

Some Recent Aspects and Problems of Chaparral Plant Water Relations¹

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Water is a critically important resource for plants and is often limiting with respect to plant growth, development, and distribution. Environmental water availability may also be quite variable in space and time. In view of both the significance of water to plant processes and its variability in nature, any mechanisms by which plants might stabilize their internal water environment against a changing external water regime would have great adaptive significance. Chaparral shrubs must endure droughts which occur repeatedly with varying severity over the lifetime of an individual plant (Mooney and Dunn 1970). The objective of this paper is to briefly review some current research results on the water relations of selected chaparral and matorral plants and to characterize aspects of the plant responses to developing water deficits during drought.

CHAPARRAL FIELD WATER RELATIONS

Field measurements of xylem pressure potential and leaf conductance were made through a summer drought cycle for *Adenostoma fasciculatum* H. & A., *Ceanothus greggii* var. *perplexens* (Trel.) Jeps. [C. p. Trel.], *Quercus dumosa* Nutt., and *Arctostaphylos glauca* Lindl. [A. g var. *eremicola* Jeps.], four common and widespread southern California chaparral shrub species (Munz and Keck 1959). Measurements were obtained from June through November 1978 at the Echo Valley research site in San Diego County, California. The research site has been previously described (Poole and Miller 1975, Mooney 1977, Thrower and Bradbury 1977). Measurements in *A. fasciculatum*, *C. greggii*, *Q. dumosa*, and *A. glauca* were obtained for individuals growing in close association on a north (pole-) facing slope. Additional measurements were made in a pure stand of *A. fasciculatum* growing on an adjacent south (equator-) facing slope.

Seasonal patterns of leaf water potential, measured with a pressure bomb (Scholander and

Abstract: Current research on the water relations of shrub species in the southern California chaparral and the central Chilean matorral vegetations is reported. A fair data base is now available to characterize water potentials, stomatal conductances, and plant water use patterns in some of the more common shrubs in the chaparral and matorral vegetations. Much less is known about the water relations of the herbaceous plants, succulents, and tree species of these areas. Osmotic relations appear particularly important in understanding adaptation of these plants to the mediterranean-climate water environment.

others 1965), appeared to segregate by species rooting distribution (fig. 1). *Ceanothus greggii* and *A. glauca*, which tend to be shallow-rooted (Hellmers and others 1955, Miller and Ng 1977) showed similar seasonal water potentials which were increasingly more negative than the water potentials in *A. fasciculatum* and *Q. dumosa*, which tend to be deep-rooted. Site effects can override species differences, however. *Adenostoma fasciculatum*, measured during the same time period in a pure stand on an adjacent equator-facing slope, showed consistently more negative minimum water potentials than *A. glauca* and *C. greggii* on the pole-facing slope (fig. 1). It thus appears that particular water potential values should not in general be taken as a

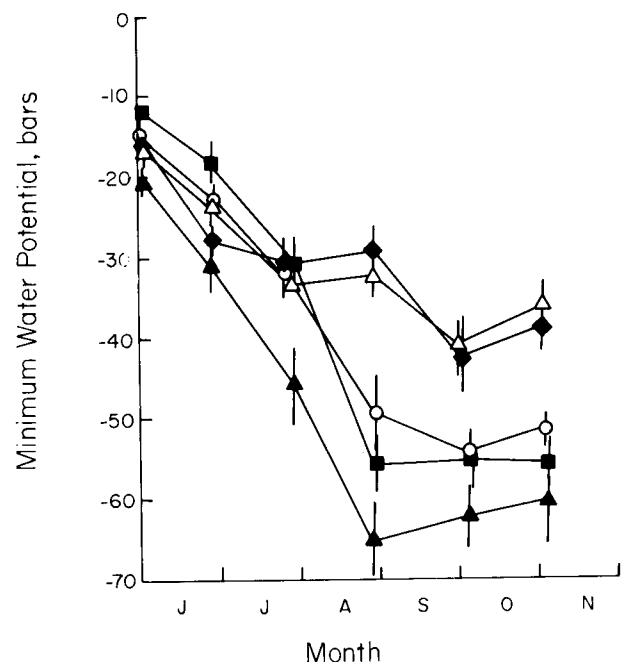


Fig. 1. Seasonal course of mean minimum leaf water potentials with standard errors estimated with a pressure bomb in *Adenostoma fasciculatum* on the pole- (Δ) and equator-facing slopes (\blacktriangle), and *Quercus dumosa* (\blacklozenge), *Ceanothus greggii* (\blacksquare), and *Arctostaphylos glauca* (\circ) on the pole-facing slope.

¹Presented at the Symposium on Dynamics and Management of Mediterranean-type Ecosystems, June 22-26, 1981, San Diego, California

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species-specific property. The water potential measurements may serve as a relative index of drought stress among several species occupying the same local site, but the variation in water potential within a species from site to site can be often greater than the interspecific water potential variation within a site.

Additional measurements of stomatal conductance were made using the "null-balance" porometer approach (Beardsell and others 1972). Maximum conductances showed differences between species and in *A. fasciculatum* there were further differences by leaf age class (fig. 2). All conductances reported here are based on the total leaf surface area. Conductances based on a projected leaf area would be twice the values reported here for the broadleaf species *A. glauca*, *C. greggii*, and *Q. dumosa*, and approximately three times the values reported here *A. fasciculatum*. Early season measurements showed *A. fasciculatum* with the highest conductance and new *A. fasciculatum* leaves with conductances of about 0.8 centimeters per second in mid-June. There were no differences in maximum conductances between old and new leaves of *A. glauca*, which generally showed the lowest maximum conductances. *Ceanothus greggii* and *Q. dumosa* showed maximum conductances intermediate to *A. fasciculatum* and *A. glauca*. In all species maximum conductance decreased as the drought cycle progressed, reaching late

season values of 0.05-0.15 centimeters per second.

Within *A. fasciculatum* maximum leaf conductances differed with leaf age class and shrub exposure (fig. 2). *Adenostoma fasciculatum* shrubs on the pole-facing slope showed higher maximum conductances than did *A. fasciculatum* on the equator-facing slope and on each slope the new leaves showed higher early season maximum conductances. The early October peak in maximum conductance was associated with a short period of precipitation. The effect of precipitation was more pronounced in the conductance response of the equator-facing slope shrubs, but can be noted in the pole-facing slope shrubs as well (fig. 2).

Contrasts in leaf conductance between leaf age classes have not been studied previously in these species. Roberts and others (1979) measured consistent differences in leaf conductance in *Ilex opaca* Ait. early in the growing season with new tissue showing lower conductance than old tissue. These differences were gone by midseason. The controls determining conductance differences between the new and old leaves in *A. fasciculatum* may be related to both endogenous developmental patterns of leaf maturation and external conditions related to the water history of the tissue. For example, the early season conductance differences were greater in *A. fasciculatum* on the pole-facing slope than for *A. fasciculatum* on the equator-facing slope and the differences were maintained further into the regional drought cycle in *A. fasciculatum* on the pole-facing slope (fig. 2). The seasonal water potential data showed that *A. fasciculatum* on the equator-facing slope developed water stress sooner and to a greater degree than did *A. fasciculatum* on the pole-facing slope (fig. 1). This suggests that stomatal behavior becomes increasingly conditioned by the water status of the tissue as water becomes increasingly limited.

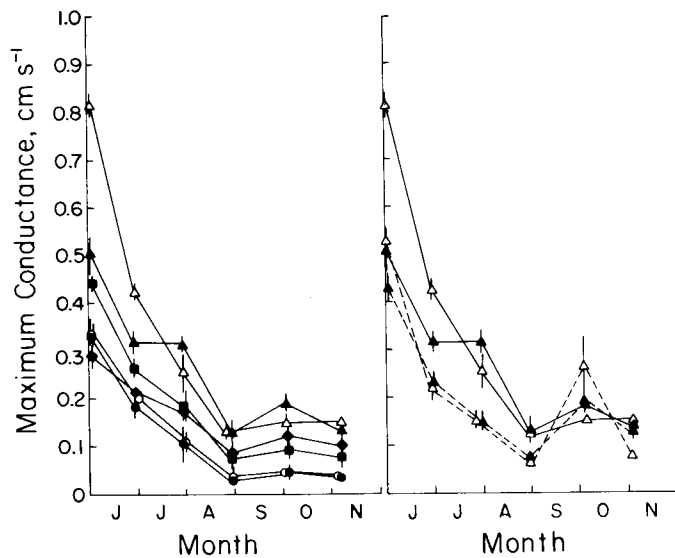


Fig. 2. A. Seasonal course of mean maximum leaf conductance with standard errors, measured on the pole-facing slope for *Adenostoma fasciculatum* (Δ current year's leaves, ▲ old leaves), *Quercus dumosa* (◆ old leaves), *Ceanothus greggii* (■ old leaves), and *Arctostaphylos glauca* (○ current year's leaves, ● old leaves). B. Comparison of seasonal courses of mean maximum leaf conductance with standard errors in *Adenostoma fasciculatum* old (▲) and new (Δ) leaves, growing on the pole- (—) and equator-facing (---) slopes.

The magnitude and duration of differences in conductance between leaf age classes appears strongly influenced by the water history of the tissue. Shrubs which tend to be deep-rooted, such as *A. fasciculatum*, and which are located on sites producing less water stress, pole-facing slopes, showed larger age class differences in leaf conductance and maintained the differences further into the regional drought cycle. Shallow-rooted shrubs, such as *A. glauca*, showed much reduced leaf age class conductance differences. Age class differences in conductance were diminished earlier in the season in plants occupying sites of greater water stress (*A. fasciculatum* on the equator-facing slope) compared to plants of the same species occupying sites of lesser water stress (*A. fasciculatum* on the pole-facing slope). This may result from the earlier dominance of leaf water status on the equator-facing slope as a major control affecting stomatal behavior.

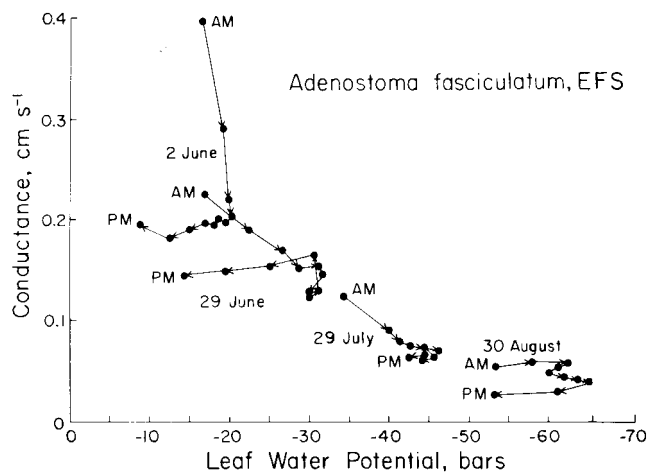


Fig. 3. Seasonal course of leaf conductance-leaf water potential relation in *Adenostoma fasciculatum* on the equator-facing slope, showing large hysteresis from morning (AM) to afternoon (PM) in the early season June measurements and decreasing hysteresis as the drought progresses. Environmental measurements are shown in Figure 3. Details are discussed in the text.

The increasingly dominant role of tissue water status in determining stomatal behavior as the drought cycle progresses is indicated by the seasonal course of the daily conductance hysteresis curves (fig. 3). Presumably, stomata respond to a complex of environmental factors, including light, temperature, carbon dioxide, humidity, wind, and tissue water status (Jarvis 1976). The large hysteresis in the early season leaf conductance-water potential relation indicates that several factors are operating simultaneously to determine stomatal responses and that leaf water status is only one factor functioning in concert with others to affect overall stomatal behavior. The seasonal tendency to decreasing hysteresis in the conductance-water potential relation suggests that tissue water status assumes an increasingly dominant role in controlling stomatal behavior under sustained drought conditions.

Specht (1972) has suggested that evergreen shrubs in mediterranean climates may moderate water use such that soil moisture would be conserved and processes such as photosynthesis and growth would be possible throughout the year. Miller and Poole (1979) suggest that such moderation of water use by a species may be adaptive in pure stands, but not in mixed stands due to interspecific competition for soil moisture. The present study showed that *A. fasciculatum* in a pure stand on the equator-facing slope had generally lower leaf conductance than did *A. fasciculatum* growing in a mixed stand on the pole-facing slope, supporting the suggestion of Miller and Poole (1979). However, water potentials in *A. fasciculatum* on the equator-facing slope were consistently more

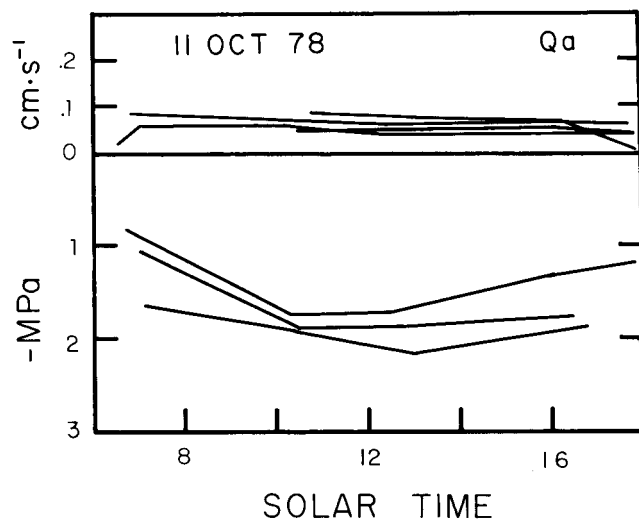


Fig. 4. Stomatal conductance and water potential in *Quercus agrifolia* at the Thousand Oaks site.

negative than for *A. fasciculatum* on the pole-facing slope, so that the observed conductance differences in *A. fasciculatum* cannot be ascribed solely to interspecific competitive effects, but must be conditioned as well by the differing water history the plants experience on the two slopes.

OAK FIELD WATER RELATIONS

Late summer measurements of water potential and stomatal conductance in *Quercus agrifolia* Nee and *Quercus lobata* Nee at a study site near Thousand Oaks, California showed conservative patterns of water use, with low stomatal conductances and water potentials much higher than values measured in the shrubs (fig. 4). Water potential measurements in *Q. agrifolia* and *Q. lobata* indicated *Q. lobata* undergoing slightly more negative midday water potentials compared to *Q. agrifolia* (fig. 5). Experimentation with partial root system removal (approximately 70% of lateral roots) showed an immediate negative shift in *Q. agrifolia* of approximately 1.0 MPa (fig. 6). This pattern of increased water stress persisted over time, both in terms of more negative midday values, and also in a reduced ability to recover overnight from the previous days transpirational water losses. Early morning and pre-dawn measurements in the root-cut tree were always 1.0 - 1.5 MPa more negative than those of a nearby control tree (fig. 6).

MATORRAL FIELD WATER RELATIONS

Comparative measurements in the Chilean matorral (nomenclature follows Muñoz Pizarro, 1966) showed differing species sensitivity to drought severity. *Trevoa trinervis* Miers, *Satureja gilliesii* Grah., *Lithraea*

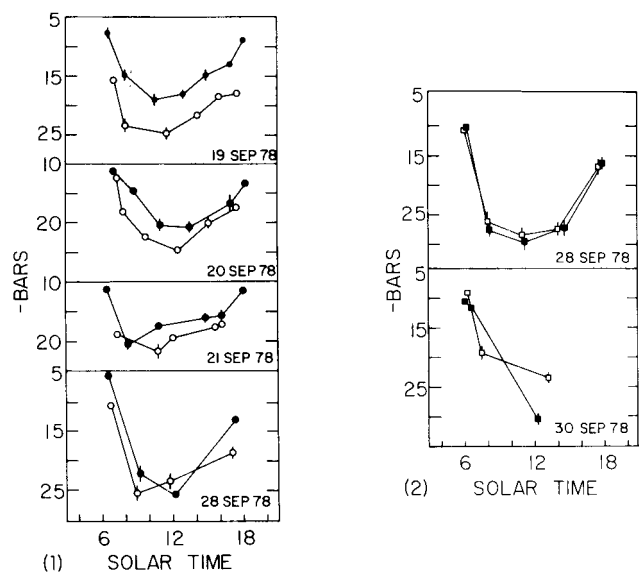


Fig. 5. Daily courses of water potential measured in *Quercus agrifolia* (A) and *Quercus lobata* (B) at the Thousand Oaks site.

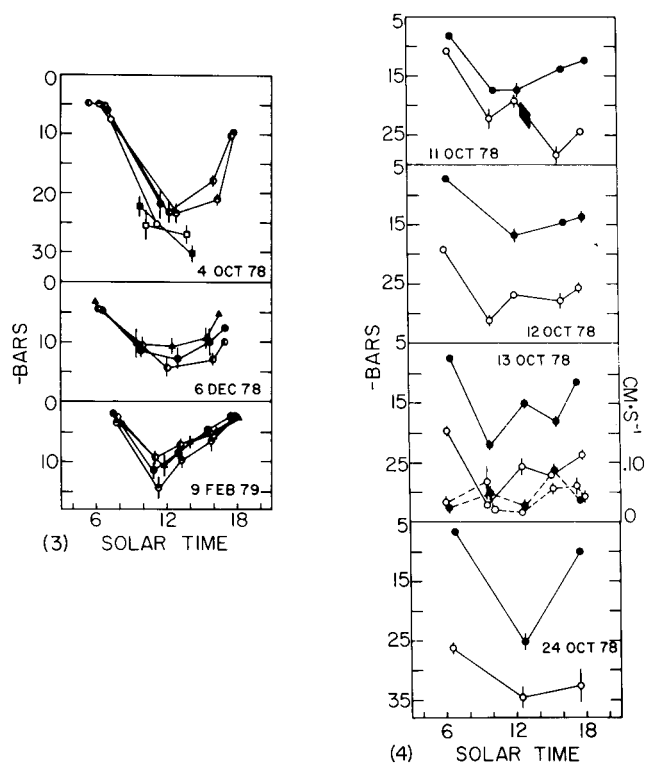


Fig. 6. Daily course of water potential and stomatal conductance measured in *Quercus agrifolia* at the Thousand Oaks site. Shaded area on 11 October 1978 indicates time of root cutting on an experimental tree.

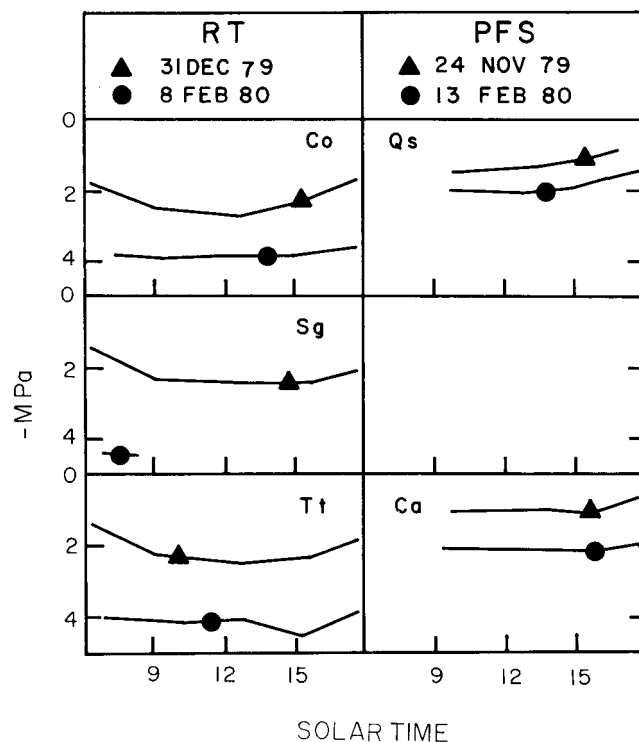


Fig. 7. Daily courses of water potential in the Chilean matorral species *Colliguaya odorifera* (Co), *Satureja gilliesii* (Sg), *Trevoa trinervis* (Tt), *Quillaja saponaria* (Qs), and *Cryptocarya alba* (Ca) on a ridge-top (RT) and a pole-facing slope (PFS).

caustica (Mol.) H. et Arn., and *Colliguaya odorifera* Mol., four shrub species located on a ridgetop site at Fundo Santa Laura, near Til-Til in central Chile (site described in Throrer and Bradbury 1977), all showed seasonal decreases in daily courses of both water potential (fig. 7) and stomatal conductance (fig. 8). *Quillaja saponaria* Mol., *Cryptocarya alba* (Mol.) Looser, and *L. caustica* on an adjacent pole-facing slope showed an opposite seasonal pattern in stomatal conductance, with higher values in February, late in the Chilean drought season, compared to measurements in November. Water potentials of pole-facing slope plants did decrease from November to February, but the decreases were less and the values were generally higher than the equator-facing slope values.

CHAPARRAL WATER POTENTIAL COMPONENTS

The capacity of many chaparral plant species to develop and endure very negative tissue water potentials is now well recognized. The question remains, however, as to just how the tissue water potential is partitioned into its turgor, osmotic, and matric components. Increasingly, the importance of characterizing the components of water potential has been recognized (Hsiao and others 1976, Fereres and others 1978) as well as the importance of understanding osmotic and

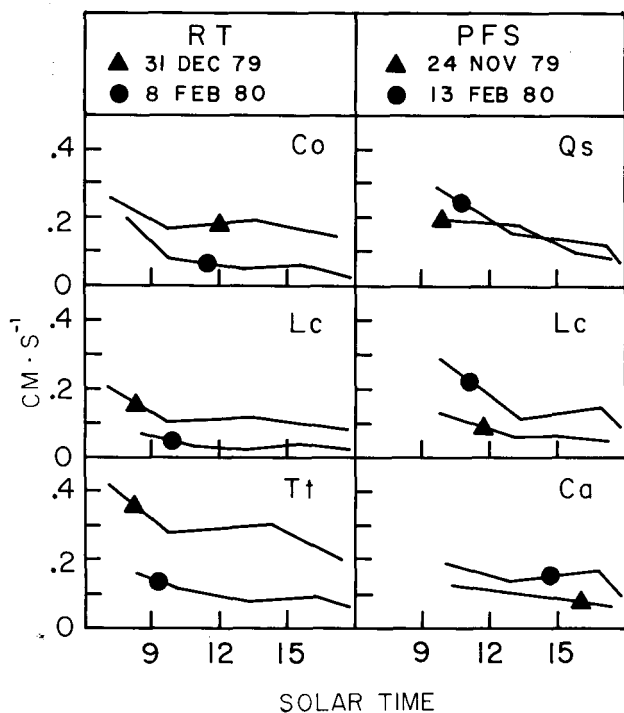


Fig. 8. Daily courses of stomatal conductances on the Chilean matorral species *Colliguaya odorifera* (Co), *Lithraea caustica* (Lc), *Trevoa trinervis* (Tt), *Quillaja saponaria* (Qs), and *Cryptocarya alba* (Ca), on a ridge-top (RT) and on a pole-facing slope (PFS).

structural properties of tissue which determine the component potentials. The pressure-volume technique (Tyree and Hammel 1972, Roberts and Knoerr 1977) is an analytical approach which allows the tissue water potential to be partitioned into components.

The pressure-volume approach has been applied in several southern Californian chaparral shrub species. Water potential component diagrams (fig. 9), showing water potential with its pressure (turgor) and nonpressure (osmotic plus matric) components, indicated that osmotic potentials were unexpectedly high (approximately -3 MPa). The potentials are shown as functions of relative water deficit $WD = (Turgid\ wt - Fresh\ wt) / (Turgid\ wt - Dry\ wt)$. *Ceanothus greggii*, *A. fasciculatum*, and *A. glauca* showed similar initial osmotic potentials (osmotic potential at full turgor) of approximately -2.7 to -3.0 MPa. *Quercus dumosa* showed an initial osmotic potential of approximately -4.6 MPa. The turgor responses were summarized by plots of the turgor component, the "volume-averaged" turgor of Tyree and Hammel (1972), versus the total water potential (Fig. 11). The rate of change of turgor per change in water potential was similar for all the species. Species differences were associated with displacements of the magnitude of the turgor component, with *Q. dumosa* showing the highest turgor values at any given water

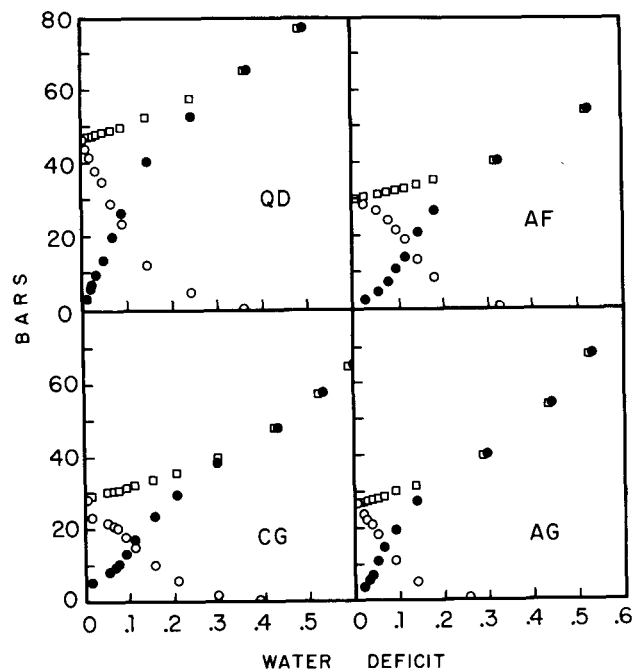


Fig. 9. Water potential component diagram for *Quercus dumosa* (QD), *Adenostoma fasciculatum* (AF), *Ceanothus greggii* (CG), and *Arctostaphylos glauca* (AG), showing water potential (●) and its turgor (○) and non-pressure (□) components. Turgor is positive, other components are negative.

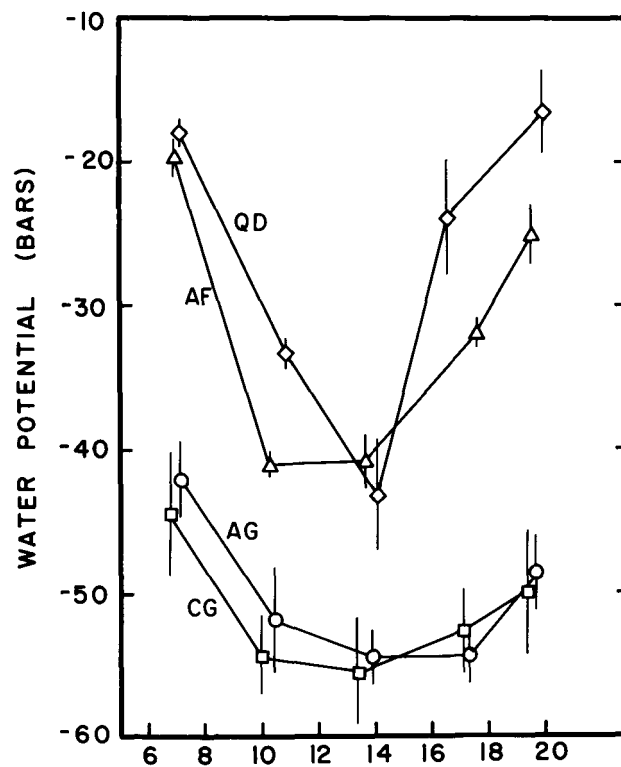


Fig. 10. Daily course of water potential measured during the late summer period when pressure-volume analyses were concurrently performed. Species symbols are as in figure 9.

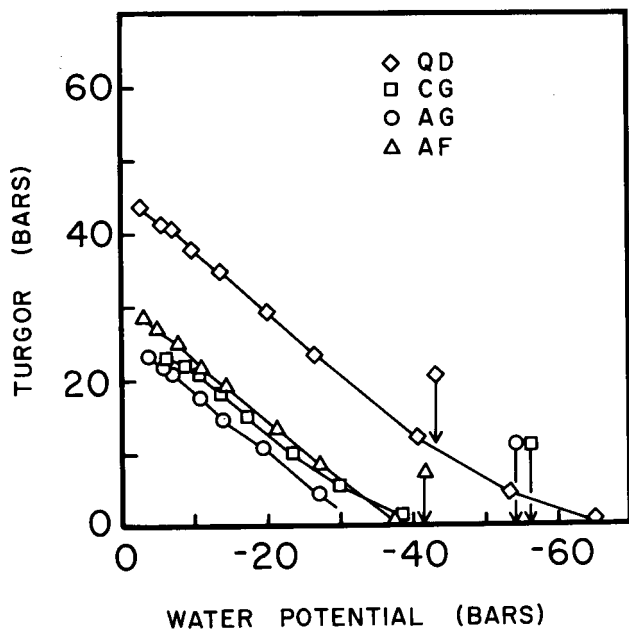


Fig. 11. Turgor pressure plotted as a function of water potential. Arrows show the point of zero turgor as determined by the pressure-volume analysis. Species symbols are as in Figure 9.

potential, resulting largely from the more negative osmotic potentials in that species.

The high osmotic values were unexpected in regard to concurrent field measurements of water potential and stomatal conductance, which showed that the plants were regularly undergoing water potentials substantially more negative than the osmotic plus matric components estimated by pressure-volume analysis (fig. 10). Diurnal patterns of xylem pressure potentials showed clear species segregation, with *C. greggii* and *A. glauca* developing similar minimum potentials of approximately -5.5 MPa during midday, about 1.3 MPa more negative than the midday values for *Q. dumosa* and *A. fasciculatum*. In addition, *Q. dumosa* and *A. fasciculatum* showed higher early morning potentials and more rapid water potential recovery in the afternoon compared to *C. greggii* and *A. glauca*. From the diagrams in figure 9 we would predict loss of bulk leaf turgor at a water potential of about -3.6 MPa in *Arctostaphylos glauca*. Yet, from daily course field data on the same plants within five days of the pressure-volume analyses we know these plants are commonly reaching -5.5 MPa in midday water potentials (fig. 10), well beyond the turgor-loss point predicted by the pressure-volume analyses. The *a priori* expectation was that seasonal osmotic adjustment would occur such that increasingly negative water potentials could develop, with concurrent osmotic adjustment allowing maintenance of turgor. Figure 11 shows that pressure-volume results would predict less of turgor at water potentials substantially higher than those actually measured in the field,

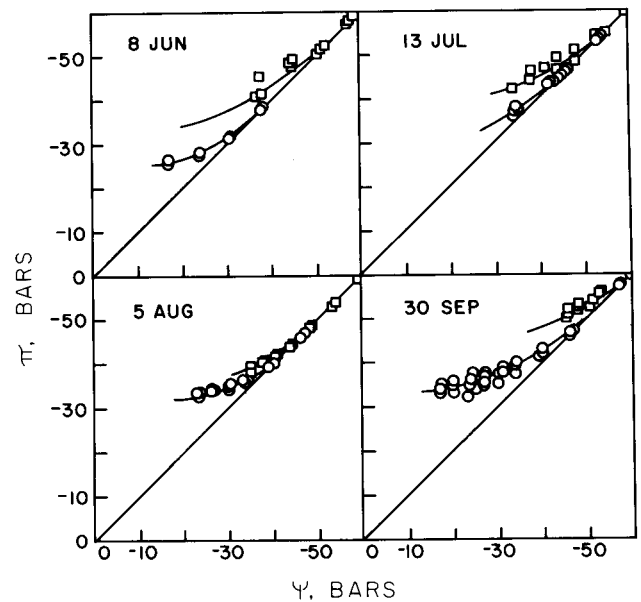


Fig. 12. Osmotic potential plotted as a function of water potential during the season for *Quercus dumosa* showing daily shifts in the osmotic component from morning (O) to afternoon (□).

indicating the plants would go through a large part of the day with zero turgor.

This seemed inconsistent with the notion of plant osmotic adjustment and adaptation to environment. The pressure volume results presented here reflect measurements on tissue rehydrated overnight and, thus, subjected to water availability conditions quite dissimilar from the conditions the tissue experiences in the field. If the tissue alters its osmolality or effective elasticity during the rehydration period, the analysis results will reflect tissue responses which will not be directly applicable to the field situation, at least for these species. Short-term osmotic adjustments of approximately 0.8 MPa over a few hours have been measured in field-grown maize (Acevedo 1975, Hsiao et al. 1976) and in apple (Davies and Lakso 1979). Measurements of short-term osmotic adjustments in two forest tree species (*Ilex opaca* and *Cornus florida*) showed only small (<0.1 MPa changes from morning to afternoon (Roberts et al. 1980). Thus, it appears that species may differ with regard to their ability to undergo short-term changes in tissue osmolality. The results of the present study suggest that these chaparral species may undergo daily shifts in tissue osmolality. The shifts might result from accumulation of photosynthate during the day, from a more direct response of the tissue to water deficits by interconversion of solute molecules to more osmotically active species, or by importation and accumulation of solute from the xylem stream. The possibility that the chaparral leaf samples were adjusting osmotically during the overnight rehydration period implies that the resulting analysis would

not reflect osmotic and turgor properties of the in situ field material.

In order to resolve this question, pressure-volume curves were analyzed from leaf tissue sampled without rehydration at dawn and at midday, corresponding to times of minimum and maximum water stress, respectively. Results of these analyses with Quercus dumosa indicated possible 10- to 12-bar osmotic adjustments from dawn to midday (fig. 12). The morning to afternoon change in the osmotic component was always a negative shift, but varied in magnitude at different times during the season. The largest shift appeared to occur in June, where the turgor loss point (the point at which the osmotic component departs from the diagonal in figure 12) shifted from a morning value of approximately -4 MPa to an afternoon value of -5.1 MPa. These results indicate that, at least for some chaparral species, the standard pressure-volume method may not predict field performance correctly.

CONCLUSIONS

A fair amount of data are now available to characterize water potentials and stomatal conductances of some of the more common shrubs in the worlds mediterranean climate regions. Relatively little is known about the water relation of the herbaceous species or the chaparral Quercus tree species. Apart from a few initial studies (Hinckley and others 1980, Roberts and others 1981) nearly nothing is known about osmotic adjustments and turgor relations in mediterranean-type vegetation. Osmotic relations may be particularly important for growth and gas exchange in plants which experience recurring drought, and thus represent an important area to focus on in ecophysiological research in the worlds mediterranean regions.

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