STRESS TOLERANCE AND ADAPTIVE VARIATION IN LEAF ABSORPTANCE AND LEAF ANGLE

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ABSTRACT. Leaf absorptance and leaf angle are two morphological means by which chaparral plants can adapt to avoid stress during chaparral long summer drought periods in mediterranean climates. Both features tend to reduce the solar radiation absorption by leaves, thus reducing leaf temperatures and transpiration rates. Leaf absorptance changes do occur within chaparral species but intra- and interspecific changes are most common along aridity gradients. Leaf angles appear to be steep in chaparral plants and to show seasonal fluctuations, which further reduce radiation absorption during the drought periods.

INTRODUCTION

Leaf absorptance (the fraction of incident solar radiation absorbed by a leaf) and leaf angle (the angular deviation from the horizontal) are two leaf parameters linking a leaf with its surrounding physical environment. These parameters influence both the amount and the temporal pattern of solar radiation absorption by leaves. While variation in both leaf absorptances and angles in plants from different habitats have been known since the early studies of Haberlandt (1884), it is only recently that the ecophysiological significance of these features on leaf temperature, transpiration, and photosynthesis have been quantitatively evaluated (Raschke 1960, Gates 1962, Parkhurst and Loucks 1972, Ehleringer and Mooney 1978).

Changes in leaf absorptance and/or leaf angle will affect the leaf temperature, photosynthesis, and transpiration through both direct and indirect interactions. The linkages between parameters are illustrated in Figure 1. The arrows indicate the direction of the influence, and it can be seen that both leaf absorptance and leaf angle affect the amount of solar radiation absorbed by the leaf. Their impact is somewhat different with leaf angle influencing the diurnal/seasonal patterns of incident solar radiation and leaf absorptance reducing the total amount of solar radiation absorbed by the leaf irrespective of orientation effects. The amount of energy absorbed will have a direct influence on both photosynthesis and on leaf temperature. Because of the secondary influence of parameters on each other, changes in leaf angle and absorptance will have both direct and indirect influences on physiological processes. Ultimately, the changes in leaf angle and absorptance will have a net effect on water use and carbon gain by the plant, which will influence at a higher level of integration both survival and fitness.

Within the chaparral, few studies have considered the importance of leaf angle and/or leaf absorptance changes to the survival and fitness of the plants. Yet there is ample evidence to suggest that this is an important, overlooked aspect of adaptation within the chaparral. This paper reviews the limited data available for chaparral species.

SPECIES REPLACEMENT GRADIENTS

Leaf pubescence is a character commonly associated with arid habitats (Haberlandt 1884, Johnson 1975). Within the vegetation of southern California, increases in leaf pubescence along a gradient of decreasing precipitation has been observed among many different genera and families (Ehleringer 1984). No single species spans the transect from the relatively wet montane habitats to the drier desert sites, but there is a pattern such that on the wetter, more mesic sites species possess less pubescent leaves. Moving to progressively drier sites, species replacements within several genera possess leaves with increasing pubescence. *Brickellia, Encelia, Eriogonum, Salvia, Tetradymia,* and *Viguiera* are examples of genera which each contain a set of species

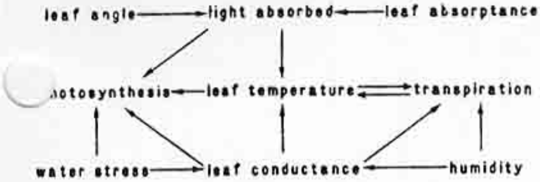

Figure 1. Interactions between leaf angle and leaf absorptance with other physiological processes and with net carbon gain. From Ehleringer and Clark (1988).

exemplifying this aridity-pubescence replacement series.

As the degree of leaf pubescence increases, leaf absorptance decreases. The *Salvia* replacement series through the chaparral illustrates this point. *Salvia mellifera* occurs on the wettest sites, and is first replaced by *S. leucophylla*, and by *S. apiana* on the driest sites (Ehleringer 1984). Figure 2 shows the absorptance spectra for leaves of these three species. *Salvia mellifera*, with a green, glabrate leaf has an absorptance spectrum between 400 and 700 nm (visible waveband) that is typical of most green leaves. In the gray-leaved *S. leucophylla*, the absorptances at all wavelengths are reduced, but otherwise the spectrum is similar to that of *S. mellifera*. *Salvia apiana* leaves are white in appearance and absorptance is clearly reduced at all wavelengths. Similar patterns also occur among species of *Arctostaphylos* (Shaver 1978) and *Encelia* (Ehleringer and Björkman 1978).

Intrageneric studies of leaf angle changes with habitat are less common, but among *Arctostaphylos* species, leaf angles do become steeper with aridity (Shaver 1978). At the community level, Ehleringer (1988) has shown that increasing leaf angles are common among all species as habitat aridity increases.

LEAF ABSORPTANCE AND ANGLE OF MEDITERRANEAN-CLIMATE PLANTS

Leaf absorptances range from 75 to 84% with a mean of 81% for the Chilean coastal scrub and 82% for the California coastal scrub. Within the evergreen sclerophyllous vegetation, leaf absorptances ranged from 70 to 87%, with the mean of the California and Chile plants being 78 and 82%, respectively. These values are not different from the leaf absorptances measured by Ehleringer (1988) for plants in habitats receiving 300–500 mm precipitation annually along the Wasatch Front of Utah. The point is that while leaf absorptance variation exists within the coastal scrub and evergreen sclerophyllous species, there is no evidence to suggest that large changes in leaf absorptance occur in a major fraction of the flora.

There are fewer survey data for leaf angles of mediterranean-climate plants. From those data available, the indication is that leaf angles can be steep (Lawrence 1975, Shaver 1978, Comstock and

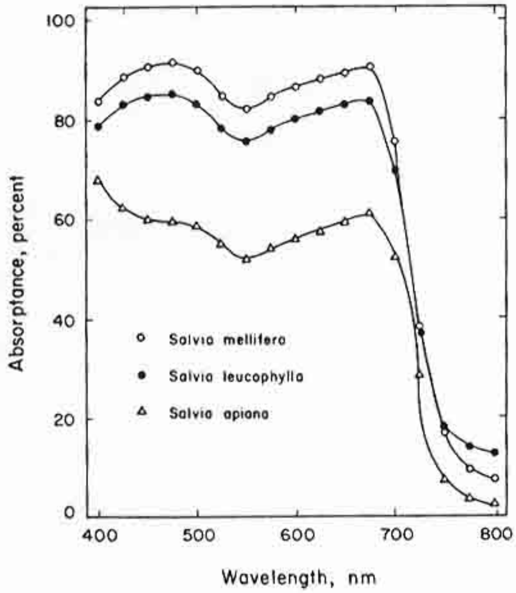

Figure 2. Leaf absorptance between 400 and 800 nm for three *Salvia* species occurring along an aridity gradient in southern California. From Ehleringer (1984).

Mahall 1985) and that leaf angles become progressively steeper with increased aridity (Shaver 1978).

STRESS AVOIDANCE BY REDUCING SOLAR RADIATION ABSORPTION

Within chaparral ecosystems, limited water represents a major stress affecting plant performance. Under these water-limited conditions, water stress results in a decreased leaf conductance and, since the carbon dioxide supply rates decrease with leaf conductance, there is a decreased need for photons to operate the photosynthetic light reactions. Photon flux levels beyond that required to saturate photosynthesis serves only to increase the leaf energy load and heat the leaf. Excessive solar radiation absorption may also be detrimental to the photosynthetic apparatus resulting in photoinhibitory damage (see contribution by Mahall for further details). Increased leaf temperatures could only serve to aggravate plant water stress. It appears reasonable that as an adjustment to water-limited conditions, natural selection may favor features which result in the reduction of the amount of solar radiation absorbed by the leaf. Leaf angles are often presumed to remain stationary through the season. If this is the case, we would expect that steep leaf angles, such as have been measured in several chaparral shrubs, should result in a greatly reduced solar radiation load at midday during the summer (Ehleringer and Werk 1986). The potential benefit to plant performance is that both transpirational demand and leaf temperature would be reduced.

An interesting observation by Comstock and Ma-

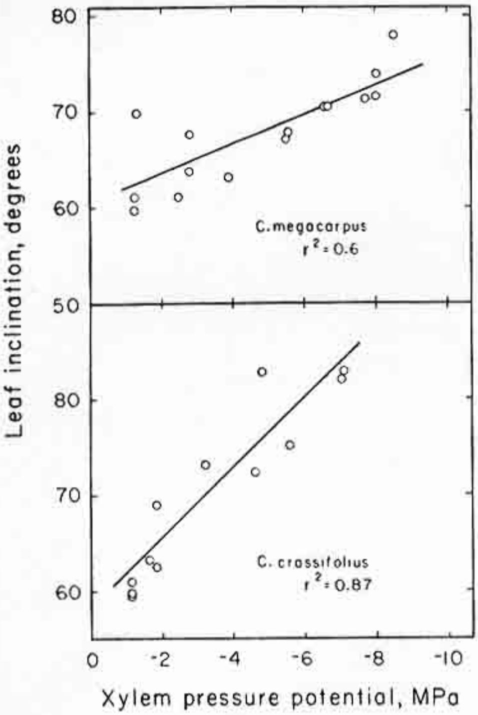

Figure 3. Average leaf angle of *Ceanothus megacarpus* and *Ceanothus crassifolius* as a function of leaf water potential. From Comstock and Mahall (1985).

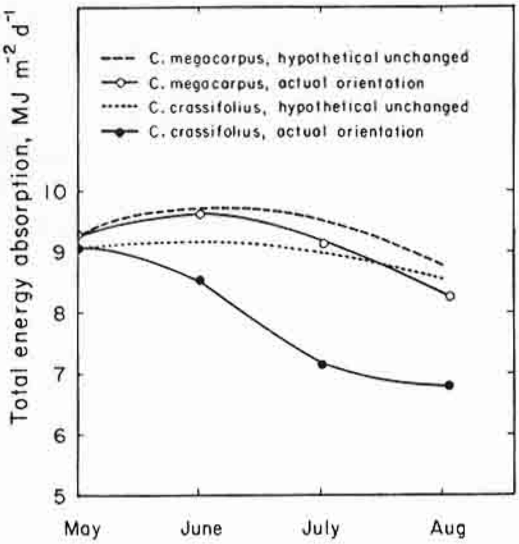

Figure 4. Simulated values for the average, total daily energy absorption using the measured leaf orientations and leaf absorptances for leaves of *Ceanothus megacarpus* and *Ceanothus crassifolius.* "Hypothetical unchanged" refers to the energy absorption that would have occurred had the leaf orientation remained unchanged from their values on 15 May. From Comstock and Mahall (1985).

hall (1985), however, suggests that studies of leaf angles of chaparral shrubs may be more revealing than previously considered. Comstock and Mahall (1985) measured leaf angles of two *Ceanothus* species in the chaparral near Santa Barbara over an annual cycle from the wet, active growth season through the long, summer drought period. They observed that leaf angles did not remain at a specific angle, but that leaf angles increased as leaf water potentials decreased (Fig. 3). Leaf angles of both *Ceanothus* were relatively steep at approximately 60°C during the wettest part of the year. However, by August when the summer drought was greatest, leaf angles had increased to almost 85° in *C. crassifolius* and 75° in *C. megacarpus.*

The consequence of these increased leaf angles was to decrease the solar radiation incident on the leaf. These changes in leaf orientation were sufficient to cause substantial reductions in the total amount of absorbed solar radiation (Fig. 4). During the peak water stress period in August, *C. megacarpus* leaves were absorbing 6% and *C. crassifolius* leaves 20% less solar radiation than if the leaf angles had not changed from the late springtime values. Comstock and Mahall (1985) calculated that the reduced thermal load on these leaves would reduce transpiration by 5%. Even though transpiration rates at this time of the year would be depressed by the overall low soil moisture availability, this 5% savings could be important in improving the probability of plant survival during extreme water stress periods.

The changes in leaf angle in *Ceanothus* leaves are completely reversible. This is an important feature since the life span is 14–15 months and leaf production is limited to the springtime. Photosynthetic activity in mediterranean-climate sclerophylls such as *Ceanothus* requires a lengthy period of time for leaves to cover all production costs and to achieve a net positive lifetime carbon gain (Miller and Stoner 1979). The low instantaneous rate of carbon gain may militate against irreversible leaf angle changes or morphological changes such as leaf pubescence, which tend to be irreversible (Ehleringer and Werk 1986), because these changes would be detrimental to productivity in the subsequent growing season.

The full implications of leaf angle or leaf absorptance changes to modify solar radiation absorptance patterns by chaparral species are not well understood. However, the recent literature available clearly suggests that major insights into plant adaptation and water stress avoidance are likely to emerge in the coming years.

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