·96	0·92	0·57	0·88	0·90	0·17	−0·77	−0·08
Ln/Tl	−0·74	−0·73	1·00	−0·83	−0·88	−0·70	0·63	−0·59	−0·56	0·46	0·17
L mg	0·93	0·96	−0·83	1·00	0·98	0·47	0·81	0·83	−0·29	−0·71	−0·06
L cm^2	0·90	0·92	−0·88	0·98	1·00	0·50	0·77	0·77	−0·47	−0·63	−0·14
T len	0·64	0·57	−0·70	0·47	0·50	1·00	0·60	0·52	−0·33	0·36	−0·27
T dia	0·91	0·88	−0·63	0·81	0·78	0·60	1·00	0·91	−0·15	−0·67	0·34
T m/l	0·93	0·90	−0·59	0·83	0·77	0·52	0·91	1·00	−0·00	−0·92	0·08
L a/m	0·17	0·17	−0·56	0·29	0·47	0·33	0·15	0·00	1·00	0·15	−0·37
T a/m	−0·80	−0·77	−0·46	−0·71	−0·63	−0·36	−0·67	−0·92	0·15	1·00	−0·46
T m/v	−0·08	−0·08	−0·17	−0·06	−0·14	−0·27	−0·34	0·08	−0·37	−0·46	1·00
with *Brickelia californica* excluded:											
L a/m	0·34	0·37	−0·67	0·53	0·64	0·26	0·28	0·07	1·00	−0·07	−0·03

Morphological parameters	*Abbreviations*
ln (*T*otal *mass per* new *S*hoot, g)	T m/S
ln (Total *Leaf mass per* new *S*hoot, mg)	L m/S
ln (*Leaf number per* unit *T*wig *l*ength, n m^{-1})	L n/Tl
ln (*Leaf* size, *mg*)	L mg
ln (*Leaf* size, *cm*^{2})	L cm^2
ln (*T*wig *len*gth, m)	T len
ln (*T*wig *dia*meter, mm)	T dia
ln (*T*wig *mass per* unit *l*ength, kg m^{-1})	T m/l
ln (*Leaf* projected *a*rea *per* unit *m*ass, cm^2 g^{-1})	L a/m
ln (*T*wig projected *a*rea *per* unit *m*ass, cm^2 g^{-1})	T a/m
ln (*T*wig *mass per v*olume, kg m^{-3})	T m/v

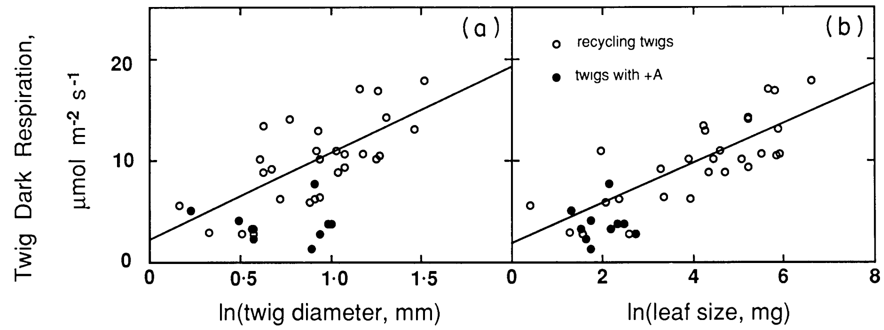

Fig. 2. Relationships between shoot morphology and the twig dark respiration rate per unit projected area. Closed circles represent species which achieved positive net assimilation rates in the twigs, while open circles represent species in which twig photosynthesis only recycled respiratory CO_2. Regression lines are based only on species limited to recycling activity. (a) The relationship among species between the mean twig diameter, mm and the twig dark respiration rate, μmol m^{-2} s^{-1} (projected area). The line is the least-squares best fit to the data: $y = 2{\cdot}10 + 8{\cdot}52 \times \ln(x)$; ($r^2 = 0{\cdot}47$; $P < 0{\cdot}001$). (b) The relationship among species between the average mass (mg dry weight) of an individual leaf and the twig dark respiration rate on a projected area basis. The line is the least-squares best fit to the data: $y = 1{\cdot}83 + 1{\cdot}97 \times \ln(x)$; ($r^2 = 0{\cdot}61$; $P < 0{\cdot}001$).

Table 3. Correlations between twig CO_2-exchange rates and selected morphological characters of the current season's shoots for 28 species. None of the twigs ever had positive net assimilation of atmospheric CO_2 and efflux from the stem (positive respiration rate) is here defined as a negative flux. Gross photosynthesis represents the difference between the efflux in the light and the efflux in the dark. All masses refer to dry weight. The critical value of the correlation coefficient ($P < 0{\cdot}05$) is 0·37.

	Df a	Df m	Lf a	Lf m	G P a	G P m	L fr
Df a	1·00	0·80	0·49	0·28	−0·98	−0·80	0·63
T m/S	−0·75	−0·37	−0·41	0·01	0·73	0·40	−0·53
L m/S	−0·78	−0·32	−0·41	0·00	0·76	0·44	−0·55
Ln/Tl	0·63	0·55	0·18	0·09	−0·64	−0·57	0·57
L mg	−0·78	−0·46	−0·36	0·00	0·77	0·50	−0·59
T len	−0·41	−0·36	−0·16	−0·12	0·41	0·37	−0·37
T dia	−0·68	−0·33	−0·38	−0·03	0·66	0·36	−0·44
T m/l	−0·66	−0·18	−0·40	0·10	0·63	0·22	−0·43
T a/m	0·53	0·08	0·36	−0·19	−0·50	−0·12	0·35
T m/v	0·14	0·39	0·00	0·28	−0·15	−0·36	0·07

Photosynthetic parameters	*Abbreviations*
*D*ark CO_2 *f*lux μmol m^{-2} s^{-1}	Df a
*D*ark CO_2 *f*lux, nmol g^{-1} s^{-1}	Df m
High *L*ight CO_2 *f*lux, μmol m^{-2} s^{-1}	Lf a
High *L*ight CO_2 *f*lux, nmol g^{-1} s^{-1}	Lf m
*G*ross *P*hotosynthesis, μmol m^{-2} s^{-1}	G P a
*G*ross *P*hotosynthesis, nmol g^{-1} s^{-1}	G P m
Dark Respiration eliminated in *L*ight, *fr*action	L fr

Morphological parameters	Abbreviations
ln (*T*otal *m*ass *per* new *S*hoot, g)	Tm/S
ln (*L*eaf *m*ass *per* new *S*hoot, mg)	Lm/S
ln (*L*eaf *n*umber *per* unit *T*wig *l*ength, n m^{-1})	Ln/Tl
ln (*L*eaf size, *mg*)	L mg
ln (*T*wig *len*gth, m)	T len
ln (*T*wig *dia*meter, mm)	T dia
ln (*T*wig *m*ass *per* unit *l*ength, kg m^{-1})	Tm/l
ln (*T*wig projected *a*rea *per* unit *m*ass, cm^2 g^{-1})	Ta/m
ln (*T*wig *m*ass *per* *v*olume, kg m^{-3})	Tm/v

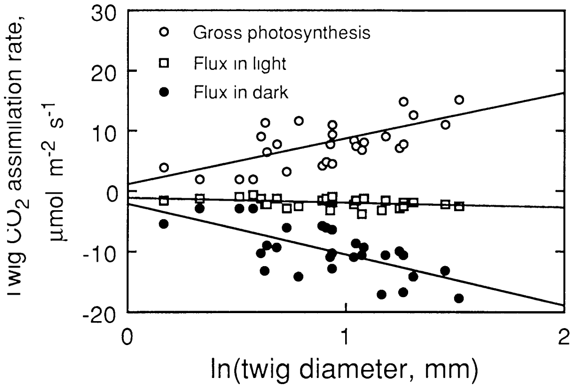

Fig. 3. The relationship among species between twig diameter, mm and the twig CO_2 assimilation rate expressed per unit projected area. The CO_2 fluxes in light and darkness were directly measured. The gross photosynthetic rate was calculated as the difference between the two measured fluxes, and it was taken to represent the rate at which respired CO_2 is photosynthetically recycled to carbohydrate in the light. The lines are the least-squares best fits to the data. In dark: $y = -2{\cdot}10 - 8{\cdot}52 \times \ln(x)$; ($r^2 = 0{\cdot}47$; $P < 0{\cdot}001$). In light: $y = -1{\cdot}15 - 0{\cdot}931 \times \ln(x)$; ($r^2 = 0{\cdot}15$; $P < 0{\cdot}05$). Gross photosynthesis in light: $y = 0{\cdot}95 + 7{\cdot}59 \times \ln(x)$; ($r^2 = 0{\cdot}44$; $P < 0{\cdot}001$). Only the 28 species that did not exhibit net assimilation of atmospheric CO_2 are included in the analyses.

resulted in lower than expected (based on twig diameter) respiration rates in these species because of reduced transport costs and differences in tissue composition.

The rate of CO_2 exchange between the twigs and the surrounding atmosphere differed substantially between high irradiance and dark conditions (Table 3, Fig. 3). The difference between the light and dark CO_2-exchange rates was attributed to the photosynthetic activity of the chloroplasts in the cortical and vascular parenchyma rather than to changes in the actual respiration rates between light and dark measurement conditions. Because none of these twigs ever achieved positive net CO_2 assimilation from the atmosphere, the magnitudes of their gross photosynthetic rates were limited by their respiration rates.

CO_2 exchange in the light was always negative but near zero. Although the net assimilation rate in the light became increasingly negative with increasing twig diameter ($r^2 = 0{\cdot}15$; $P < 0{\cdot}05$), the absolute magnitude of the slope in the light was only 0·11 times that of the slope in the dark. The fractional reduction of apparent respiration in the light relative to that in the dark is one measure of the efficiency of photosynthetic recycling (Fig. 4). Rather than showing a tendency for recycling capacity to become saturated by high rates of respiration, the efficiency of recycling actually increased with increases in dark respiration rate.

The respiration rates unit^{-1} mass reported here for the twigs (the leaf-bearing portion of the stem) were rather high for woody tissues and this may have been related to the fact that the young twigs were composed largely of living ground tissues and not an accumulation of secondary xylem. For seven of the 28 species, gas-exchange rates were measured for 1-year-old stems as well as the current season's shoots (Table 4). The current season's twigs still consisted of mostly primary tissues, while 1-year-old stems had all undergone lateral thickening (secondary growth) and sometimes had replaced the epidermis with corky bark. This difference in tissue structure is reflected in the much higher mass volume^{-1} of the older stems. The much higher mass projected area^{-1} of the older twigs was primarily due to their higher mass volume^{-1} rather than the effects of their slightly larger diameter stems on surface volume^{-1}. The dark respiration rates of current-season twigs were 4·2 and 1·9 times greater than those of 1-year-old twigs when expressed on a unit mass or projected area basis, respectively. In the light, the efflux of CO_2 was reduced in both age classes and the difference in respiration rates between current season twigs and 1-year-old stems was reduced. The efficiency of recycling was greater in the metabolically more active current season twigs.

The gross photosynthetic rate of twigs that achieved positive net uptake of atmospheric CO_2 was independent of twig diameter (Fig. 5a). At the larger twig diameter classes, there was little

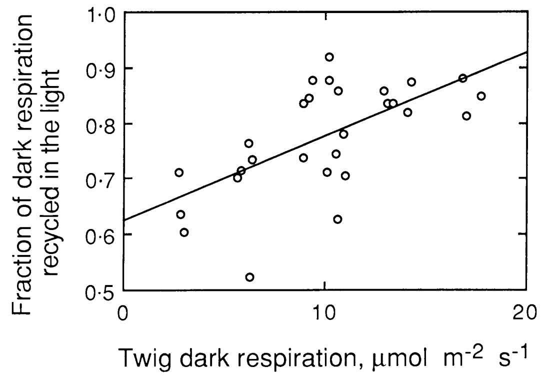

Fig. 4. The efficiency with which dark respiration was recycled in the light, calculated as the fractional reduction of the CO_2 efflux between dark and light-saturated conditions, as the dark respiration rate varies among species. The line is the least-squares best fit to the data: $y = 0{\cdot}623 - 0{\cdot}015 \times x$; ($r^2 = 0{\cdot}40$; $P < 0{\cdot}001$). Only the 28 species that did not exhibit net assimilation of atmospheric CO_2 are included in the analysis.

Table 4. The effect of stem age on apparent respiration rates in the dark and in the light. Gas-exchange measurements were made on both 1-year-old stems and current season twigs in seven of the species whose twigs lacked net photosynthetic capacity. The seven species were *Acer grandidentatum, A. negundo, Chilopsis linearis, Fraxinus velutina, Prunus fasciculata, P. virginiana* and *Rhus trilobata*. All measurements of twig mass refer to dry weight. Significance values were determined using Student's *t*-test on the hypothesis that the mean of the difference between the seven pairs of values (the two age classes within each species) was different from zero. * $P < 0{\cdot}05$; ** $P < 0{\cdot}01$; *** $P < 0{\cdot}001$; NS = not significant.

	New twigs mean ± SE	1-year-old stems mean ± SE	
Twig diameter, mm	2·7±0·3	3·6±0·4	**
Twig mass per projected area, g m^{-2}	560±50	1210±80	***
Twig specific mass, kg m^{-3}	260±20	450±50	**
Dark respiration, μmol m^{-2} s^{-1}	11·1±1·6	5·9±1·4	**
Dark respiration, nmol g^{-1} s^{-1}	20·0±2·5	4·8±1·0	***
Apparent Respiration in light, μmol m^{-2} s^{-1}	1·8±0·2	1·7±0·3	NS
Apparent Respiration in light, nmol g^{-1} s^{-1}	3·2±0·3	1·4±0·3	**
Fraction of dark CO_2 efflux eliminated by light	0·18±0·03	0·33±0·07	*

difference in twig gross photosynthetic rate depending on the CO_2 source used, although twig dark respiration rates were lower for species whose twigs had positive net assimilation rates (Fig. 1a). When twig diameters were very small, however, CO_2 recycling became limited by low respiration rates (Fig. 3) and only species utilizing atmospheric CO_2 could achieve high gross photosynthetic rates. These relationships were even more pronounced when twig gross photosynthesis was plotted as a function of leaf size (Fig. 5b). Thus, the difference in photosynthetic activity between these two species groups depended on the twig diameters and leaf sizes of the species involved in the comparison, but they were categorically distinguished by the CO_2 source utilized to support photosynthetic activity. In species whose twigs were anatomically specialized for net uptake, twig gross photosynthesis was strongly correlated with net CO_2 assimilation from the atmosphere in the light, but not with the rate of endogenous CO_2 production in the dark (Table 5). The opposite relationship was observed for species which lacked the anatomical specializations. The very high correlation between gross photosynthesis and dark respiration in this latter group was possible because there was little variation among species in their ability to photosynthetically recycle most of the respired CO_2 in the light, regardless of their rate of respiration in the dark (Figs. 3 and 4).

An important physiological difference for

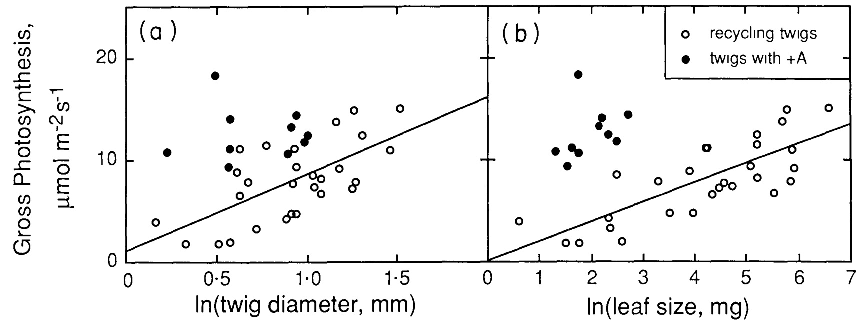

Fig. 5. The relationships among species between gross photosynthetic rate (μmol m^{-2} s^{-1}) of the twigs under light-saturating conditions and selected aspects of shoot morphology. Closed circles represent species which achieved positive net assimilation rates in the twigs, while open circles represent species in which twig photosynthesis only recycled respiratory CO_2. Regression lines are based only on species limited to recycling activity. (a) The relationship among species between the mean twig diameter, mm and the twig gross photosynthetic rate per unit projected area. The regression is the least-squares best fit to the data: $y = 0{\cdot}95 + 7{\cdot}59 \times \ln(x)$; ($r^2 = 0{\cdot}44$; $P < 0{\cdot}001$). (b) The relationship among species between the mass (dry weight) of an individual leaf and the twig gross photosynthetic rate per unit projected area. The regression line is the least-squares best fit to the data: $y = -0{\cdot}45 + 1{\cdot}91 \times \ln(x)$; ($r^2 = 0{\cdot}61$; $P < 0{\cdot}001$). The relationship between either leaf size or twig diameter and twig gross photosynthetic rate was not significant among species whose twigs achieved net photosynthesis.

Table 5. Correlation coefficients of gross photosynthetic capacity (Gross PS) with dark respiration rate (DR) and net assimilation rate under high irradiance conditions (HI PS) for: (A) the 10 species listed in Table 1 whose twigs do achieve positive net assimilation of atmospheric CO_2 in the light; (B) all 28 species that lack net photosynthetic (net-PS) uptake in the twigs; and (C) the seven species included in B whose mean leaf size falls into the same range as the species in A (< 20 mg). A CO_2 efflux from the stem has a positive sign for dark respiration rate and a negative sign for photosynthesis under high irradiance. The twigs of all species in group B (and C) had a net efflux of CO_2 even in the light. Correlation coefficients marked with * are significant at the $P < 0{\cdot}01$ level or better. Unasterisked coefficients are not statistically significant.

Species group	Gross PS *vs* DR	Gross PS *vs* HI PS
(A) net-PS twigs	0·12	0·77*
(B) no net-PS, all leaf sizes	0·98*	−0·23
(C) no net-PS, small leaves	0·98*	−0·60

photosynthetic activity in the two species groups was the internal CO_2 concentration (c_i) in the light. Foote & Schaedle (1976a) reported that gross photosynthesis in stems of *Populus tremuloides* (net photosynthesis was always negative) was insensitive to ambient CO_2 over the range 0–580 $\mu l\ l^{-1}$. They concluded that resistances to diffusion between the chlorenchyma and atmosphere must be very high and that CO_2 concentrations in the stem chlorenchyma were non-limiting, although actual values were not calculated. From previous studies (Ehleringer, Comstock & Cooper, 1987; Osmond *et al.*, 1987; Smith & Osmond, 1987; Comstock & Ehleringer, 1988), it is known that c_i values of twigs of desert species capable of positive net assimilation of CO_2 are similar to (or slightly lower than) those expected for C_3 leaves, and fall in the range of 200–220 $\mu l\ l^{-1}$ when plant water potentials are high. In contrast, the minimum possible c_i for the recycling twigs at the Cove Wash and Red Butte Canyon sites was 427 ± 44 $\mu l\ l^{-1}$ (mean ± SD; CO_2 ambient (c_a) = 350 $\mu l\ l^{-1}$). This is presented as a minimum value for two reasons. First, the calculation of c_i during standard gas-exchange measurements assumes a common pathway for the water flux leaving the plant organ, from which the stomatal conductance is calculated, and for CO_2 entering the organ. The conductances measured for the recycling twigs were very low ($0{\cdot}034 \pm 0{\cdot}015$ mol $m^{-2}\ s^{-1}$; mean ± SD), and did not vary significantly between light and dark measurements. A substantial fraction of total conductance may have been cuticular conductance which does not represent a pathway for diffusion of CO_2. This would cause an overestimate of stomatal conductance and, since the net flux of CO_2 is leaving the twig, an underestimate of c_i. Secondly, the chlorenchyma tissues involved may not have been immediately subtending the epidermis, but more diffusely extended through the outer cortex of the stem. Airspace continuity exists in the twig cortical parenchyma for gaseous diffusion (Hook, Brown & Wetmore, 1972; Armstrong, 1979), but represents a much smaller fraction of the total tissue volume than would be found in a leaf (or a positive net photosynthesizing twig), and large internal concentration gradients may have existed between the inner epidermis and the sites of carboxylation. Thus, c_i at the chloroplasts of the recycling twigs was at least twice the value present in the positive net photosynthesizing twigs and could possibly have been much higher.

Discussion

In presenting these data, we have emphasized the importance of twig surface to volume relationships in determining twig respiration rates. This functional link is easily understood and successfully explains a large fraction of the variation in twig respiration. Nonetheless, many other factors such as growth rate, degree of secondary thickening, tissue composition, environmental temperature, expected twig life-span, and amount of associated leaf area and transport costs are also undoubtably important. The correlations between leaf size and twig respiration and photosynthetic rates (Table 3) were actually higher than the analogous correlations with twig diameter (Figs. 2, 3, 4 and 5). This indicates that leaf size is related to twig respiration by functional links other than just its relationship with twig diameter. One likely possibility is that total leaf mass, which is highly correlated with leaf size (Fig. 1), also determines factors such as transport cost and possibly tissue composition in the twigs.

No species measured was found to lack photosynthetic capacity in the twig tissues. In species where positive net photosynthesis was not found in twig tissues, a reduction of 77 ± 10% (mean ± SD; n = 28 species) in the respiratory CO_2 efflux occurred in the light. This reduction was interpreted to be a measure of gross photosynthesis, but actual reductions in mitochondrial respiration would also be consistent with the gas-exchange data. The degree to which mitochondrial activity is inhibited by light is still not fully understood even in leaves, which have been studied intensively. Estimates of the actual rate of leaf mitochondrial activity in the light range from 0 to 100% of the rate in the dark (Farrar, 1985) with higher, intermediate values being the most likely (McCashin, Cossins & Canvin, 1988). The presence of carboxylation capacity in the twigs has been confirmed by ^{14}C labelling studies and the stem chloroplasts are known to produce starch even if the shoots are defoliated or the stem is girdled (Pearson & Lawrence, 1958; Strain & Johnson, 1963).

Although a capacity for substantial photosynthesis was ubiquitous, the physiology of photosynthesis appeared to be constrained in different ways in photosynthetic twigs which differed in their anatomical specialization. When twigs are anatomically specialized for assimilation of atmospheric CO_2 by having: (1) a high stomatal density; (2) a concentrated chlorenchyma (often palisade) developed in the most superficial layers of the cortex; (3) a large fraction of the chlorenchyma volume composed of airspace (high porosity) to facilitate diffusion of CO_2; and (4) delayed formation of periderm (Gibson, 1983), then they exhibit positive net CO_2-exchange rates over a wide range of light, temperature and humidity conditions throughout most of the growing season (Fig. 4; Adams & Strain, 1969; Smith & Osmond, 1987; Comstock *et al.*, 1988).

Physiologically, twigs engaged in positive net uptake must draw down the intercellular CO_2 concentration (c_i) to a level substantially below ambient in order to achieve a net influx of CO_2 by diffusion. High rates of carboxylation at these low c_i values further require very high concentrations of RuBP carboxylase (Collatz, 1977; Farquhar, Caemmerer & von Berry, 1980; Seeman, Tepperman & Berry, 1980; von Caemmerer & Farquhar, 1981), which can represent a large fraction of the soluble protein in leaves (Evans, 1989). In contrast, twigs that are only recycling endogenously derived CO_2 require no anatomical specializations. They generally do not exhibit net uptake under any conditions, but will recycle CO_2 at a variable rate depending on changes in the respiration rate (Figs. 3 and 4; Foote & Schaedle, 1976b; Brayman & Schaedle, 1982). Intermediate twig photosynthetic types lacking specialized anatomy but nonetheless operating at below ambient c_i are generally lacking (but see *Artemisia tridentata* in DePuit & Caldwell [1975] for an exception). Thus recycling twigs show a wide range of gross photosynthetic capacities, but are somehow constrained to always operate at negative net assimilation rates regardless of what the gross photosynthetic rate may be. A possible explanation for this behaviour lies in biochemical specialization of the recycling twigs for functioning under conditions of high c_i. Low concentrations of RuBP carboxylase in twigs specialized for recycling could explain: (1) the inability of such twigs to ever achieve positive net uptake since high carboxylation rates could only occur at $c_i > c_a$; and (2) the tendency towards greater efficiency of recycling in species with higher respiration rates by postulating that all species operate at high c_i values. The gradient for CO_2 loss by diffusion may always be large, but uncorrelated with the actual rate of dark respiration. When twig respiration rates are much higher than those of leaves of the same species, divergent specialization of leaves and twigs for positive net assimilation and recycling of respiratory CO_2 respectively may maximize the photosynthetic nitrogen use efficiency at the whole shoot level (Comstock, 1989).

When twigs lack high stomatal densities and a high cortical porosity to facilitate CO_2 diffusion between the atmosphere and the deeper tissues, large CO_2 concentrations can build up in the internal tissues. Studies of tree trunks have indicated that CO_2 concentrations in the wood can reach levels of 5–20% (200 000 $\mu l\ l^{-1}$) (Jensen, 1969; Hook *et al.*, 1972). The vascular cambium, however, is a major barrier to gaseous diffusion (Hook & Brown, 1972; Hook *et al.*, 1972), and the CO_2 concentrations in the bark and especially the cortex of young stems are presumably much lower than this. Standard gas-exchange calculations estimated the mean c_i of species from the Cove Wash and Red Butte Canyon sites at 427 ± 44 $\mu l\ l^{-1}$ (c_a = 350 $\mu l\ l^{-1}$) or twice that of the twigs that had positive net uptake. As discussed above, this is considered a minimum estimate of the actual c_i in the airspaces adjacent to the chloroplasts in these twigs and the actual value may be assumed to lie between it and the very high CO_2 concentrations (up to 1·5% by volume or 15 000 $\mu l\ l^{-1}$) measured in the centres of hollow current season stems (Billings & Godfrey, 1967; Osmond *et al.*, 1987).

The light environment of the twigs may also be important in selecting for patterns of net uptake by twigs. Although photosynthesis in Aspen bark light saturates at only moderate light intensities (Foote & Schaedle, 1976a), it has nonetheless been shown to be light limited during much of the summer when leaf area development is maximal (Foote & Schaedle, 1978). Little is known about variation in irradiances experienced by the current season's twigs of species in this survey, though it is likely that it decreased in the larger species that had much greater total leaf area development. In the largest-leaved species in this study, light saturation of recycling photosynthesis would not be expected with less than one-quarter to one-third full sunlight, even if the incident quantum yield was equal to that of a typical C_3 leaf. Similar light requirements for saturation of photosynthesis in mature stems have been reported in previous work (Keller, 1973; Foote & Schaedle, 1976a; Coe & McLaughlin, 1980).

In summary, twig respiration rates of desert species were quite low compared to the other species in this survey. This could be explained in large part by reduced twig diameters in the smaller-leaved desert species, and by the concomitant high twig surface volume^{-1}. There is also an indication that low levels of leaf area development were associated with low twig respiration rates independently of twig diameter and this was especially apparent for the species which had twigs specialized for positive net assimilation. This may be due to reduced transport costs and variations in twig tissue composition with low levels of leaf area development, but these relationships will require further investigation. Low twig respiration rates limit the potential gross photosynthetic rate which can be maintained purely by recycling respired CO_2 and may predispose desert species to the development of both anatomical and physiological specializations which facilitate the uptake of atmospheric CO_2. There appears to be a dichotomy in photosynthetic behaviour such that sufficient biochemical capacity to draw down c_i to levels below c_a and hence achieve positive net uptake, only occurs in twigs which are also fully specialized anatomically for high rates of gaseous diffusion from the atmosphere to the intercellular airspaces. Among small-leaved species, twig photosynthetic behaviour is variable with respect to assimilation of atmospheric CO_2, but no large-leaved species have been reported to have twigs which achieve positive net rates.

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