Physiological Plant Ecology IV

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7 Productivity of Desert and Mediterranean-Climate Plants

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CONTENTS

7.1 Introduction

Mediterranean-climate and desert ecosystems are prominent on all continents at latitudes between approximately 15° and 30° (BROWN 1968; McGINNIES 1969; MOONEY 1977a). Mediterranean-climate systems generally occur at these latitudes on the western or southwestern edges of the continent, whereas towards the more equatorial latitudes and also to the continental interior, there is a transition of vegetation types from mediterranean-climate types to desert forms (SHREVE 1936; McGINNIES 1969; DI CASTRI and MOONEY 1973; MOONEY 1977a).

Both mediterranean-climate and desert ecosystems have a high diversity of life forms (SHREVE and WIGGINS 1969; DI CASTRI and MOONEY 1973; MOONEY 1977a). The dominant life form of both ecosystem types, however, is the shrub, although subshrub, herbaceous, and ephemeral life forms constitute a significant fraction of the vegetation, and under some conditions may actually become the dominant life forms. For the most part trees are not an important component of these ecosystems, except under riparian situations.

As is characteristic of arid lands, mediterranean-climate and desert ecosystems receive low precipitation. Typically, precipitation for mediterranean-
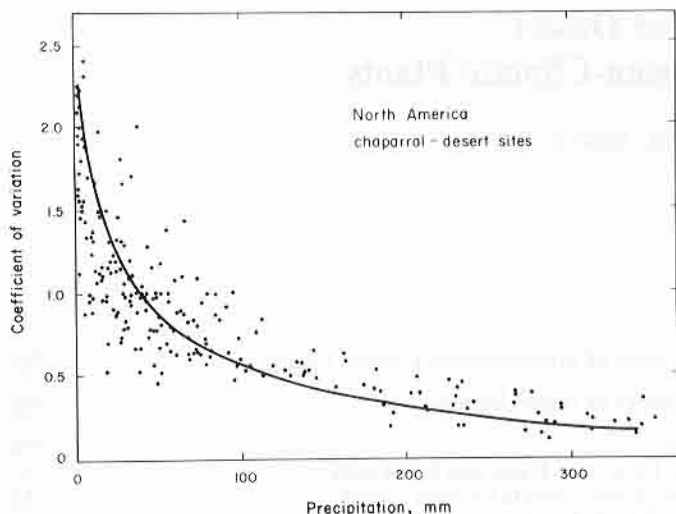
Fig. 7.1. The coefficient of variation in mean precipitation plotted as a function of mean precipitation for different locations in mediterranean-climate and desert habitats of southwestern North America. (Data from Hastings and Humphrey 1969a, b, and U.S. Weather Bureau records)

climate systems is in the range of 250–900 mm annually, with precipitation occurring almost exclusively in the cool winter months (Aschmann 1973). In contrast desert ecosystems receive 0–250 mm annually, and seasonally precipitation may occur predominantly during either the winter months or the summer months, or in some regions during both seasons. There is a strong positive correlation between the mean precipitation level and the predictability of that precipitation in mediterranean-climate and desert ecosystems (Fig. 7.1). This relationship indicates that desert ecosystems which have lower mean precipitation levels also have less predictable precipitation than do mediterranean-climate systems. Desert habitats which have less than 100 mm precipitation annually have a very low predictability of precipitation. Schaffer and Gadgil (1975) have shown that within such habitats the fraction of the flora which is ephemeral increases linearly as precipitation predictability decreases.

7.2 Biomass and Productivity of Mediterranean-Climate Plants

In mediterranean-climate regions of the world a wide range of plant growth forms may be found, ranging from evergreen trees to herbaceous annuals. Various combinations of these growth forms can be segregated in a more or less comparable manner in the different mediterranean climatic regions in response to particular climatic, soil, and disturbance gradients (Naveh 1967; Specht 1969a, b; Mooney et al. 1970; Mooney et al. 1974a). For example, in both Chilean and Californian coastal regions, progressing from the more humid

Table 7.1. Productive characteristics of mediterranean-climate evergreen forests, evergreen scrub, and a subligneous scrub community. (From MOONEY 1980)

Vegetation type	Evergreen forest		Evergreen scrub		Subligneous scrub
Community name Locality	Pine France[a]	Evergreen oak France[b]	Chaparral California[c]	Garrigue France[b]	Phrygana Greece[d]
Stand age, yr	30	150	17–18	17	?
Height, m	10.4	11	~1.5	–	<1
Leaf area index, m^2 m^{-2}	–	4.5	2.5	–	1.7
Biomass, kg ha^{-1}					
Shoot	156,800	269,000	20,390	22,500	10,950
Wood	144,100	262,000	16,720	19,500	8,860
Leaves	12,700	7,000	3,670	4,000	2,090
Roots	22,000	~50,000	~12,230	–	16,180
Litter	–	11,400	13,590	–	–
Total biomass	–	330,400	46,210	–	–
Allocation, %					
Shoot					
Wood	91.9	97.4	82.0	83.0	80.9
Leaves	8.1	2.6	18.0	17.0	19.1
Shoot	86.0	84.3	62.5	–	40.4
Root	14.0	15.7	37.5	–	59.6
Root:shoot ratio	0.16	0.19	0.60	–	1.48
Production, kg ha^{-1} yr^{-1}					
Above-ground biomass accumulation		2,600	1,300	1,100	2,020
Litter fall	7,830	3,900	2,820	2,300	2,100
Shoot, net	14,300	6,500	4,120	3,400	4,120
Root, net	1,100				
Decomposition, kg ha^{-1} yr^{-1}					
Litter	–	3,000	2,640	–	–

[a] CABANETTES 1979
[b] LOSSAINT 1973
[c] Composite data from SPECHT 1969b; KITTREDGE 1955; root biomass estimate based on KUMMEROW et al. 1977; leaf area index estimate from MOONEY et al. 1977b
[d] MARGARIS 1975 for spring

regions to the drier parts, there is a shift in community type from evergreen forests to evergreen scrub to a drought-deciduous scrub. In more interior regions or in modified sites there may be woodlands and grasslands. In regions of complex topography, substrate diversity, or land-use history, communities of widely disparate structure may co-occur within the same rainfall regime.

All of the mediterranean-climate community types have quite different productive structures and distributions of biomass, as can be seen by a comparison of the characteristics of a composite of mediterranean-climate community types (Table 7.1), as well as by a comparison of a number of community types, both natural and cultivated, found in southern France (Table 7.2).

The above-ground standing biomass of the various mediterranean woody community types varies by over an order of magnitude, from about 10,000 kg ha^{-1} for a subligneous scrub to nearly 300,000 kg ha^{-1} for an ever-

Table 7.2. Productive characteristics of four diverse Mediterranean-climate vegetation types in southern France. (ECKARDT et al. 1975)

Vegetation type	Dominant species	Growth form	Leaf specific wt. (mg cm^{-2})	Leaf area index (m^2 m^{-2})	Above-ground live biomass	Net leaf photosynthesis at 400 W m^{-2} PAR (mg CO$_2$ g^{-1} s^{-1})	Annual photosynthetic period (mo)	Above-ground production (kg ha^{-1} yr^{-1})
Evergreen forest	*Quercus ilex*	Phanerophyte	16	4.4	27	1.8	12	6,500
Halophytic scrub	*Salicornia fruticosa*	Chamaephyte	12.5	–	2.4	2.6	7	5,000
Wet meadow	*Arrhenatherum elatius*	Hemicryptophyte	4.2	3.6	0.4	11	10–12	11,000
Annual crop	*Helianthus annuus*	Therophyte	9.2	1.8	0.9	15.6	2	9,000

Table 7.3. Biomass accumulation in evergreen scrub communities of various mediterranean-climate regions. (Format from MOONEY 1977b)

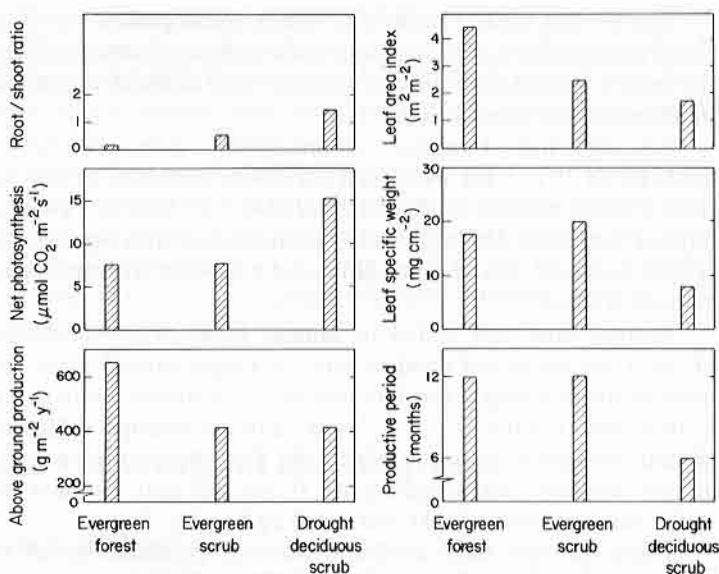| Locality	Vegetation type	Annual biomass increment (kg ha^{-1})	Estimate period (yr)	Standing living biomass and age of mature stand (kg ha^{-1})	(yr)	Reference
California						
San Dimas	Chamise chaparral	1,200	0–5	27,260	37	SPECHT 1969b
		1,000	0–10			
Boulder Creek	Chamise chaparral	1,000	0–23	23,080	23	MOONEY et al. 1977b
Northern California (average)	Chamise chaparral	1,600	0–8	31,470	?	SAMPSON 1944
Santa Ynez Mts.	Ceanothus chaparral	1,750	0–12	48,710	21	SCHLESINGER and GILL 1980
Santa Maria	Chamise-red-shank					
	Ceanothus chaparral	840	0–24	20,120	24	DEBANO and CONRAD 1978
France						
Montpellier	Garrigue	1,500	0–5	23,500	17	SPECHT 1969b
LePuech du Juge	Garrigue	1,380	0–17			LOSSAINT 1973
Australia						
Dark Island Soak	Heath	640	0–5			SPECHT et al. 1958
South Africa						
Jonkershoek	Fynbos – broad sclerophyll scrub	2,500	0–6	25,700	17	KRUGER 1977
		1,500	0–10			
		1,840	0–10			
		1,500	0–17			

Fig. 7.2. Productive structure of three mediterranean-climate type plant communities. Specific leaf weights and photosynthetic rates are average values for plants from a wide range of communities (MOONEY 1980). Other values are from Table 7.1

green oak forest (Table 7.1). Herbaceous communities, such as Californian annual grassland, have still lower values, ranging from 500 kg ha^{-1} early in a growing season to about 5,000 kg ha^{-1} at the peak of the season (DUNCAN and WOODMANSEE 1980). These differences in biomass reflect, of course, the differences in the dominant growth forms, including their life spans, which vary from less than a year for the annuals, to tens of years for the shrubby types, to hundreds of years for the forest species. Comparable differences in biomass can be noted for the community series studied in southern France by ECKARDT et al. (1975) (Table 7.2).

The comparison of the woody community types, which is based on composite data, illustrates that, because of compensating factors in the productive structure in the community, comparable aboveground productivities can be attained (Fig. 7.2). For example, the drought-deciduous type has leaves with a high photosynthetic capacity and a low construction cost yet a short photosynthetic duration (MOONEY and DUNN 1970; MILLER and STONER 1979; see also the discussion about plant life forms in Chap. 18, Vol. 12 B). In contrast, the evergreen scrub has plants with costly leaves of a low photosynthetic capacity but a higher leaf area index, and lower allocation to roots than the drought-deciduous scrub. These factors compensate each other, resulting in similar aboveground productivities between these two vegetation types. The evergreen forest has a potentially higher productivity than the evergreen scrub since, although photosynthetic capacities, duration and leaf cost are comparable, allocation to roots is less.

The French study (Table 7.2), which encompassed forest, scrub, and herbaceous communities, also indicates such internal compensation. These communities have a 30-fold difference in aboveground biomass yet only a 2-fold difference in aboveground production.

Aboveground biomass accumulation averages between 1,000 and 2,000 kg ha^{-1} y^{-1} for evergreen scrub communities in the various mediterranean-climate regions of the world (Table 7.3). Specht (1981) indicates that the annual increment declines in such communities with age. Schlesinger and Gill (1980), however, found no decline over a 22-year regrowth span for a California chaparral stand.

Annual litter fall added to annual biomass accumulation gives an index of total aboveground productivity. Average annual litter fall for a range of mediterranean-climate scrub communities is somewhat over 3,000 kg ha^{-1} y^{-1}, a little over 1,000 kg ha^{-1} y^{-1} less than an average value for mediterranean-climate evergreen forests (Table 7.4). For the evergreen scrub, then, average annual aboveground productivity (litter fall and biomass accumulation) lies in the range between 4,000 and 5,000 kg ha^{-1} y^{-1}.

There are few data available on root productivity of mediterranean-climate communities. Cabanettes (1979) indicates a value of a little over

Table 7.4. Mean annual litter fall for various evergreen forest and scrub communities

Vegetation type and dominant species	Locality	Litter fall (kg ha^{-1} yr^{-1})	Reference
Evergreen forest			
Dominant species			
Quercus agrifolia	Echo Valley, Calif.	5,130–6,460	Mooney et al. 1977b
Quercus ilex	Montpellier, France	3,900	Lossaint 1973
Pinus pinea	Montpellier, France	7,830	Cabenettes 1979
Quercus ilex	Italy	4,600	Susmel et al. 1976
Pinus halepensis	Southern France	2,900–4,900	Lossaint and Rapp 1971
Cryptocarya alba	Chile	1,830–3,260	Mooney et al. 1977b
	Overall mean =	4,760	
Evergreen scrub			
Ceanothus megacarpus	California	3,350–8,250	Schlesinger and Gill 1980
Adenostoma fasciculatum	California	2,730	Mooney et al. 1977b
Mixed spp.	Chile	1,630	Mooney et al. 1977b
Adenostoma fasciculatum	California	2,820	Kittredge 1955
Quercus coccifera	France	3,800	Lossaint 1973
	Overall mean =	3,360	
Drought-deciduous			
Phlomis fruticosa	Greece	2,100	Margaris 1976

1,000 kg ha^{-1} y^{-1} for a mediterranean-climate closed cone pine forest, whereas values of nearly 6,000 kg ha^{-1} y^{-1} have been measured for annual grasslands (DUNCAN and WOODMANSEE 1980). KUMMEROW et al. (1977) indicate that certain California evergreen shrub species may have root productions in excess of 10,000 kg ha^{-1} y^{-1}.

OECHEL (1980a) calculated total annual productivities for four Californian evergreen shrubs, using physiological data and simulation models. These values were lower for these plant types than indicated from the survey data given above. They do indicate, however, that a large carbon cost is required for the production and maintenance of evergreen sclerophyll tissues, a point well-documented by MILLER and STONER (1979).

7.3 Biomass and Productivity of Desert Systems

The standing biomass of desert ecosystems is low relative to that present in other ecosystems (RODIN and BAZILEVICH 1968; WHITTAKER 1975). The amount of biomass present will depend on the density and spacing of individuals in the population. For the most part the spacing of desert plants is random, although a number of studies have shown that the distribution of desert plants can be regular and/or clustered under very low precipitation conditions (BARBOUR 1969; WOODELL et al. 1969; FONTEYN and MAHALL 1978). Stand biomass will, of course, vary with shrub density, but typical values are in the range of 1,000–6,000 kg ha^{-1} (Table 7.5). These values are characteristic of desert shrub communities globally and are substantially less than values we have presented for mediterranean-climate ecosystems.

The annual productivity of the shrubs in the desert shrub ecosystems ranges widely, from a low of 300 kg ha^{-1} yr^{-1} to a high of about 1,800 kg ha^{-1} yr^{-1} (Table 7.5). The variation in annual aboveground productivity can be attributed to two factors: (1) differences in biomass between different shrub communities and (2) year-to-year variation in the amount of precipitation. When the relative productivity (annual productivity/stand biomass for aboveground components) for these desert shrub communities is calculated, it is seen to be quite high. The relative productivity reaches levels of 40%–50% for several shrub communities and falls to levels of 20%–30% for the seemingly least productive community types. It is likely that the low relative productivity of *Zygophyllum dumosum* (22%) and *Larrea-Ambrosia* (27%) shrub communities may be attributed to low precipitation during the measurement period. On the other hand, it is also likely that the high relative productivity of *Artemisia herba-alba* communities may be attributed to a high photosynthetic potential by desert plants (see Sect. 7.4) and high seasonal precipitation.

The distribution of biomass within these desert shrub communities is primarily in wood and belowground components (Table 7.6). Typically much less than one-fifth of the total biomass is found in leaves. Belowground biomass varies substantially, and as a result so does the root:shoot (weight:weight) ratio. These

Table 7.5. Stand biomass, annual above ground productivity, and relative productivity for selected desert shrub vegetation types

Stand biomass (kg ha^{-1})	Annual productivity (kg ha^{-1} yr^{-1})	Relative productivity (%)	Desert shrub type	Location	Reference
4,185	1,768	42	*Artemisia herba-alba*	Algeria	1
890	440	49	*Artemisia herba-alba*	Israel	2
6,113	2,380	39	*Artemisia sieberi*	Syria	1
1,610	470	29	*Artemisia + Zygophyllum*	Israel	2
4,600	1,440	31	*Artemisia + Atriplex*	Utah, U.S.A.	3
4,610	1,220	26	*Atriplex confertifolia*	Utah, U.S.A.	4
2,228	ca. 900	40	*Atriplex vesicaria*	Australia	5
2,810	780	28	*Ceratoides lanata*	Utah, U.S.A.	4
3,780	1,048	28	*Cercidium + Franseria*	Arizona, U.S.A.	6
2,370	795	34	*Eremophila gilesii*	Australia	7
3,320	1,430	43	*Hammada scoparia*	Israel	2
5,000	1,730	35	*Larrea divaricata*	New Mexico, U.S.A.	3
1,070	286	27	*Larrea + Ambrosia*	Nevada, U.S.A.	3
1,560	350	22	*Zygophyllum dumosum*	Israel	8

References: 1 RODIN et al. (1972); 2 EVENARI et al. (1972); 3 SZAREK (1979); 4 CALDWELL et al. (1977b); 5 CHARLEY and COWLING (1968); 6 WHITTAKER and NIERING (1975); 7 BURROWS (1972); 8 ORSHAN and DISKIN (1968)

Table 7.6. Biomass and root:shoot ratios for several dominant desert scrub communities

Community and location	Reference	Biomass (kg ha^{-1})					Root:shoot
		Above-ground	Wood	Leaves	Below-ground	Total	
Eremophila (Australia)	1	2,370	1,406	964	776	3,146	0.33
Larrea (U.S.A.)	3	4,290	3,870	420	1,550[b]	5,840[b]	0.36[a]
Atriplex (Australia)	2	2,228	1,403	825	910	3,138	0.41
Artemisia (Syria)	4	2,600	2,400	200	3,500	6,100	1.35
Hammada (Syria)	4	2,360	2,200	160	7,300	9,600	3.09
Atriplex (U.S.A.)	6	4,610	3,620	990	18,860	23,470	4.09
Ceratoides (U.S.A.)	6	2,810	2,110	700	19,010	21,820	6.77
Artemisia (U.S.S.R.)	4	530	400	130	3,800	4,300	7.17
Artemisia-Ceratoides (U.S.S.R.)	5	530	400	130	4,210	4,740	7.94

[a] Average from CHEW and CHEW (1965) and BARBOUR (1973)
[b] Calculation based on root:shoot value

References: 1 BURROWS (1972); 2 CHARLEY and COWLING (1968); 3 WHITTAKER and NIERING (1975); 4 RODIN and BAZILEVICH (1968); 5 LITVINOVA (1972); 6 CALDWELL et al. (1977b)

Table 7.7. Root:shoot ratios (weight:weight) for perennial desert shrubs from cool-winter and cold-winter desert habitats

Species	Reference	Location	Root:shoot
Cool-winter			
Atriplex vesicaria	4	Australia	0.41
Brickellia incana	6	California	0.55
Eremophila gilesii	2	Australia	0.36
Ephedra nevadensis	5	California	0.84
Franseria dumosa	6	California	0.64
Grayia spinosa	10	Nevada	0.64
Hymenoclea salsola	6	California	0.72
Krameria grayi	6	California	0.37
Larrea divaricata	6	California	0.33
Lycium andersonii	10	Nevada	0.73
Cold-winter			
Artemisia badhysi	9	U.S.S.R.	3.31
Artemisia rhodantha and	8	U.S.S.R.	6.58
Acantholimon diapensioides			
Artemisia rhodantha and	8	U.S.S.R.	7.94
Ceratoides papposa			
Atriplex confertifolia	3	Utah	4.09
Ceratoides lanata	3	Utah	6.77
Eurotia lanata	1	Utah	6.67
Eurotia ceratoides and	7	U.S.S.R.	6.30
Artemisia terra-alba			

References: 1 Bjerregaard (1971); 2 Burrows (1972); 3 Caldwell et al. (1977b); 4 Charley and Cowling (1968); 5 Evenari et al. (1972); 6 Garcia-Moya and McKell (1970); 7 Kurochkina et al. (1972); 8 Litvinova (1972); 9 Rustanov (1972); 10 Wallace et al. (1974)

root:shoot ratios vary from 0.33 in *Larrea divaricata* to as high as 7.94 in *Artemisia rhodantha-Ceratoides papposa* communities (Table 7.7). There does appear to be a systematic trend in root:shoot ratios between desert shrub communities. In those desert shrub communities with cool winters where plants can potentially be active through most of the winter season, the root:shoot ratios are less than one. However, in those desert shrub communities with long, cold winters where plants are likely to be inactive in the winter, the root:shoot ratios are generally much higher than three.

The biomass and productivity of desert annuals is quite variable and depends very much on the amount of precipitation (Beatley 1969; Evenari et al. 1976; Patten 1978). Patten (1978) reported an order of magnitude difference (952 kg ha^{-1} in 1972 and 94 kg ha^{-1} in 1973) in the biomass of desert annuals in a *Larrea-Cercidium* community in Arizona (U.S.A.) when the precipitation levels between years differed. Table 7.8 summarizes studies by Beatley (1969) and Evenari et al. (1976) in two different desert shrub communities where precipitation is strongly correlated with the seasonal productivity of annuals. The study by Evenari et al. (1976) suggests that there is a minimum precipitation level below which the annuals will not germinate. Similar observations have

Table 7.8. Biomass of desert annuals (kg ha^{-1}) in two different desert shrub community types in different years. [Data for the *Larrea* community type (USA) are from BEATLEY (1969) and for the *Hammada* community type (Israel) from EVENARI et al. (1976)]

	Peak biomass of annuals (kg ha^{-1})	Precipitation (mm)
Larrea community		
1963	67.9	102
1964	41.6	91
1965	161.7	162
Hammada community		
1970	80.0	94
1971	2,700.0	163
1972	0.0	54
1973	1,150.0	134

been made on annuals found in the Californian deserts (WENT 1949; TEVIS 1958).

The timing and phenology of desert plants plays an important role in determining rates of biomass accumulation. However, for most desert systems the factors controlling phenology and dynamics of primary production are poorly understood. Perhaps the best understood of the desert ecosystems in this respect is the Mohave Desert of North America (WENT 1949; TEVIS 1958; BEATLEY 1974; ACKERMAN and BAMBERG 1974). These studies suggest that the seasonal success of most primary producers is dependent on precipitation events occurring at particular points in time. Differences in the amounts of precipitation and temperatures during the precipitation period will have a direct effect on the germination success of different species and therefore on the potential for biomass production. Vegetative growth generally precedes flowering activities in all desert species, both woody and herbaceous.

The biomass of lower plant life forms such as lichens and mosses is quite low in desert systems and does not contribute substantially to the overall productivity within the system (KAPPEN et al. 1975; NASH et al. 1977; KAPPEN et al. 1979).

7.4 Photosynthetic Rates

There are now abundant values in the literature on the photosynthetic capacity of plants in nature from a variety of habitats. We will use many of these for our comparisons. However, rather than compiling all the available rates, we shall be somewhat selective, often choosing the most complete set by a given worker to make a particular point. We feel that this is a valid approach, considering the great amount of variability one finds in rates for a given plant dependent on measurement techniques and season. Both the light-saturated photosyn-

thetic rates, as well as the temperature optimum of photosynthesis, can be affected by physiological, environmental, or experimental factors.

This variability will be more noticeable on some plant types than on others. For example, plants with leaves with a short life span often have very high photosynthetic rates while young, but their capacity declines rapidly with age – often without a noticeable visible sign. Then plants with particularly sensitive stomata may have quite variable rates, dependent on premeasurement handling, as well as measurement conditions.

Much of this variability can be assessed, and even compensated for if full environmental and physiological parameters such as stomatal conductance, internal CO_2 concentration, vapor pressure gradient, leaf age and some measure of carboxylating capacity are given for each photosynthetic rate reported. However, such information is rarely available to accompany any data set on photosynthetic rates.

7.4.1 Photosynthetic Pathways, Rates and Life Form

A number of recent studies have focused on determining the distributions of different photosynthetic pathways among life forms and within mediterranean-climate and desert ecosystems (MOONEY et al. 1974b; SCHULZE and SCHULZE 1976; TEERI and STOWE 1976; SYVERTSEN et al. 1976; MULROY and RUNDEL 1977; MOONEY et al. 1977a; EICKMEIER 1978; WINTER and TROUGHTON 1978; TEERI et al. 1978). In mediterranean-climate systems, the C_3 pathway predominates in all life forms; only in the coastal zones and at mediterranean-climate – desert ecotones does CAM become of any importance. Within desert ecosystems, trees and shrubs possess the C_3 pathway, except for halophytic shrubs which often possess the C_4 pathway. Succulent subshrubs are usually CAM or FCAM (facultative CAM). Among the grasses, herbs, and annuals, we find that cool season (winter) species are generally C_3, whereas warm season (summer) species are generally C_4. (For detailed discussion of the functional significance of the different pathways of CO_2 fixation in photosynthesis see Chap. 15, Vol. 12B.)

7.4.1.1 Mediterranean-Climate Growth Forms

There are now a number of studies that indicate that there are intrinsic differences in the photosynthetic capacities of different mediterranean-climate life forms. For example, evergreen species generally have lower (about $1/2$) photosynthetic capacities than drought-deciduous species on a leaf area basis (HARRISON et al. 1971; MOONEY et al. 1977c; GIGON 1979). In a survey of the net photosynthetic rates of mediterranean-climate growth measured in field plants, MOONEY (1981) gives an average rate of 8 µmol CO_2 m^{-2} s^{-1} for evergreen shrubs and trees and 15 µmol CO_2 m^{-2} s^{-1} for drought-deciduous shrubs.

A recent study by MARTINEZ (1979) compared the photosynthetic capacities of a whole range of Chilean mediterranean-type growth forms. Using ^{14}C techniques on field plants throughout the year, he found that the maximum photosynthetic rates observed declined in order of growth form in the following se-

Table 7.9. Maximum observed seasonal gross photosynthetic rates as determined by ^{14}C techniques on different growth forms of Mediterranean-climate Chilean plants. (MARTINEZ 1979)

Growth form	Range of photosynthetic rates (μmol CO_2 m^{-2} s^{-1})	Number of species observed
Drought deciduous shrubs	25–40	2
Annuals	27–35	2
Perennial herbs	10–23	2
Evergreen sclerophyll trees and shrubs	11–16	4
Chlorophyllous stemmed shrubs	11–15	2
Hygrophyllous evergreen trees and shrubs	5–12	2
Succulents	3	2

quence: drought-deciduous shrub, herbaceous annual, herbaceous perennial, sclerophyllous evergreen, chlorophyllous-stemmed shrub, hygrophyllous evergreen, and evergreen succulent (Table 7.9). Although there were only limited representations of certain forms, these results are consistent in ranking with the results of others. In a similar comparison of Californian mediterranean-climate plants, OECHEL (1980b) found results comparable to that of MARTINEZ (1979), although the spread in rates between types was less. However, OECHEL's study was conducted during a single season at the beginning of the drought (late May and early June) when the capacity of the herbaceous types in particular would be reduced.

7.4.1.2 Desert Growth Forms

The major limiting factor for the photosynthetic process in most desert plants is water availability. As noted in the previous sections, the generally low and sporadic nature of precipitation often leads to a direct correlation between amount of rainfall and magnitudes of primary productivity. Desert plants as a general rule can respond immediately to precipitation events (moving from dormant to an active state and/or seed germination) by producing leaves which have a high photosynthetic capacity. Desert plants differ considerably in the peak rates among the most common life forms. As examples of plants from the Sonoran Desert of North America, ephemerals and plants with leaves active only a brief period of the year have extremely high photosynthetic rates (Table 7.10). These high rates are the highest or among the highest photosynthetic rates measured on terrestrial plants (SESTAK et al. 1971). In contrast, relatively low photosynthetic rates are observed in succulents and ferns.

The highest photosynthetic rates and leaf conductances for desert plants are found in ephemerals (MOONEY et al. 1976; MOONEY and EHLERINGER 1978; ARMOND and MOONEY 1978; EHLERINGER et al. 1979). These ephemerals complete their entire life cycle in a period as short as 6 weeks (BEATLEY 1974). Both C_3 and C_4 photosynthetic pathways are found in desert ephemerals

Table 7.10. Examples of peak photosynthetic rates expressed on a surface area basis for different life forms found in the Sonoran Desert of North America. These data are from plants grown and measured under field conditions

Life form	Species	Photo-synthetic pathway	Peak photo-synthesis ($\mu mol\ CO_2\ m^{-1}\ s^{-1}$)	Maximum leaf conduc-tance ($mm\ s^{-1}$)	Refer-ence
Winter ephemeral	*Camissonia claviformis*	C_3	59	24	1
Summer ephemeral	*Amaranthus palmeri*	C_4	81	20	2
Perennial herb	*Tidestromia oblongifolia*	C_4	37	5	3
Deciduous leaved shrub	*Encelia farinosa*	C_3	37	17	4
Evergreen leaved shrub	*Atriplex lentiformis*	C_4	28	3	5
Evergreen leaved shrub	*Larrea divaricata*	C_3	27	11	6
Deciduous leaved tree	*Cercidium floridum*	C_3	10	–	7
Succulent leaved subshrub	*Agave deserti*	FCAM	6	1.4	8
Stem succulent subshrub	*Opuntia basilaris*	CAM	6	1.2	9
Fern	*Notholaena parryi*	C_3	5	4	10

References: 1 EHLERINGER et al. (1979); 2 EHLERINGER (1982); 3 BJÖRKMAN et al. (1972); 4 EHLERINGER and BJÖRKMAN (1978b); 5 PEARCY and HARRISON (1974); 6 MOONEY et al. (1978); 7 ADAMS and STRAIN (1968); 8 HARTSOCK and NOBEL (1976); 9 SZAREK and TING (1975); 10 NOBEL (1978)

(MULROY and RUNDEL 1977). The winter ephemerals utilize the C_3 pathway, whereas both the C_3 and C_4 pathways occur in summer ephemerals.

Perennial life forms with leaves having life expectancies similar to ephemerals (i.e., drought-deciduous leaved shrubs and herbaceous perennials) appear to have peak photosynthetic rates approaching those of the ephemerals (BJÖRKMAN et al. 1972; EHLERINGER and BJÖRKMAN 1978b). Both drought-deciduous shrubs and herbaceous perennials are active for somewhat longer periods than ephemerals. Both C_3 and C_4 pathways are found among these life forms.

Evergreen leaved shrubs have high photosynthetic rates (STRAIN 1969, 1970; OECHEL et al. 1972; PEARCY and HARRISON 1974; MOONEY et al. 1978) relative to evergreen leaved species from other habitats (SESTAK et al. 1971; DUNN 1975). Succulent subshrubs possessing crassulacean acid metabolism (CAM) and facultative CAM (FCAM, succulents which shift between C_3 photosynthesis and CAM depending on aridity conditions) and ferns have the lowest photosynthetic rates of all the life forms. These life forms also have the lowest leaf conductances.

Yet it is the CAM plants and ferns that have the greatest capacity to survive extended periods of drought (SZAREK et al. 1973; SZAREK and TING 1975; NOBEL 1978). The next most tolerant group to drought is evergreen leaved shrubs followed by drought-deciduous leaved shrubs, and the least tolerant life forms are the ephemerals (STRAIN 1970; ODENING et al. 1974; WALTER and STADELMANN 1974).

There is a direct positive correlation between maximum leaf conductance and photosynthetic rate among the C_3 plants and among C_4 plants (Table 7.10). The C_3 plants have higher leaf conductances than C_4 plants for any given photosynthetic rate, suggesting that water use efficiency should be better in C_4 plants. It is interesting to note that photosynthetic rates in C_3 plants can equal and exceed rates measured for C_4 plants. While it may be generally true that photosynthetic rates of C_4 plants exceed those of C_3 plants, there is ample evidence to suggest that this is certainly not true for plants of desert habitats. (For a general discussion of plant life forms and their carbon and water relations see Chap. 18, Vol. 12 B).

7.4.2 Temperature and Light Response

7.4.2.1 Mediterranean-Climate Forms

Just as there are considerable differences in the absolute photosynthetic capacity between leaves of various mediterranean-climate life forms, there are also differences in the season of optimum photosynthesis capacity (to a certain degree) as well as the seasonal duration of activity. In MARTINEZ' 1979 study of 16 Chilean species, encompassing seven different growth forms, he found that the period of optimum photosynthetic capacity was concentrated in the period spanning late winter to late spring (August to December), with the herbaceous plants having their highest capacity more toward the end of this period.

Herbaceous species of mediterranean climates have a photosynthetic period that coincides with the approximately 5- to 6-month winter wet season (MARTINEZ 1979). Drought-deciduous species have a photosynthetic period that is about a month or so longer than for the herbaceous plants, because of their greater rooting volume and hence greater available water stores.

The evergreen species of mediterranean-climate regions have the capacity to fix carbon year-round (DUNN 1970; ECKARDT et al. 1975; MOONEY et al. 1975; MARTINEZ 1979; OECHEL 1980b), although at somewhat reduced rates during the drought (MOONEY et al. 1975).

In a survey of the photosynthetic temperature response of a number of Californian and Chilean shrubs, it was found that most of the species could be characterized as having rather broad central regions of relative temperature insensitivity (e.g. 85% of maximum rates of certain species occurring over a 25 °C temperature range) (OECHEL 1980b). There was, however, a range of thermal optima of photosynthesis extending from near 15 °C to about 30 °C. Most of these woody species, however, had their thermal optimum near 20 °C

when measured under full light in the springtime. This seems to be the characteristic optimum temperature for a wide range of mediterranean climate evergreens (MOONEY 1981).

In the study of OECHEL (1980b) noted above it was found that at optimum temperatures most species saturated at less than full sunlight. A notable exception was an evergreen with vertically oriented leaves (*Arctostaphylos*), which had a high light requirement. MOONEY (1981) proposed that the generally low light requirement of the evergreen sclerophylls was related to their low intrinsic photosynthetic capacity. One drought-deciduous species, *Encelia californica,* in contrast, has a high photosynthetic rate, which is typical for the life form, and does not saturate, even at full sunlight (EHLERINGER and BJÖRKMAN 1978b). A systematic analysis of life forms, photosynthetic capacity and light requirement of mediterranean-climate plants would be valuable.

7.4.2.2 Desert Forms

Leaves of desert plants are usually not photosynthetically light-saturated under midday irradiances (BJÖRKMAN et al. 1972; SCHULZE et al. 1972; PEARCY and HARRISON 1974; MOONEY et al. 1976; MOONEY and EHLERINGER 1978; EHLERINGER and BJÖRKMAN 1978b). Associated with the lack of light saturation are high photosynthetic capacities and high leaf conductances to water loss (Table 7.10). The initial slope of the light response curve, the quantum yield (ratio of photosynthetic rate over absorbed light quantum flux, see Chaps. 2 and 3, Vol. 12A), is $0.052 \text{ mol } E^{-1}$ for C_3 plants and $0.053 \text{ mol } E^{-1}$ for C_4 plants at 30 °C (EHLERINGER and BJÖRKMAN 1977). Quantum yield values measured for C_3 plants from the light response curve at 30 °C were $0.050 \text{ mol } E^{-1}$ for the shrub *Larrea divaricata* (MOONEY et al. 1978), $0.052 \text{ mol } E^{-1}$ for the shrub *Encelia farinosa* (EHLERINGER and BJÖRKMAN 1978b), and $0.055 \text{ mol } E^{-1}$ for the annual *Camissonia claviformis* (MOONEY et al. 1976). A quantum yield of $0.077 \text{ mol } E^{-1}$ has been reported for the C_3 fern *Notholaena parryi* at 15 °C (NOBEL 1978). Values of the quantum yield for C_4 plants are not generally available and are difficult to estimate based on the photosynthesis–light response curves in the literature.

The temperature response of light-saturated photosynthesis by leaves of desert plants has been the subject of intense investigations over the last decade (STRAIN and CHASE 1966; STRAIN 1969; HELLMUTH 1971; BJÖRKMAN et al. 1972; PEARCY and HARRISON 1974; LANGE et al. 1974; PEARCY et al. 1974; DEPUIT and CALDWELL 1975; LANGE et al. 1975; BJÖRKMAN et al. 1976; CALDWELL et al. 1977a; PEARCY et al. 1977; NOBEL 1978; EHLERINGER and BJÖRKMAN 1978b; BJÖRKMAN et al. 1978; LANGE et al. 1978; MOONEY et al. 1978; NOBEL et al. 1978). Generally it has been found that plants growing in desert environments show a wide variation in the thermal optima for photosynthesis, and that this optima in many species is dependent on phenology, growth temperature, and/or drought stress. Temperature optima for net photosynthesis ranging from 15° to 47 °C have been measured; these optima depend somewhat on photosynthetic pathway, with C_3 species showing lower optima than C_4 species.

7.5 Photosynthetic Adaptation to Arid Conditions

7.5.1 Mediterranean-Climate Forms

The different mediterranean-climate growth forms respond in a dissimilar manner to the seasonal drought. Annual and many perennial herbs pass through the drought in a dormant state. Many shrub species (generally subligneous, subshrubs), particularly those occupying disturbance or xeric habitats also lose all or most of their leaves during the unfavorable period. They have little stomatal control of transpiration, and they rapidly have lowered water potentials in the early drought (POOLE and MILLER 1975; GIGON 1979). These plants are thus drought avoiders. As noted earlier, it is plants of these types that generally have a high photosynthetic capacity.

Many mediterranean-climate subshrubs have seasonally dimorphic leaves (ORSHAN 1964; MARGARIS 1976, 1977; MONTENEGRO et al. 1979). There is a reduction of leaf area on such plants during the drought period, with those leaves remaining differing morphologically and physiologically from the wet season leaves. On a weight basis the drought season leaves have an intrinsically lower photosynthetic capacity than the wet season leaves (MARGARIS 1977). Further studies on the comparative gas exchange characteristics of these two leaf types are needed.

It is the evergreen mediterranean-climate plants that have the capacity to carry on photosynthesis throughout the year. In a study of the seasonal photosynthetic activity of the Californian evergreen shrub, *Heteromeles arbutifolia*, in its native habitat, it was found that plants of these species had active photosynthesis at water potentials as low as -3.3 MPa. On a seasonal basis, however, drought is the principal limiting factor to photosynthesis. During annual drought periods these plants may have midday depressions in photosynthesis because of stomatal closure, and during the most severe drought periods photosynthesis may occur primarily in the morning (MOONEY et al. 1975).

In the evergreen species morphology plays an important role in drought adaptation. For example, MORROW and MOONEY (1974) found that *H. arbutifolia*, described above, had an intrinsic capacity to carry on photosynthesis at lowered water potentials comparable to those found in *Arbutus menziesii*, even though the latter species is found generally in more northerly and mesic habitats. Yet, where these species co-occur, *Arbutus* may show severe drought effects, whereas *Heteromeles* may not. This is evidently due to the smaller and more steeply angled leaves of *Heteromeles* and because of its deeper root system. Gradients of variation in leaf morphology among evergreen plants along mediterranean-region aridity gradients have been described both for within-community types (MOONEY et al. 1974a) and among species of the same genus between community types (SHAVER 1978). The general trend is for evergreen leaves to become smaller, more steeply angled and to have a decreased light absorptivity with increasing site aridity.

POOLE and MILLER (1975) found among the Californian evergreen sclerophylls that they studied that, as might be expected, the deeper-rooted species

developed less water stress during the drought than did shallow-rooted species. The shallow-rooted species evidently have stomata less sensitive to water potential and are apparently thus restricted to more mesic microsites.

Although mediterranean-climate evergreen shrubs are photosynthetically active year-round, and thus during both hot and cold seasons, studies have not demonstrated any large degree of photosynthetic thermal acclimation capacity for them (HARRISON 1971). Since many of these evergreens (both Californian and Chilean) have very broad photosynthetic thermal responses (OECHEL 1980a), photosynthetic acclimation would not be very apparent.

7.5.2 Desert Forms

For many species the temperature optimum for photosynthesis will vary with the thermal environment in which the plants are growing, such that the thermal optima remain in tune with mean daytime air temperatures (MOONEY and WEST 1964; STRAIN and CHASE 1966; STRAIN 1969; LANGE et al. 1974; BJÖRKMAN et al. 1975; LANGE et al. 1975; PEARCY 1977; MOONEY et al. 1978). In their study of the C_4 shrub *Hammada scoparia* from the Negev Desert, LANGE et al. (1974) found that the temperature optimum for photosynthesis varied from 28.6 °C in late March to 40.9 °C in mid-August (Fig. 7.3). In association with the change in temperature optimum, there were also corresponding changes in the upper temperature compensation point from a minimum of 46.3 °C in late March to 60.0 °C in mid-August. MOONEY et al. (1978) have conducted similar measurements on the C_3 shrub *Larrea divaricata* of the Sonoran Desert. They found a shift in the temperature optima from about 20 °C in January
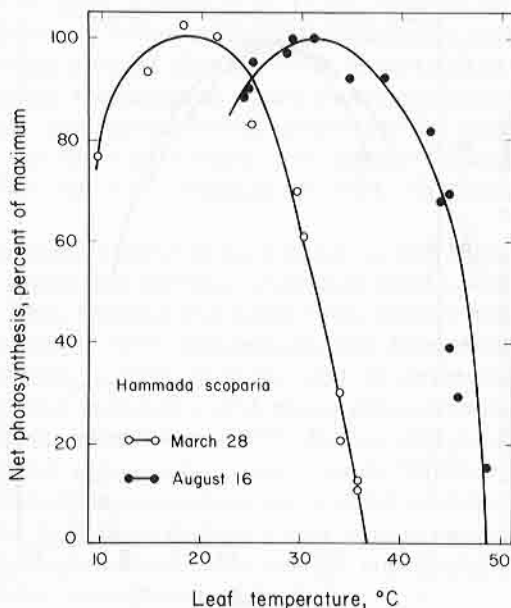

Fig. 7.3. Temperature dependence of photosynthesis at high irradiances for field-grown plants of the C_4 shrub *Hammada scoparia* in the Negev Desert, Israel, during late March (spring) and mid-August (summer) conditions. (Modified from LANGE et al. 1974)

Hammada scoparia

○—○ March 28
●—● August 16

Net photosynthesis, percent of maximum

Leaf temperature, °C

to 32 °C in September. In laboratory studies under controlled growth regimes, identical changes in thermal optima were observed. While the upper temperature compensation point was found to vary in the same manner as the temperature optima of photosynthesis, MOONEY et al. (1978) do not present specific values for *L. divaricata*. These two studies demonstrate that, while temperature optima may be higher in C_4 plants, both C_3 and C_4 plants are equally capable of thermal acclimation. While for both *Hammada scoparia* and *Larrea divaricata* the temperature optimum for net photosynthesis varied in concert with the seasonal air temperatures, the absolute photosynthetic rate at the respective temperature optimum showed little change seasonally.

The upward shift in photosynthetic temperature optimum which results from growth or exposure to high temperatures has been interpreted as photosynthetic acclimation. It is presumed to be of adaptive value to the shrubs by allowing the plant to operate at a high photosynthetic capacity despite wide fluctuations and often extremely high air temperatures. Few calculations have been made to estimate the net benefits of thermal acclimation on the daily carbon gain of a leaf. LANGE et al. (1978) made such calculations for *Prunus armeniaca* (which shows thermal acclimation) and *Hammada scoparia*. Their conclusion was that thermal acclimation did result in a greater rate of daily carbon gain in *P. armeniaca*, but that it was not beneficial in *H. scoparia*. MOONEY (1980) made a similar analysis on the consequence of thermal acclimation in *Larrea divaricata* and concluded that thermal acclimation did result in a greater daily carbon gain by the leaf.

Although many desert species exhibit a capacity for thermal acclimation of their photosynthetic apparatus, a number of species, such as *Encelia farinosa* (Fig. 7.4), do not show changes in temperature optima when grown under differ-
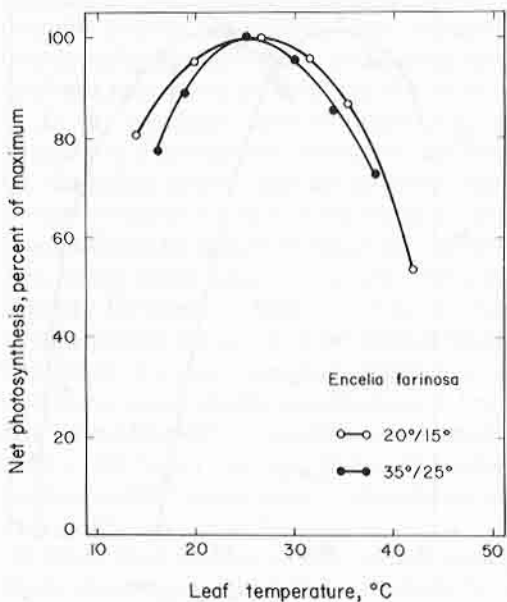

Fig. 7.4. Temperature dependence of photosynthesis of high irradiances for laboratory grown plants of the C_3 shrub *Encelia farinosa* from the Sonoran Desert. The growth temperatures presented are day–night temperatures. (Data from EHLERINGER and BJÖRKMAN 1978b)

ent thermal regimes (STRAIN 1969; PEARCY et al. 1974; BJÖRKMAN et al. 1975; EHLERINGER and BJÖRKMAN 1978b). These plants exhibit a morphological change (or acclimation) in leaf structure rather than physiological acclimation in response to changes in the thermal environment (CUNNINGHAM and STRAIN 1969; EHLERINGER et al. 1976; MOONEY et al. 1977c; EHLERINGER and BJÖRKMAN 1978a; EHLERINGER and MOONEY 1978). Plants such as the C_3 shrub *Encelia farinosa* and the C_4 shrub *Atriplex hymenelytra* show changes in leaf spectral properties under changing thermal regimes. As air temperatures and/or drought stress increase, leaves from both of these plants increase their reflectance, reducing heat load and thus leaf temperatures. The two shrubs utilize different mechanisms to achieve an increased reflectance. *Encelia farinosa* uses a thick layer of pubescence to reflect light (EHLERINGER and BJÖRKMAN 1978a), whereas the crystallization of sodium chloride in epidermal salt glands is the mechanism used by *A. hymenelytra* (MOONEY et al. 1977c). The net effect on leaf temperature is the same; temperatures are reduced and remain close to the respective thermal optima of photosynthesis (MOONEY et al. 1977c; EHLERINGER and BJÖRKMAN 1978b; EHLERINGER and MOONEY 1978).

Since precipitation events are infrequent and amounts are often low, water stress is a continual limiting factor for desert plants. Stomatal control under low soil moisture conditions is the major cause of reduced net photosynthetic activity in plants under water stress. Desert plants exhibit two fundamental adaptive patterns to adapt the photosynthetic apparatus to low soil moisture conditions: desiccation tolerance and drought avoidance.

Under moderate water stress, many desert plants respond with a partial midday closure of stomata, which results in a bimodal peak of daily photosynthetic activity (STRAIN 1969; LANGE et al. 1969; HELLMUTH 1971). Most true xerophytes and desert halophytes are able to survive extremely low leaf water potentials (WALTER and STADELMANN 1974; LANGE et al. 1976). Positive net photosynthesis, although severely depressed by low stomatal conductances, still persists for such plants under extreme drought (STRAIN 1970; KAPPEN et al. 1972; ODENING et al. 1974). Within the nonsucculent desert plants, evergreen shrubs are most desiccation-tolerant, drought-deciduous shrubs are the next most tolerant, followed by trees, and the least tolerant are ephemerals and herbaceous perennials (Fig. 7.5) (WALTER and STADELMANN 1974; ODENING et al. 1974).

An alternative to drought tolerance in photosynthetic adaptation is drought avoidance. Three life forms occur within this category: perennial shrubs with drought-deciduous leaves (ZOHARY 1961; ORSHAN and ZAND 1962; SHREVE and WIGGINS 1964; CUNNINGHAM and STRAIN 1969; EHLERINGER and BJÖRKMAN 1978a), ephemerals (SHREVE and WIGGINS 1964; WALTER and STADELMANN 1974; MULROY and RUNDEL 1977), and succulent CAM plants (NEALES et al. 1968; SZAREK et al. 1973; LANGE et al. 1976; NOBEL 1977; KLUGE and TING 1978). Drought-deciduous shrubs and ephemerals avoid drought stress by achieving high rates of photosynthesis during non-stress periods and senescing photosynthetic activity as leaf water potentials decline. CAM plants, on the other hand, avoid drought stress through internal water storage and allowing only a minimal water loss at night when stomates are open.
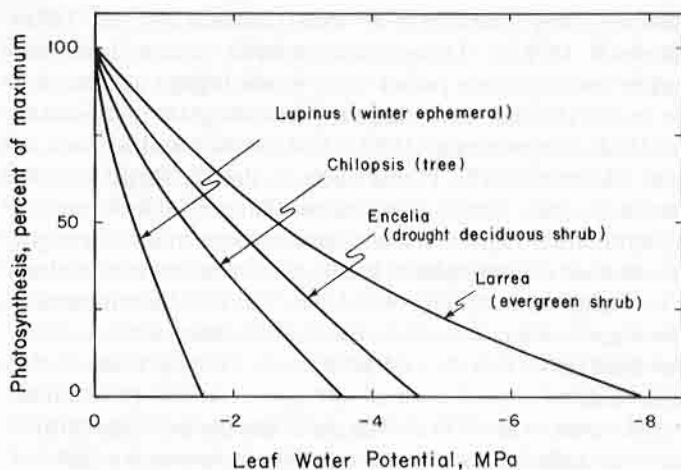
Fig. 7.5. Relationships between decreasing leaf water potential and net photosynthetic rate for different life forms found in the Sonoran Desert. (Data for *Lupinus arizonicus* calculated utilizing values from ARMOND and MOONEY 1978 and FORSETH and EHLERINGER 1980. Data for *Larrea divaricata, Encelia farinosa*, and *Chilopsis linearis* from ODENING et al. 1974)

Within drought-deciduous perennials and ephemerals, several species show adaptations which allow these plants to extend the photosynthetic activity to greater levels of drought stress. In drought-deciduous shrubs such as *Encelia farinosa* there are several changes in external and internal leaf morphology that will allow the leaves to be active to low leaf water potentials (CUNNINGHAM and STRAIN 1969; EHLERINGER and MOONEY 1978). The phenomenon of solar tracking in desert ephemerals (leaves move to become perpendicular to the sun's rays) results in leaves operating at maximum photosynthetic capacity throughout the day, greatly increasing the daily carbon gain over fixed orientation leaves (WAINWRIGHT 1977; MOONEY and EHLERINGER 1978; FORSETH and EHLERINGER 1980). Under mild drought stress, solar trackers can become solar-avoiders (leaves move to become parallel to the sun's rays) and thus extend their period of productivity (albeit severely reduced) into drought conditions (BEGG and TORSELL 1974; FORSETH and EHLERINGER 1980).

In drier habitats, especially in coastal desert zones, there is an increase in the occurrence of CAM plants (MOONEY et al. 1974b; SCHULZE and SCHULZE 1976; MOONEY et al. 1977a; WINTER and TROUGHTON 1978). Since stomates open only at night when vapor pressure deficits are lowest, CAM plants have low rates of water loss and consequently high water use efficiencies (SZAREK et al. 1973; SZAREK and TING 1975; NOBEL 1978; KLUGE and TING 1978). As leaf water potentials decline in CAM plants, leaf conductances decrease (SZAREK and TING 1975; NOBEL 1978; KLUGE and TING 1978). Total CO_2 fixation decreases as stem water potentials decline in *Opuntia basilaris,* and a point of zero net CO_2 fixation occurs at a fairly highly stem water potential of -1.5 MPa (Fig. 7.6). During periods of zero net CO_2 fixation, CAM plants are in an "idling mode" and refix internally generated CO_2. Because of their extremely

Fig. 7.6. Effects of cactus pad leaf water potential in the nocturnal acidification rate in *Opuntia basilaris* from the Sonoran Desert. (Data from SZAREK and TING 1975)
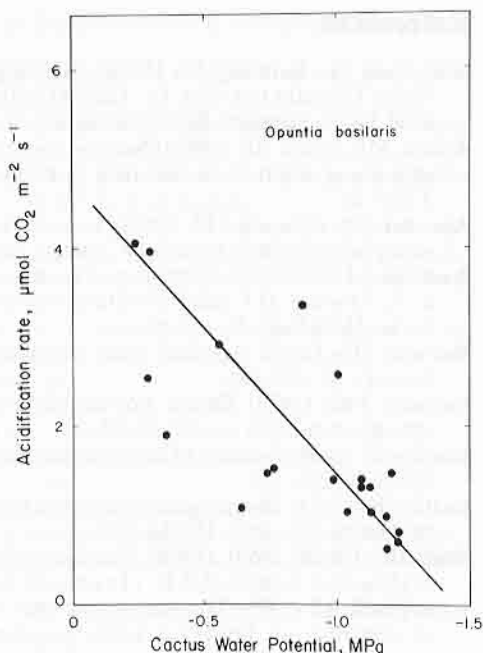
thick cuticles, which virtually eliminate any water loss, CAM plants can survive extended periods of drought in this "idling mode" (KLUGE and TING 1978).

7.6 Conclusions

Although there are many similarities in the life forms present in mediterranean-climate and desert ecosystems, rates of annual productivity and amounts of standing biomass are vastly different. Almost all of this difference can be attributed to increased precipitation in the mediterranean-climate ecosystem. One major biomass difference between these two ecosystem types is the very high root:shoot ratios that occur in cold-winter desert habitats; a high root:shoot ratio evidently does not occur in mediterranean-climate plants.

There are differences in the photosynthetic adaptations of plants in these two ecosystems. These differences seem related to the seasonality as well as the predictability of precipitation events. In mediterranean-climate systems, precipitation and plant growth occurs almost exclusively in the winter and spring months. Since both temperature and precipitation are fairly predictable, mediterranean-climate plants exhibit a broad temperature response in photosynthesis and apparently lack a thermal acclimation potential. In contrast, in desert systems precipitation and growth can generally occur over a wide range of temperatures and are less predictable. Consequently, most desert plants either show adaptations to morphologically or physiologically acclimate to changes in thermal environments or to be active during thermally favorable periods, and remain dormant or inactive during unfavorable periods.

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