2 Modifications of solar-radiation absorption patterns and implications for carbon gain at the leaf level

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Introduction

At the end of the nineteenth century and during the early part of the twentieth century there was interest in determining the relationships between leaf form and function and in determining how morphology was involved in adapting plants to specific environments. Studies by Haberlandt (1884), Schimper (1903), and Warming (1909) showed that leaves of plants from arid habitats tended to possess characteristics different from those of plants from more mesic habitats. Characteristics often found in arid-zone plants included more leaf pubescence, an increase in the frequency of compound leaves, sclerophyllous anatomy, generally smaller leaves, and more steeply inclined leaves. They regarded these characters as "adaptations" for reducing water loss, but any potential effect on photosynthesis was not considered. These studies did not have an experimental basis, and although a correlation could be established between certain leaf characteristics and environmental factors, the potential functional significance has been investigated more thoroughly only in recent times.

Raschke (1956) and Gates (1962) provided a theoretical basis for the leaf energy balance, linking water loss, leaf temperature, and certain leaf characteristics such as size, spectral characteristics, and leaf orientation. The linkage between the processes of water and energy transfer and photosynthesis was made by Mooney (1972), Parkhurst and Loucks (1972), Givnish and Vermeij (1976), Cowan and Farquhar (1977), and Mooney and Gulmon (1979), in which the environmental constraints imposed on photosynthesis, transpiration, and net carbon gain were simultaneously evaluated.

In this chapter we shall focus on the consequences of variations in leaf spectral characteristics and leaf orientation for the processes of photosynthesis and transpiration and on how the importance of such morphological traits is affected by constraints imposed by the physical and biotic environ-
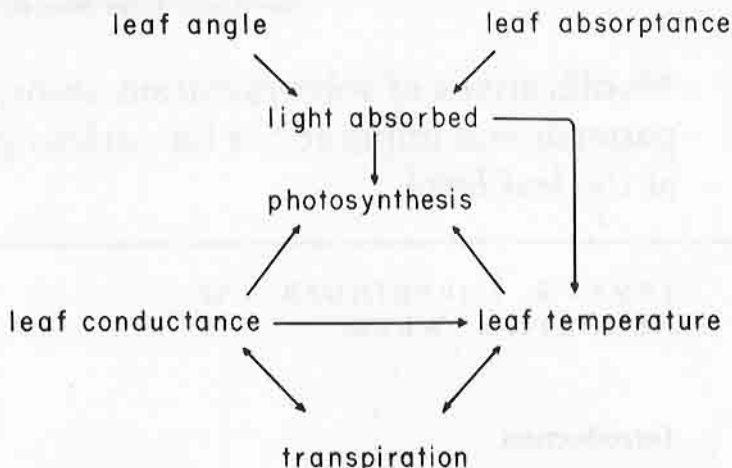
leaf angle   leaf absorptance
        ↘   ↙
              light absorbed ─────┐
                   ↓   │
            photosynthesis   │
           ↗   ↖   │
          ╱   ╲   ↓
leaf conductance ──────────→ leaf temperature
         ↘   ↗
          ↘   ↗
            transpiration

Figure 2.1.   Interactions between effects of leaf angle and leaf absorptance on leaf temperature and the processes of photosynthesis and transpiration.

ment. At the leaf level, photosynthesis and transpiration are tightly coupled to each other via energy and gas exchange, which are influenced by properties of the leaf (Figure 2.1). In this chapter we shall focus on the effects of changes in leaf absorptance and leaf angle.

The leaf angle will directly influence the amount of solar radiation incident on a leaf through its effect on determining the cosine of the angle of incidence ($\cos i$) between the normal to the leaf lamina and the direct solar beam, as outlined in equation (2.1):

$$\cos i = (\cos a_l)(\sin a_s) + (\sin a_l)(\cos a_s)[\cos(z_s - z_l)] \qquad (2.1)$$

where a_l and a_s are the angles of the leaf and sun above the horizontal, and z_l and z_s are the azimuths (compass directions) of the leaf and the sun.

The leaf absorptance will determine what fraction of the incident solar radiation is absorbed by the leaf. Two different leaf absorptances to solar radiation need to be considered: the leaf absorptance to the 400–700-nm waveband for photosynthetic studies and the leaf absorptance to the 400–3,000-nm waveband for heat-balance studies. The two leaf absorptances as percentages are empirically related by equation (2.2) (Ehleringer 1981):

$$a_{400-3,000} = (0.73)(a_{400-700}) - 11.9 \qquad (2.2)$$

Thus, the amount of direct-beam solar radiation absorbed by a leaf, which can influence the photosynthetic rate and/or leaf temperature, is

$$Q_k = (a_k)(\cos i)(I_p) \qquad (2.3)$$

where Q_k is the total direct-beam solar radiation absorbed by the leaf (either as 400–700-nm photon flux or 400–3,000-nm thermal radiation), a_k is the absorptance to that waveband, and I_p is the intensity of the solar beam on a perpendicular to that beam.

Only about 1% of the photons in the 400–700-nm waveband are used to drive the light reactions of photosynthesis; most of the solar radiation is converted to heat, raising the leaf temperature (T_l). A change in leaf temperature will directly affect photosynthesis (A), and thus the amount of light absorbed by the leaf will have both direct and indirect effects on the rate of this process. A third parameter directly influencing the photosynthetic rate is the leaf conductance to water vapor (g), which affects the rate of carbon dioxide diffusion into the leaf, as shown in equation (2.4):

$$A = g(c_a - c_i)/1.6 \qquad (2.4)$$

where c_a and c_i are the ambient and intercellular carbon dioxide concentrations and 1.6 is the ratio of the molecular diffusion rates of water and carbon dioxide in air.

As shown in equation (2.5), the leaf conductance will also directly affect the transpiration rate E, because water vapor must diffuse through the same stomatal pore openings as does carbon dioxide:

$$E = g(\Delta w) \qquad (2.5)$$

The magnitude of E is also dependent on the water vapor concentration gradient between the leaf and the air (Δw), and thus T_l has a direct effect on E. Because E imparts a significant heat loss from the leaf, it both affects and is affected by T_l (Gates 1962).

From the preceding it should be clear that a quantitative evaluation of the "adaptive or evolutionary significance" of a change in leaf absorptance or leaf angle for plant fitness is not possible without first understanding its effects on photosynthesis, leaf temperature, and water relations.

As a reference point for our discussion of changes in leaf angle or leaf absorptance, let us use a hypothetical green leaf with a leaf angle of 0° (a horizontal leaf). If for this hypothetical green leaf we assume that air temperatures and nutrient and water availabilities are optimal for growth, the leaf photosynthetic rate will increase with increasing irradiance and may or may not become saturated by typical midday irradiance levels (see Chapter 1). Leaves with greater enzyme content and photochemical capacity should become light-saturated at proportionally higher irradiances (see Chapter 1). As irradiance levels increase, the stomata also open, resulting in increased transpiration. It is this inevitable loss of water via transpiration through the stomata in order for the leaf to take up carbon dioxide via

photosynthesis that establishes a tradeoff between photosynthesis and transpiration.

Recent experimental evidence indicates that under well-watered conditions, the responses to irradiance of stomatal opening and photosynthetic rate appear coupled, such that c_i remains nearly constant, although there may be variation in c_i between species (Körner et al. 1979; Wong et al. 1979; von Caemmerer and Farquhar 1981; Farquhar and Sharkey 1982).

The question we would like to ask is what would happen to this hypothetical green leaf if g is decreased in response to less water availability (e.g., increased Δw or decreased leaf water potential)? What are the effects on A, E, and T_l? If there were no physiological changes at the leaf level other than a decreased g, then we would expect to observe three changes at the leaf level. First, A should become light-saturated at a lower irradiance level because of the decreased g. Second, as a consequence of a decreased g, T_l will be higher. This could raise Δw sufficiently that E would not be decreased in exactly the same proportion as g was decreased. Also, T_l could become sufficiently high and result in thermal damage to the photosynthetic apparatus. Third, in response to leaf exposure to supersaturating photon fluxes, photochemical damage may occur (i.e., photobleaching or photoinhibition).

What are the observed patterns in the field?

Before addressing the difficult questions of the costs and benefits of leaf angle or leaf absorptance changes, let us examine what trends are observed in the field. We analyze these trends at three levels: the community-level patterns, intrageneric patterns, and intraspecies seasonal patterns.

Community-level patterns of leaf absorptance and leaf angle

Precipitation and temperature gradients are often steep over short distances in the western United States, especially when elevated changes are involved. As a consequence, there can be large variations in habitat aridity over short geographical distances. Billings and Morris (1951) initially demonstrated that if the dominant species at two community extremes along an aridity gradient in central Nevada (saltbrush and coniferous forest) were compared, the species at the drier sites tended to have higher leaf reflectances.

In a recent survey of leaf energy-budget parameters for 192 species common to the Wasatch Front in Utah, intercommunity-level trends were analyzed for changes in leaf absorptance and leaf angle along an altitudinal

Table 2.1. *Average values of leaf absorptance to solar radiation (400–700 nm) and leaf angle for the dominant species in communities along the Wasatch Front, Utah*

Community[a]	Average leaf absorptance (%)	Average leaf angle (degrees)
Saltbush (13)	75.2	57.8
Grassland (36)	80.9	53.2
Oak-maple (17)	82.6	51.7
Juniper woodland (28)	76.4	43.8
Mountain brush (13)	84.3	23.1
Coniferous forest (28)	81.4	34.1
Alpine meadow (27)	79.5	38.7
Lower riparian (21)	82.1	46.4
Upper riparian (9)	83.3	36.1

[a] Plant communities are arranged in order of decreasing aridity. Values in parentheses are species sample sizes.

cline (Table 2.1). The lowest leaf absorptances, the greatest range of leaf absorptance values, and the steepest leaf angles were observed in the saltbush community. This plant community also occupies the most arid site along the transect. The low leaf absorptances observed in plants from this habitat resulted from increased leaf surface reflectance. Proceeding to less arid sites, the average leaf absorptance increased and reached a maximum in the mountain brush community. At higher elevations the average leaf absorptance decreased slightly because of increased leaf transmittance in the herbaceous species of the coniferous forest and alpine meadow communities. Average leaf angles showed a trend similar to that of leaf absorptance, decreasing as one proceeds from the saltbrush community up to the mountain brush community. It is interesting that there is a small but significant increase in the average leaf angle as one proceeds from the mountain brush community up through the alpine meadow community.

Although the saltbush community is the driest plant community along the Wasatch Mountains, still drier plant communities occur in the Mohave and Sonoran deserts to the south. In a survey of the common species in these deserts, Ehleringer (1981) found average leaf absorptances of the perennial vegetation to be lower than reported for the saltbush community (Figure 2.2). Thus, at the plant community level, there was a consistent trend for leaf absorptance to decrease as aridity (= decreased precipitation) increased.

Decreases in leaf absorptance can result from increased reflectance or from increased transmittance. Several surface modifications can result in increased reflectance, including waxes (Reicosky and Hanover 1978; Mulroy 1979; Ehleringer 1981), hairs (Pearman 1966; Sinclair and
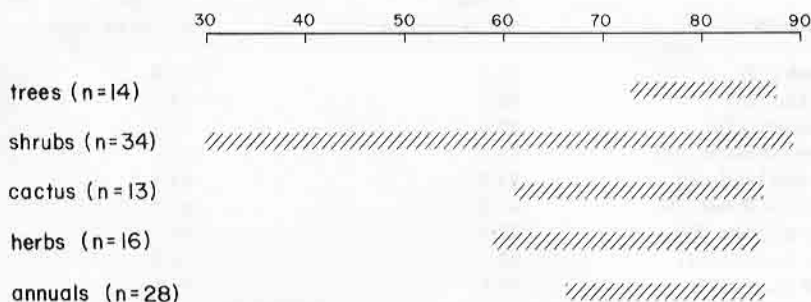
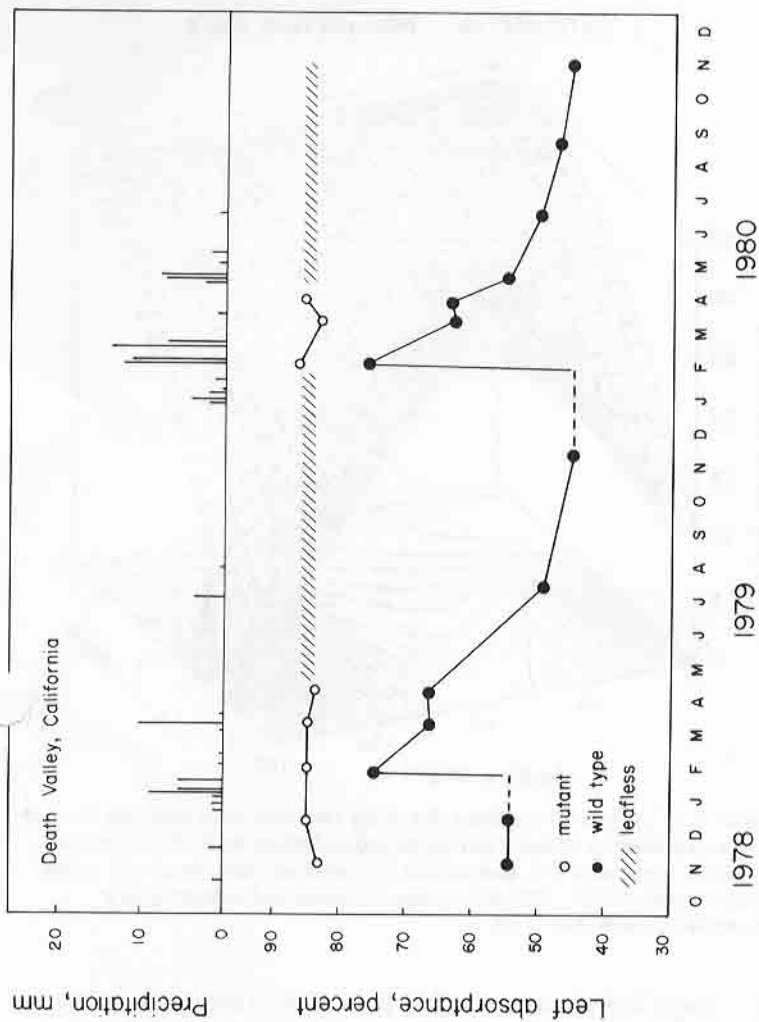Figure 2.3. Seasonal courses of precipitation and of leaf absorptance of solar radiation (400–700 nm) in leaves of *Encelia farinosa* in Death Valley, California. Also plotted are the in situ seasonal leaf absorptances for a mutant form of this species that lacks the reflective leaf hairs. (From Ehleringer 1983a.)
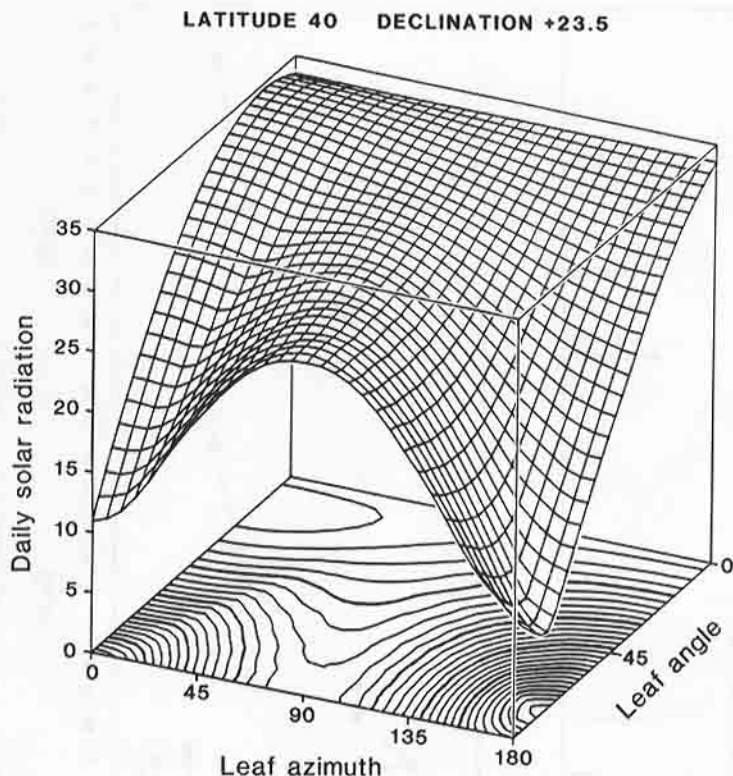
LATITUDE 40   DECLINATION +23.5

Figure 2.4. A three-dimensional plot of the total daily solar radiation incident on leaves possessing different leaf angles and leaf azimuths. Leaf azimuths are measured from south (0°). Calculations are based on a latitude of 40°, a solar declination of +23.5°, 10% diffuse solar radiation, and an atmospheric transmission coefficient of 0.8.

Green leaves (high leaf absorptance, low pubescence) are produced at the beginning of the growing season when soil water availability is high. As soil water availability decreases (leaf water potential decreases), new leaves are produced that are more pubescent and have lower absorptances (Ehleringer and Björkman 1978; Ehleringer 1982). The relationship between degree of leaf pubescence and leaf water potential is linear and without an initial threshold, so that the plant is constantly adjusting the leaf spectral characteristics in response to decreased soil water availability (as measured by decreasing leaf water potential) (Ehleringer 1982).

Variation in leaf angle and azimuth

The orientation of a leaf (angle and azimuth) affects three separate aspects of solar radiation intercepted by its lamina: (1) daily integrated

Table 2.2. *Mean leaf angles for a number of common perennial species in the Mohave and Sonoran deserts*

Species	Leaf angle (degrees)	Leaf type
Ambrosia dumosa	36.6	Drought-deciduous
Atriplex hymenelytra	67.5	Evergreen
Datura meteloides	19.9	Drought-deciduous
Encelia asperifolia	33.0	Drought-deciduous
Encelia farinosa	26.0	Drought-deciduous
Encelia frutescens	31.1	Drought-deciduous
Larrea divaricata	48.4	Evergreen
Simmondsia chinensis	84.2	Evergreen
Viguiera laciniata	31.8	Drought-deciduous
Viscainoa geniculata	67.8	Evergreen

radiation, (2) peak instantaneous irradiance, and (3) diurnal distribution of instantaneous incident irradiance. The interaction between leaf angle and azimuth is frequently ignored by investigators (because it is often assumed that the leaves have a random distribution of leaf azimuths), and most of the data on leaf orientation presented in the literature provide informa-ɔn on leaf inclination only.

A response surface for daily integrated solar radiation as a function of both leaf angle and leaf azimuth is presented in Figure 2.4 (for the summer solstice at 40° N latitude). In general, increasing leaf angle will result in a decrease in the amount of irradiance incident on a leaf. Thus, along the Wasatch Mountain transect, the leaves at the most arid sites will have less solar radiation incident on them. However, this holds true only if the distribution of azimuths is random (most of the species). In the warmer Mohave and Sonoran deserts, leaf angles for evergreen-leaved perennials tend to be more steeply inclined than those for deciduous-leaved perennials (Table 2.2).

Nonrandom leaf azimuths

There can be large variations in the amount of solar radiation incident on a leaf, depending on the specific leaf orientation. For instance, a vertical leaf with its lamina facing east receives as much solar radiation over the course of a day as a leaf facing northeast or northwest with an inclination of 30° from horizontal or a leaf facing southeast or southwest with an inclination of 55°. Steeper leaf angles need not necessarily reduce the solar radiation received during the summer or increase the solar radiation received during the winter if particular leaf azimuths are considered. For the Wasatch Mountain transect, the distributions of leaf azimuths
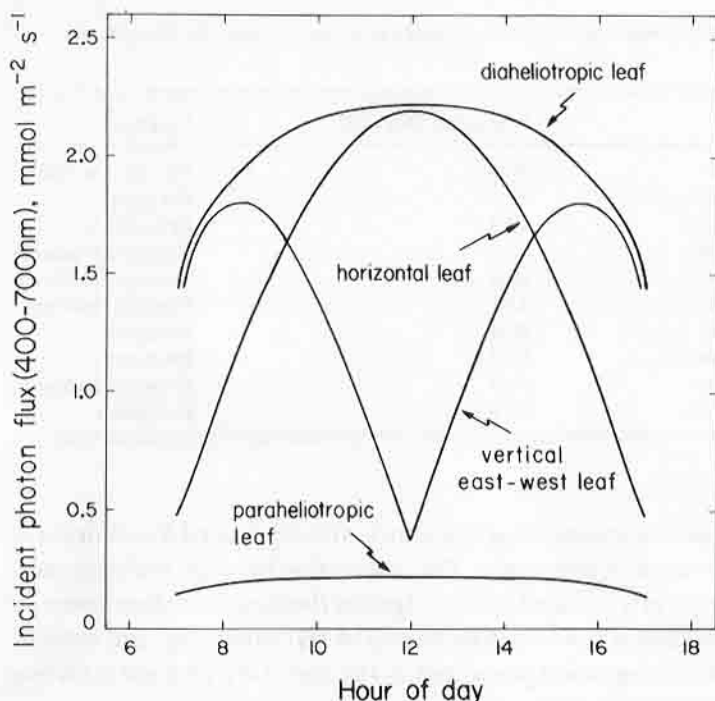
Figure 2.5. Photon flux (400–700 nm) incident on leaves with different orientations on a diurnal basis. Calculations are based on a latitude of 40° and a declination of 10°. The diffuse solar radiation was assumed to be equal to 10% of the incident perpendicular solar beam.

appear to be random, except for two notable exceptions: compass plants and solar-tracking plants, which will be discussed later.

The effect of nonrandom leaf azimuths on the solar radiation received by a plant is dependent on the specific orientation and the solar declination and latitude. East–west lamina orientations greatly reduce winter solar radiation while only slightly reducing summer radiation. The diurnal distribution on a steeply angled leaf facing east–west is heavily weighted toward the early morning and late afternoon, reducing midday irradiance (Figure 2.5). The steeper the leaf angle, the more the irradiance is shifted away from noon. The so-called compass plants (e.g., *Lactuca serriola, Silphium* species) are examples of species whose leaves are steeply inclined, with their lamina facing east–west. The frequency of species with this unusual leaf orientation is low.

North–south lamina orientations result in a simple parabolic distribution of solar irradiance over the course of a day. The amount received is

reduced by steep inclinations in the summer and low inclinations during the winter. This lamina orientation can result in enhanced daily integrated irradiance if the inclination is approximately equal to the latitude minus the solar declination. Thus, low inclinations during the summer, intermediate inclinations during the spring and fall, and steep inclinations during the winter will maximize the daily integrated irradiance received by a south-facing leaf growing in the middle latitudes (see Chapter 3 for examples of this with cacti).

Leaf solar tracking

Leaves from a number of species do not remain in a fixed position diurnally, but move through the day such that the lamina remains perpendicular to the sun's direct rays (Figure 2.6). Such leaves are called diaheliotropic (= solar tracking) and receive a more or less constant irradiance throughout the day (Figure 2.5). As a consequence of this higher instantaneous solar irradiance, diaheliotropic leaves may receive as much as 35% more solar radiation over the day than a fixed leaf with a horizontal orientation (Shackel and Hall 1979; Ehleringer and Forseth 1980).

Leaf solar tracking occurs in herbaceous species and is most common in annuals. In the Wasatch Mountain transect, leaf solar tracking was effectively restricted to the grassland community. In drier sites, Ehleringer and Forseth (1980) noted that the frequency of leaf solar tracking in the annual flora of a community was inversely related to the length of the growing season and reached as high as 75% of the species in the summer annuals of the Sonoran Desert.

Costs and benefits of morphological changes for photosynthesis and transpiration

Leaf absorptance

To illustrate the costs and benefits of a leaf spectral change in plants, let us consider *Encelia*, a common genus of shrubs in the arid western United States. Members of the genus *Encelia* produce drought-deciduous leaves covered to different extents with leaf pubescence on both upper and lower surfaces. Along geographical clines of decreasing precipitation, there is a replacement of species such that leaves exhibit increases in both the density and thickness of the pubescence layer (Ehleringer 1980, 1983b). The effect of the leaf pubescence is to cause the leaf absorptance (400–700 nm) to decrease (via increased reflectance) from 85% at the
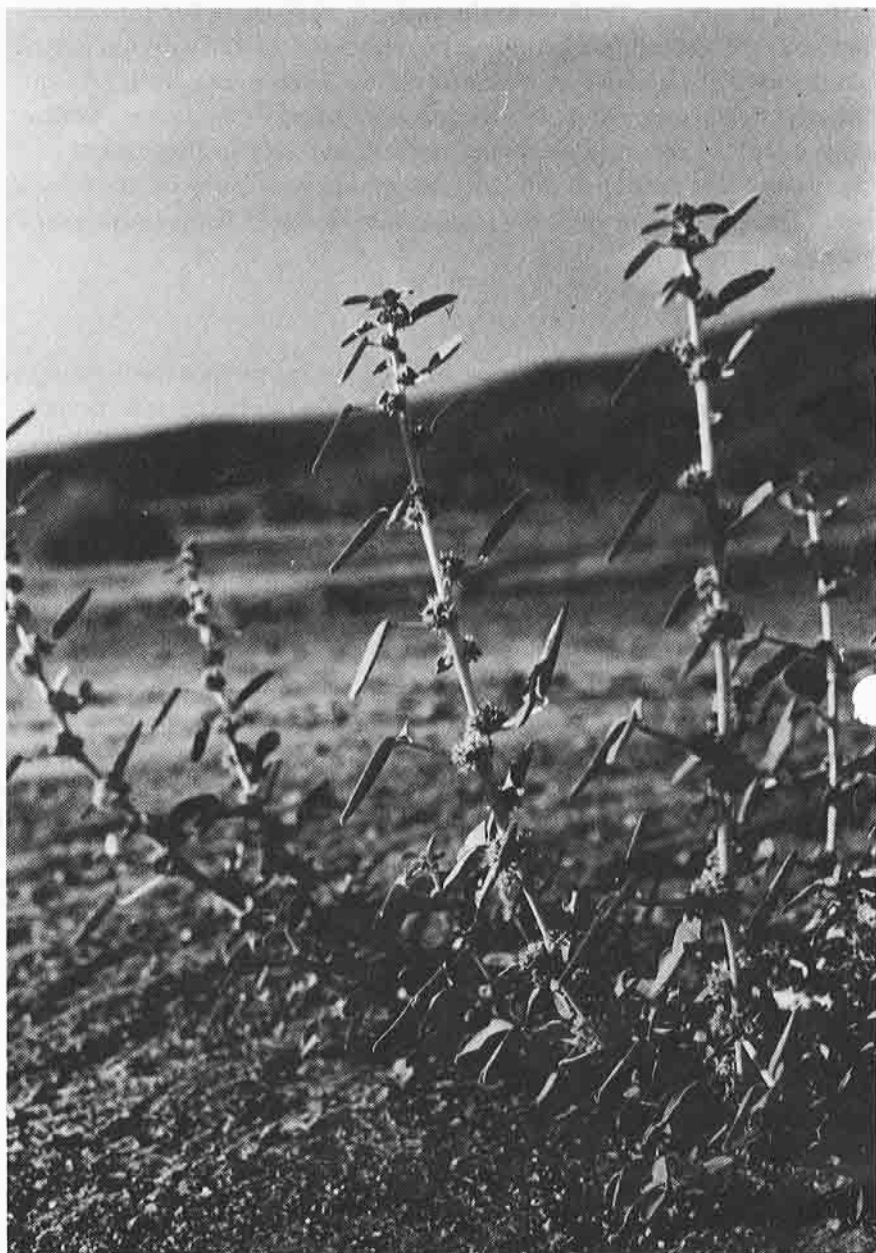
Figure 2.6.   Leaves of *Oxystylis lutea* showing the diaheliotropic leaf orientation.
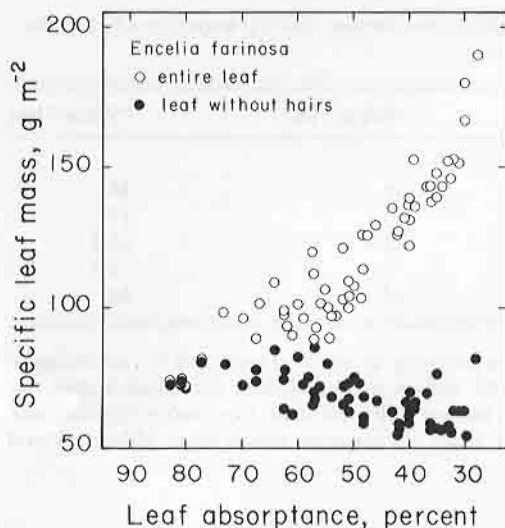
Figure 2.7. Relationship between specific leaf weight of *E. farinosa* leaves, with and without hairs, as a function of leaf absorptance of the intact leaf. (From Ehleringer and Cook 1984.)

wettest sites to as low as 29% at the driest sites (Ehleringer et al. 1976; Ehleringer and Björkman 1978).

Encelia farinosa occurs at the dry end of *Encelia*'s distribution and varies its leaf absorptance on a seasonal basis in response to changes in drought (Figure 2.3). During wet periods, leaves are green, with an absorptance of 80%. However, as leaf water potential decreases, new leaves are produced, with progressively lower absorptances (Ehleringer 1982). The relationship between midday leaf water potential and the extent of leaf pubescence development is linear, with a change in leaf absorptance of approximately 9% per MPa.

As a minimum, the caloric cost to produce an *E. farinosa* leaf with reduced leaf absorptance is the caloric cost to produce the mass of the hairs responsible for leaf absorptance changes. Figure 2.7 plots the specific leaf weight of intact leaves with pubescence and the same leaf after the pubescence has been removed as a function of leaf absorptance. These data indicate that the mass of the photosynthetic and conducting tissues remains constant at all leaf absorptances. All of the specific leaf weight differences are due to hair production. At the heavily pubescent end (low leaf absorptance), the cost to produce a leaf is high, because the hairs represent approximately 55% of the total leaf mass.

Table 2.3. *Calculated values of photosynthesis, transpiration, and leaf temperature for* Encelia farinosa *under midday summer conditions*[a]

Variable	"Green" leaf	"White" leaf
Absorptance (%)		
400–700 nm	85	40
400–3,000 nm	50	17
Leaf temperature (°C)	43.5	37.5
Transpiration (mmol m^{-2} s^{-1})	6.1	4.1
Photosynthesis (% of maximum)	36	82

[a] Energy-budget calculations assume the following values: wind speed 1 m s^{-1}, soil temperature 50°C, air temperature 40°C, 10% diffuse solar radiation, sky infrared radiation 350 W m^{-2}, air vapor density 10 g m^{-3}, leaf angle 25°, leaf width 4 cm, and leaf conductance 0.09 mol m^{-2} s^{-1}. Photosynthetic rate based on response curves from Ehleringer and Mooney (1978).

We can use the production-value approach of Penning de Vries et al. (1974) to estimate the cost to produce different leaf types in *E. farinosa*. If we assume that the pubescence consists only of cellulose and hemicellulose, we calculate a cost of 92.5 g glucose per m^2 leaf for very lightly pubescent leaves and a cost of 188 g glucose per m^2 leaf for heavily pubescent leave Production of pubescent leaves thus represents a significant investment on the part of the plant, and it is of interest then to understand just how the plant benefits from this additional investment in leaf structure.

One immediate benefit of the reduced leaf absorptance in pubescent *E. farinosa* leaves is a reduction in the heat load. This translates into a reduced leaf temperature and thus a lower transpiration rate (because Δw is reduced). The calculations from Table 2.3 illustrate that the pubescent leaf will have a temperature 6°C lower than the nonpubescent leaf. As a result of this lower leaf temperature, the transpiration rate will be approximately 33% less in the pubescent leaf. This saving in water loss at the single leaf could allow the plant to maintain more leaves (and thus more photosynthesis) under water-limited conditions or to maintain activity for a longer period of time into the drought period.

There are two additional benefits of the increased pubescence that directly affect photosynthesis. Ehleringer and Mooney (1978) showed (1) that the pubescence lowered leaf temperatures enough that the "upper lethal leaf temperature" was avoided and (2) that at temperatures above 30°C (thermal optimum for photosynthesis), the increase in photosynthetic rate by having a lowered leaf temperature was greater than the potential decrease in photosynthetic rate caused by increased photon re-

flectance. More recently, Ehleringer and Cook (unpublished data) have shown that under lower leaf water potentials, the photosynthetic rate becomes light-saturated at irradiances lower than midday levels. Thus, the pubescence is serving the additional benefit of reflecting excess photons that cannot be effectively used in photosynthesis under water-limited conditions.

We can very roughly estimate the net benefits of having the "more expensive" pubescent leaf in terms of water loss or carbon gain. Because a pubescent leaf is transpiring at a rate approximately one-third less than that of a nonpubescent leaf, it can remain photosynthetically active for a period about one-third longer. Calculating a conservative photosynthetic rate of $10 \ \mu\text{mol m}^{-2} \text{ s}^{-1}$ over a 12-hr day will result in fixation of approximately $0.43 \ \text{mol CO}_2 \ \text{m}^{-2}$. At this rate, the extra investment in leaf pubescence in a leaf can be recovered in approximately eight days ($81 \ \text{g m}^{-2}$ pubescence on a low-absorptance leaf whose specific leaf weight is $150 \ \text{g m}^{-2}$ will cost $95.6 \ \text{g glucose m}^{-2}$, divided by daily carbohydrate gain of $13.0 \ \text{g glucose m}^{-2}$). Thus, as a rough approximation, if the pubescence allows a leaf to remain active for a period eight days longer than a nonpubescent leaf, that should result in an overall net carbon gain by the leaf.

Leaf solar tracking

The biochemical energy costs to achieve solar tracking are thought to be small, because the movements usually are accomplished by small turgor changes in the pulvinal region of the petiole. There are definite costs, though, associated with the presence of diaheliotropism. One such cost is that because only a small fraction of the incident solar radiation passes beyond the solar-tracking leaf, the extent of potential canopy development becomes restricted. In the arid western United States, diaheliotropic plants usually have very low leaf area indices (Ehleringer and Forseth 1980). A second cost associated with solar tracking is that the leaf is exposed to much higher irradiances, resulting in a greater thermal load on the leaf and thus higher leaf temperatures (Forseth and Ehleringer 1983b).

There are distinct advantages associated with diaheliotropic leaf movements, particularly in habitats with short growing seasons. A diaheliotropic leaf will receive approximately 30% more photons over the day than will a horizontally fixed leaf (Figure 2.5). In order to take advantage of these higher irradiances, leaves of solar-tracking species should not be light-saturated at midday irradiance levels. Werk et al. (1983) studied the photosynthetic rates of a large number of desert winter annuals and found that species with solar-tracking leaves tended to have higher photosyn-
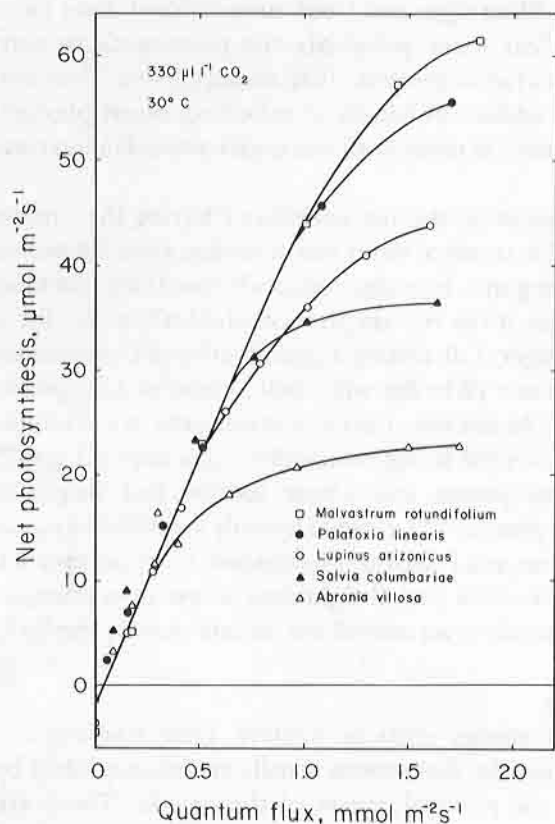
Figure 2.8.   Dependence of net photosynthesis on incident photon flux (400–700 nm) in leaves of several winter desert annuals. *Lupinus arizonicus*, *Malvastrum rotundifolium*, and *Palafoxia linearis* exhibit diaheliotropic leaf movements. (From Werk et al. 1983.)

thetic rates than species with nontracking leaves at midday irradiances (Figure 2.8). Moreover, the solar-tracking leaves (*Lupinus*, *Malvastrum*, and *Palafoxia* in Figure 2.8) were not light-saturated at light levels comparable to what the leaves would receive over the course of the day in the field.

Paraheliotropic leaf movements

The higher heat load of a solar-tracking leaf places the leaf in an unfavorable water-relations position during periods of limited water availability. In this situation, a large fraction of species with diaheliotropic leaves also exhibit paraheliotropic movements (Ehleringer and Forseth 1980). That is, during periods of low water availability, the leaf will move

during the day such that the leaf lamina is parallel to the sun's direct rays (Figure 2.9). As a consequence, the leaf is exposed to much lower light levels and heat loads (Figure 2.5).

One example of such a plant with both diaheliotropic and paraheliotropic leaf movements is *Lupinus arizonicus,* a common annual in the Mohave and Sonoran deserts (Forseth and Ehleringer 1980). In response to lower leaf water potentials, the cosine of the leaf's angle of incidence to the sun's direct rays decreases (Figure 2.10). Forseth and Ehleringer (1983b) have shown that at the same time as soil water becomes less available, the leaf conductance and photosynthetic rate also decrease (Figure 2.10). Even though there is also a reduction in the intercellular CO_2 concentration as the leaf water potential decreases, these results should not be interpreted as meaning that stomata are necessarily imposing a greater limitation on photosynthetic rate. Calculations of the stomatal limitation on photosynthesis (using the equation from Farquhar and Sharkey 1982) indicate that there is no increase in the stomatal limitation with decreasing leaf water potential. Rather, the parallel nature of the declines in these parameters suggests that the reduction in light incident on the leaf reduces electron-transport rates to a degree similar to the reduction in the rate of CO_2 supply by diffusion through the stomata so that the rates of these two processes remain in balance. Therefore, we can conclude that the paraheliotropic leaf movements are not advantageous in terms of increasing net productivity per se, but rather are advantageous in allowing the leaf to avoid higher leaf temperatures and exposure to high photon fluxes that cannot be used by the photosynthetic apparatus.

A major advantage of leaf solar tracking is that it allows the leaf to achieve maximal rates of photosynthesis early in the morning when Δw is lowest (Forseth and Ehleringer 1983b; Forseth et al., unpublished data). This feature will be of significant advantage in habitats with low midday humidities, because the stomata of most plants close in response to increased Δw.

Simulations comparing the performances of paraheliotropic leaves with fixed leaf orientations strongly suggest that under water-limited conditions, daily water-use efficiency (A/E) is higher in the paraheliotropic leaf (Forseth and Ehleringer 1983b). Additionally, by having a reduced heat load, the paraheliotropic leaf avoids higher leaf temperatures and thus higher transpiration rates.

Steep fixed leaf angles

When a canopy is composed of many leaves with random azimuths but nonrandom inclinations, the situation becomes complex. Individual

Figure 2.9.   Leaves of *Lupinus arizonicus* showing the cupped nature of the paraheliotropic leaves under water-stressed conditions.
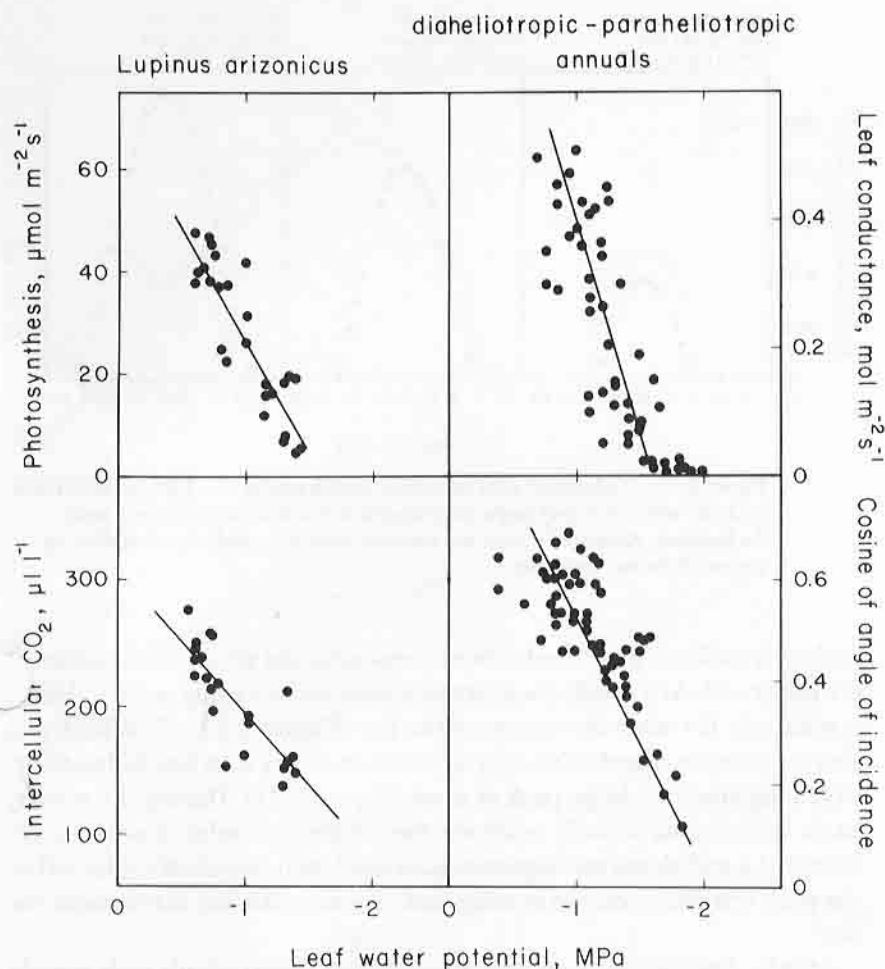
Figure 2.10. Relationships of the cosine of the angle of incidence, the photosynthetic rate at high irradiance, leaf conductance, and intercellular CO_2 concentration to leaf water potential in leaves of *Lupinus arizonicus*, a plant whose leaves exhibit both diaheliotropic and paraheliotropic movements. (Modified from Forseth and Ehleringer 1980, 1983a.)

leaves within the canopy are subject to very different patterns of solar irradiance (Figure 2.4). The simplest method used to understand these patterns is to average the irradiance received by all the leaves. This provides us with an overview of a canopy-level phenomenon, but ignores details such as the peak irradiance received by any one leaf.

On average, steep leaf inclinations reduce the light intercepted by leaves during the summer. The diurnal distribution is also changed, so that
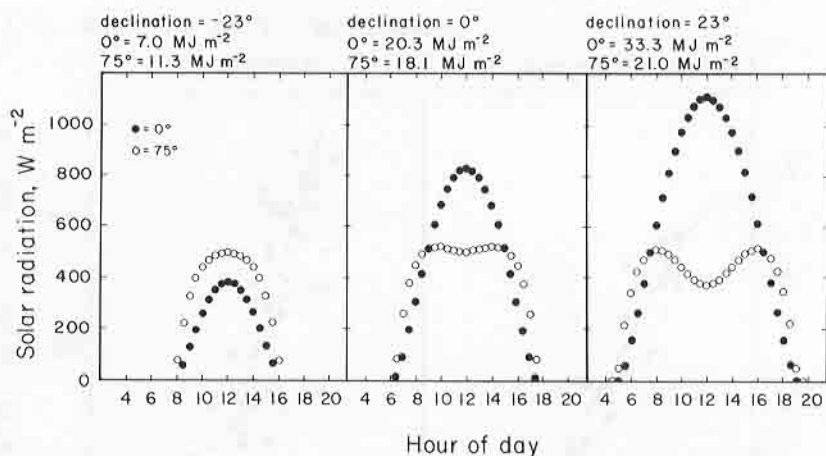
Figure 2.11.   Calculated solar radiation levels incident on a horizontal leaf and on a leaf with a 70° leaf angle (and random leaf azimuth) at different solar declinations. Above each plate are the total daily solar radiations incident on the two different leaf types.

midday irradiance is reduced, whereas morning and afternoon irradiance are enhanced. As a result, the average irradiance of steeply inclined leaf is relatively flat over the course of the day (Figure 2.11). This contrasts sharply with the distribution of irradiance on leaves with low inclinations, which experience a large peak at noon (Figure 2.11). During the winter, steep inclinations actually enhance the amount of solar irradiance received. An additional consequence associated with steep leaf angles is that the peak irradiance on the average leaf remains constant throughout the year.

Atriplex hymenelytra is an evergreen-leaved desert shrub with steeply inclined leaves oriented randomly with respect to azimuth (Mooney et al. 1977). Photosynthesis is light-saturated at relatively low irradiances (Mooney et al. 1982), similar to the maximal irradiance incident on the steeply inclined leaves in Figure 2.11. *A. hymenelytra* is also characterized by having salt bladders on the leaf surface that dry out during drought. This causes the salts within the bladders to crystallize and results in decreased leaf absorptance. The implications of the steep leaf inclination for photosynthesis and transpiration can be evaluated by asking what would happen if the leaf angle were lower or if the leaf absorptance were higher. We can calculate how much photosynthesis and transpiration would be affected by these changes during the summer months, which represent the drought period for these plants. Changing both leaf absorptance and angle

Atriplex hymenelytra   summer day   leaf conductance, 0.02 mol m^{-2} s^{-1}

	Leaf temperature (°C)	Transpiration (mmol m^{-2} s^{-1})	Photosynthesis (μmol m^{-2} s^{-1})	WUE (μmol / mmol)
	50	1.9	4	2.1
	47	1.7	7	4.1
	43	1.4	10	7.1

Figure 2.12.   Predicted relationships between leaf temperature, transpiration, photosynthesis, and water-use efficiency (ratio of photosynthesis to transpiration) as functions of different leaf absorptances and leaf angles. (Modified from Mooney et al. 1977, and based on photosynthetic data from Mooney et al. 1982.)

results in a 7°C decrease in leaf temperature from that of a horizontal green leaf (Figure 2.12). As a consequence only of this leaf temperature difference, the transpiration rate is predicted to be reduced by 34% and photosynthetic rate increased by 70%. These differences are quite large and should have a significant impact on plant performance, because these leaves are maintained throughout the prolonged drought periods. Morphological changes such as these not only may enhance plant performance in marginal habitats but also may be essential to their survival in these zones.

It is important to understand that when studying the average effect of leaf inclination on solar irradiance, we are overlooking the variation that exists within a plant. While reducing average irradiance during the summer, steeply inclined leaves also increase the range of solar irradiance incident on individual leaves. As leaf angles are increased, the difference between the highest peak irradiance received by a single leaf and the lowest is amplified (Figure 2.13). For the example presented in Figure 2.13, for a leaf inclination of 75° from horizontal, at least one leaf never receives more than 200 W m^{-2}, while another leaf receives more than 900 W m^{-2} peak irradiance. The importance of this type of variation on the overall performance of a plant is not known. It is likely that physiological and morphological differences exist between leaves with different orientations within a plant in the same way that differences exist between inner and outer leaves in dense canopies.
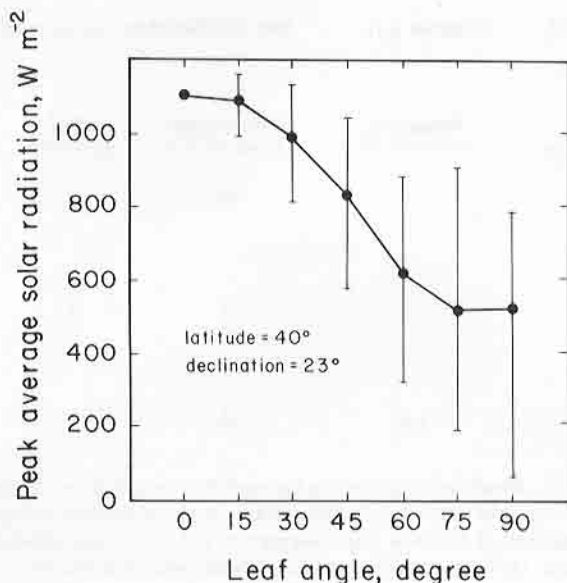
Figure 2.13.   Relationship between peak average solar radiation and leaf angle. Calculations were made using a latitude of 40° and a solar declination of +23.5°. Filled circles represent average values for all possible leaf azimuths; vertical lines represent absolute ranges of values by different leaf azimuths.

Steep leaf angles and nonrandom azimuths

In contrast to the case of randomly oriented leaves, the significance of specific nonrandom lamina orientations is much simpler to understand in functional terms. The effects of a specific orientation on daily irradiance, peak irradiance, and diurnal distribution of irradiance can all be related to their effects on leaf temperature, photosynthesis, and water loss. For example, north–south lamina orientations have been studied in several species of cactus (see Chapter 3). In these examples the specific orientation has been determined to increase the solar irradiance on the growing meristems or cladodes during the winter, the active growing season. Interception of irradiance during the summer drought periods is reduced, lowering the risk of excessive heating and/or desiccation.

East–west lamina orientations have been studied in cactus (Gibbs and Patten 1970; Nobel 1980) and in herbaceous plants (Dolk 1931; Werk and Ehleringer 1984). In all cases studied thus far, the east–west orientation was associated with vertical leaves. The major effect of this is that most of the solar radiation intercepted by the lamina is received early in the morn-
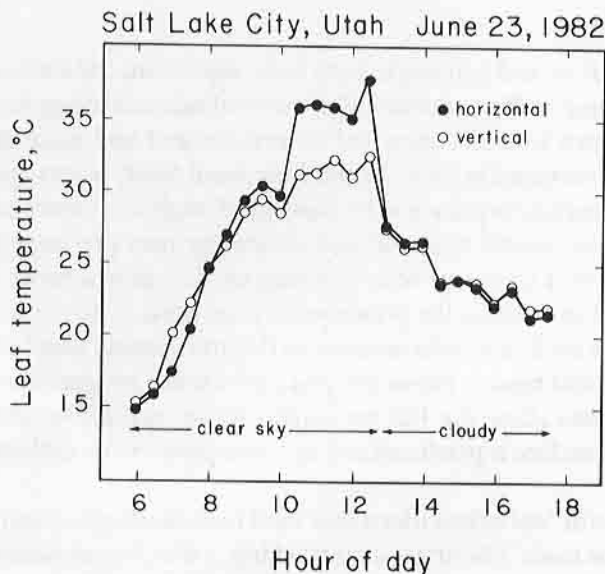
Figure 2.14. Diurnal courses of leaf temperatures on *Lactuca serriola* leaves oriented in the natural vertical position or modified so that the leaf was horizontal. (From Werk and Ehleringer 1984.)

ing and late in the afternoon. Midday irradiance is sharply reduced (Figure 2.5). Thus, the plants can be most active during the coolest time of the day when Δw is lowest. This can reduce water loss significantly, while not severely limiting photosynthesis.

Lactuca serriola is an annual that orients its leaves vertically, facing east–west (Werk and Ehleringer 1984). The effect of this leaf orientation on leaf temperature was determined by comparing the diurnal courses of leaf temperatures of adjacent leaves of a plant. One leaf was forced into a horizontal position and compared with a leaf left in its natural orientation. The patterns of leaf temperatures of these leaves closely followed the pattern of solar irradiance incident on them (Figure 2.14). The pattern of leaf-to-air vapor pressure deficits was very similar to that for leaf temperature. Leaf conductance to water vapor in *L. serriola* is reduced in response to increases in Δw (Werk, unpublished data); however, the response is not strong enough to completely offset the effect of Δw on transpiration. Thus, the horizontal leaf described in Figure 2.14 transpired approximately 10–20% more water over the course of the day than the naturally oriented leaf.

Conclusions

Leaf absorptance and leaf angle both have significant influences on leaf temperature and on the processes of photosynthesis and transpiration. In the arid western United States, leaf reflectance and leaf angle in plants increase with increased aridity. At the functional level, plants appear to use decreased leaf absorptance or increased leaf angle as a means of reducing water loss to extend their period of activity into prolonged drought periods and as a means of reducing photon flux at irradiances higher than necessary to saturate the photosynthetic process. The "cost" to produce a reflective surface may be as much as the investment "cost" to produce the glabrous leaf tissues. However, given how much longer these epidermal modifications allow the leaf to remain active into a drought period, the reflective surface is predicted to result in a positive net carbon gain to the plant.

There are two specific leaf orientations that tend to enhance photosynthetic rate on a diurnal basis. The first is solar tracking, which may enhance productivity at the leaf level because of the resulting high incident irradiances, but limits total canopy productivity by restricting the maximum canopy leaf area index. The second is fixed leaves with steep leaf angles and oriented with lamina in an east – west direction. This orientation ten to increase the incident irradiance and thus photosynthesis, early in the morning and again in the later afternoon. These are periods of the day when the transpirational demand is lowest.

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