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DROUGHT TOLERANCE AND XYLEM EMBOLISM IN CO-OCCURRING SPECIES OF COASTAL SAGE AND CHAPARRAL¹

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Abstract. Some species of coastal sage and chaparral shrubs of California are extremely tolerant of tissue dehydration, surviving water potentials as low as -9 MPa during dry summer months. Such low water potentials (high tensions on xylem water) are known to cause severe embolism formation in the xylem vessels of woody plants, blocking water transport and potentially causing shoot dieback. Thus drought hardy species of coastal sage and chaparral are either extremely resistant to water stress-induced embolism or they become severely embolized during summer drought. We compared the seasonal changes in xylem water potential and xylem embolism (percent loss in hydraulic conductivity of stem segments due to air emboli) between co-occurring *Salvia mellifera* (coastal sage) and *Ceanothus megacarpus* (chaparral) growing in the Santa Monica Mountains of southern California. We also determined the relative sensitivity of each species to water stress-induced embolism by artificially dehydrating branches and measuring percent loss in hydraulic conductivity of xylem tissues at a given water potential. We found that both species experienced the same minimum in seasonal water potentials (-8 MPa) but the xylem of *S. mellifera* lost 78% in hydraulic conductivity whereas the xylem of *C. megacarpus* lost only 17% in hydraulic conductivity. These values for a natural plant community were within 10% of those predicted by our artificial dehydration curves. Our estimate of susceptibility to water stress-induced embolism indicated that 50% loss in hydraulic conductivity would occur at -4.5 MPa for *S. mellifera* but at -11 MPa for *C. megacarpus*. Irrigation of *S. mellifera* for one summer reduced loss in conductivity from 78 to 38% and increased leaf areas 10-fold, indicating that xylem embolism and leaf drop were drought induced. Our results show that xylem tissues of *S. mellifera* are more sensitive to water stress and tissue dehydration than those of co-occurring *C. megacarpus*. The observed ability of *S. mellifera* to inhabit drier sites than *C. megacarpus* may result from drought deciduousness in summer and high growth rates in spring that facilitate rapid construction of new xylem and leaf tissues. It may be that facultative drought deciduousness in coastal sage is tightly coupled to drought-induced embolism of xylem tissues.

Key words: carbon isotope discrimination; *Ceanothus megacarpus*; chaparral; coastal sage; drought tolerance; hydraulic conductivity; nitrogen-use efficiency; *Salvia mellifera*; water-use efficiency; xylem embolism.

INTRODUCTION

Coastal sage scrub and chaparral dominate much of the lower elevational and more coastal regions of southern California (Epling and Lewis 1942, Mooney 1977, Kirkpatrick and Hutchinson 1980, Keeley 1986). Coastal sage species are half-woody (subligneous) subshrubs, rarely >2 m in height. They typically have shallow roots and mesophytic appearing leaves, the majority of which are shed during dry summer months (Hellmers et al. 1955, Westman 1981, Gray 1982). In contrast, chaparral is comprised of much taller, more deeply rooted, sclerophyllous shrubs that retain most of their leaves during summer drought (Hanes 1977, Keeley and Keeley 1988). Generally, coastal sage occupy more arid habitats than chaparral, and most in-

vestigators agree that coastal sage species appear to be more tolerant of dry conditions than are chaparral (Harrison et al. 1971, Miller and Mooney 1976, Raven 1977, Axelrod 1978, Kirkpatrick and Hutchinson 1980, Westman 1981, Mooney 1989). Several reports indicate that at least some species of coastal sage experience more negative seasonal water potentials than neighboring chaparral shrubs (Poole and Miller 1975, Mooney 1982, 1989). However, a particularly well-documented study found that *Salvia mellifera* (representing coastal sage) and *Ceanothus megacarpus* (representing chaparral), growing together at the same microsite, had virtually identical predawn water potentials over a 2-yr period, reaching extremely low mean values of -9 MPa (Gill and Mahall 1986).

The results of Gill and Mahall's study have two important implications relative to dehydration tolerance in coastal sage and chaparral. First, they indicate that at least some species of chaparral shrubs (e.g., species of *Ceanothus*) also have shallow roots and experience severe tissue dehydration during summer drought (cf.

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Hellmers et al. 1955, Saruwatari and Davis 1989). Second, with the exception of chaparral seedlings (Schlesinger and Gill 1980, Oechel 1988, Thomas and Davis 1989), -9 MPa is the lowest mean water potential recorded for drought-hardy shrubs of California (cf. Poole and Miller 1975, Davis 1989) and is even lower than values reported for desert shrubs of California (cf. Halvorson and Patten 1974, Nilsen et al. 1984). Such low water potentials (high tensions on xylem water) in woody plants are known to cause cavitation, leading to formation of air emboli in xylem vessels and tracheids, potentially blocking water transport (embolism). A recent review by Tyree and Ewers (1991) indicates that all woody species thus far examined would be 100% embolized at a water potential of -9 MPa. Thus, either *S. mellifera* and *C. megacarpus* become severely embolized during summer drought or they are extremely resistant to water stress-induced embolism.

Physiological adjustments of coastal sage and chaparral to water stress (e.g., stomatal closure, osmotic adjustment, turgor maintenance) have been shown to play a significant role in drought tolerance (Poole and Miller 1975, Bowman and Roberts 1985, Davis and Mooney 1986, Saruwatari and Davis 1989). It may be that the physical ability of xylem tissues to resist cavitation under severe water stress is also a significant component of drought tolerance. To determine if this is the case, we initiated a study with the following objectives: (1) to ascertain if co-occurring *S. mellifera* and *C. megacarpus* experience high levels of xylem embolism induced by water stress during summer drought and (2) to compare seasonal patterns of xylem transport properties, susceptibility to xylem embolism, and rates of leaf gas exchange between the two species. Even though *S. mellifera* usually occupies drier habitats, because of its drought deciduousness we suspected that the xylem of *S. mellifera* would be more embolized than neighboring *C. megacarpus*. Furthermore, we suspected that the xylem of *S. mellifera* would be more efficient in water transport than the xylem of *C. megacarpus*, primarily because of the much higher transpiration rates, on a leaf area basis, reported for coastal sage (Harrison et al. 1971, Mooney 1989).

METHODS

Study sites

Corral Canyon site.—We selected as one of our study sites a mixed stand of coastal sage (*Salvia mellifera*, *Yucca whipplei*) growing adjacent to a mixed chaparral stand (*Ceanothus megacarpus*, *C. spinosus*, *Rhus laurina*) in a coastal exposure of the Santa Monica Mountains. Nomenclature follows Munz (1974). The study site was located on a southwest-facing slope (mean incline 35°) 1.5 km north of Highway 1 ($34^\circ 02' 30''$ N, $118^\circ 43' 30''$ W), at an elevation of 430 m. *S. mellifera* had a mean height of 1.43 ± 0.05 m (mean ± 1 SE, $n = 20$) and *C. megacarpus* had a mean height of 4.05

± 0.08 m. The stand burned in a 1970 wildfire (Los Angeles County Fire Department, Fire Mapping Unit, unpublished data). A 20-yr-old age for *C. megacarpus*, a species that can regenerate only by seed after fire, was confirmed by ring counts on three individuals. The fire frequency in the Santa Monica Mountains ranges between 12 and 21 yr (Radkte et al. 1982), thus the vegetation at the Corral Canyon site was representative of a mature stand. We intentionally chose a mature stand because one criticism of Gill and Mahall's (1986) earlier comparison of *S. mellifera* and *C. megacarpus* was that they did not examine mature individuals (cf. Mooney 1989).

Pepperdine site.—A second study site, in predominantly coastal sage scrub vegetation, was selected for irrigation treatments. This site was located on the Pepperdine University campus ($34^\circ 02' 30''$ N, $118^\circ 42' 30''$ W), ≈ 2 km from the Corral Canyon site, at an elevation of 90 m.

Irrigation treatments

The Pepperdine study site facilitated the use of two irrigation treatments: a long-term irrigation (≈ 10 yr) and a short-term irrigation (6 mo during one summer). The long-term irrigation was made possible by a natural stand of *S. mellifera* and *C. megacarpus* which grew adjacent to the lawn on the Pepperdine University campus. This stand received ≈ 8 mm of landscape irrigation each day during summer months over a 10-yr period. A short-term irrigation treatment at the Pepperdine site was imposed on 20 individuals of *S. mellifera* between May 1990 and November 1990, using a trickle irrigation system. The irrigation system delivered ≈ 10 L of tap water per plant each day over a 6-mo period. Twenty individuals of *S. mellifera* that grew close to (≈ 50 m from), but were not influenced by, the irrigation treatment were used as a nonirrigated control.

Seasonal changes in water potential

We measured predawn and midday water potentials on *S. mellifera* and *C. megacarpus* at the Corral Canyon site, at 1–2 mo intervals, between October 1990 and December 1991, following the method of Scholander et al. (1965). Water potentials at predawn and midday were also measured at the Pepperdine site near the beginning and the end of each summer drought period from 1989 to 1991. We sampled one branchlet from each of 10 individuals of each species in our estimate of mean water potential. The pressure chamber was custom designed to allow us to measure water potentials as low as -14 MPa (Model 1001, PMS Instrument Company, Corvallis, Oregon, USA).

Vulnerability of xylem to water stress-induced embolism

The relationship between embolism level and water stress for *S. mellifera* and *C. megacarpus* was deter-

mined using individuals exposed to long-term irrigation at the Pepperdine site. We selected irrigated plants because it was important that we establish the native embolism values (background levels) for these species and thus determine how an increase in water stress, via artificial dehydration, promoted embolism above background levels. At the initiation of this study, southern California had received $\approx 50\%$ of "normal" annual precipitation for each of the previous 4 yr (100-yr mean = 403 mm/yr, Los Angeles Flood Control District, Malibu Beach-Dunne Station, *unpublished data*). Thus, baseline native embolism values of non-irrigated plants in the spring would not accurately reflect the minimum embolism possible.

Our measurement of percent embolism (= percent blockage of hydraulic flow) was not via an estimate of the percent of the vessels that were dysfunctional or the percent of the vessel volume or cross-sectional area filled with air. All of these values represent an estimate of the amount of foreign material (= embolus) causing an obstruction, not the functional loss in hydraulic flow itself (= embolism). We chose to measure the hydraulic flow through stem segments before and after air emboli were removed, allowing us to calculate percent embolism in physiological terms of percent loss in hydraulic conductivity (percent loss in k_h). Our method follows that of Sperry et al. (1988). Thus the terms "percent embolism" or "percent loss in k_h " used throughout this paper literally means "percent loss in hydraulic conductivity of stem segments due to the presence of air emboli as determined by the method of Sperry et al. 1988" (cf. Tyree and Sperry 1989, Tyree and Ewers 1991).

A complete susceptibility curve to water stress-induced embolism was constructed by plotting decreasing values of water potential vs. percent loss in k_h . The curves were constructed by collecting branches longer than 1 m from the field. A minimum of 1 m was selected because this was longer than the maximum vessel length of 70 cm for *S. mellifera* and *C. megacarpus* (determined on five individuals of each species by the air permeability method of Zimmermann and Jeje 1981). This prevented air from being artificially introduced into cut branches. Immediately after collection, the cut end of each branch was sealed with parafilm to reduce evaporative water loss. Branches were returned to an air conditioned laboratory and allowed to dehydrate on a laboratory bench for 0.5–6 d. Branches were placed in plastic bags the night before their hydraulic conductivity was determined to insure that all branchlets approached a uniform water status. The next morning, water potentials were measured and entire branches were submerged in water and alternately trimmed from opposite ends to produce a 10 cm long stem segment, ranging between 6 and 8 mm in diameter.

Hydraulic conductivity (k_h) and percent loss in hydraulic conductivity due to embolism (percent loss in

k_h) were measured following a method fully described by Sperry et al. (1988). Briefly, a 10 mmol/L, degassed citric acid solution was passed through a 0.1- μm filter, then through a manifold of 10 stem segments under 5–6 kPa of hydrostatic pressure. We empirically demonstrated that the low pressure treatment (6 kPa) was not sufficient to push a meniscus through a vessel that might be open at both ends of our stem segments. We did this by increasing pressures in 2 kPa steps from 2 to 6 kPa and finding that calculated k_h remained constant. The volume flow rate through each stem segment was determined by collecting the solution on an analytical balance and measuring the mass increase per unit time with a stop watch (equivalent to the volume flow rate). Hydraulic conductivity, k_h (in metres to the fourth power per megapascal per second), was calculated as $k_h = q/[dP/dx]$, where q is the volume flow rate (in cubic metres per second) and dP/dx is the pressure gradient (in megapascals per metre). The initial measurement of k_h was followed by two or three subsequent measurements, each after a 1 h long high pressure perfusion (175 kPa) to remove air emboli from vessels and tracheids. The removal of emboli resulted in an increase in k_h relative to initial measurements. The difference between initial and final values was used to calculate percent loss in hydraulic conductivity due to embolism (cf. Sperry et al. 1988).

Hydraulic transport properties of xylem

We measured the degree of xylem embolism and hydraulic transport properties in the fall of 1990 and the spring of 1991 for 20 individuals each of *S. mellifera* and *C. megacarpus* at the Corral Canyon site. As our objective was to examine the seasonal extremes in hydraulic transport characteristics of these two species, we reasoned that these extremes would occur at the end of summer drought, before the onset of fall rains, and at the end of spring growth while plants were still hydrated. We also made similar measurements on 20 individuals of irrigated and nonirrigated *S. mellifera* at the Pepperdine site five times between December 1989 and May 1991 in order to assess changes in hydraulic transport properties in response to summer irrigation.

In order to compare the hydraulic transport capacity of different stems, the hydraulic conductivity values measured as described above were normalized against either the leaf area supported by that segment or the cross-sectional area of active xylem. The leaf specific conductivity, k_l (in square metres per megapascal per second), for stem segments was calculated by dividing hydraulic conductivity by the total leaf area, A_{leaves} (in square metres), distal to the stem segments. Leaf areas were determined by an image analysis program (Image 1.35, Twilight Clone, Silver Springs, Maryland, USA) in conjunction with a video camera and a Macintosh II computer. The index k_l represents the stem's capac-

ity to supply water to leaves distal to the stem segment (Zimmermann 1983, Ewers and Cruiziat 1989).

The specific conductivity of stem segments, k_s (in square metres per megapascal per second), which is a measure of xylem efficiency in water transport, was calculated by taking the ratio in k_i to the active xylem area. The stem segments used were the same as those used to estimate percent loss in k_i . After determination of final k_i , the active xylem area of each stem segment was estimated by allowing them to take up a 0.1% (mass/volume) solution of crystal violet or basic fuchsin that had passed through a 0.1- μm filter. The stain was taken up under a suction of 5–6 kPa for 20–30 min and the cross-sectional area of stained, active xylem was measured using an ocular micrometer and an Olympus Vanox microscope at a 20 \times magnification. The radius of the pith, radius to the stained xylem vessels (usually nonfunctional, unstained xylem was the older tissue near the center of the stem), and the total radius of the xylem were estimated using the average of four perpendicular measurements. From these values, the area of the pith, total area of the xylem, and the active xylem area were calculated.

The Huber value, HV, of each stem segment was calculated by dividing the active xylem area by the leaf area distal to the stem segment (Zimmermann 1983). Thus, HV is a measure of the amount of functional xylem supplying a given leaf area.

Estimate of the gradient in shoot water potential

Leaf specific conductivity, k_l , can be used to estimate the change in water potential per unit length of shoot, $\Delta P/\Delta x$ (in megapascals per metre), if the transpiration rate per unit leaf area, E (in metres per second), is also known, $\Delta P/\Delta x = E/k_l$ (Tyree and Ewers 1991). This assumes steady-state conditions and that the k_l of the stem segment is representative of the entire shoot. These assumptions may not be valid for large trees with a central trunk because leaf specific conductivities have been shown to vary widely throughout the shoot, and water storage in trunk tissues may preclude steady-state conditions (Tyree and Ewers 1991). These assumptions are probably more realistic for small shrubs that have uniform branching near the soil surface (e.g., *S. mellifera*).

Transpiration and photosynthetic rates

We also estimated photosynthetic rates (A) in units of micromoles per square metre per second, transpiration rates (E) in millimoles per square metre per second, and instantaneous water use efficiency (instantaneous A/E) in micromoles per millimole *S. mellifera* and *C. megacarpus* at Corral Canyon on 22 April 1992 using a portable photosynthesis system (Model LI-6200, LI-COR, Inc., Lincoln, Nebraska, USA). Measurements were made between 1000 and 1100 (Pacific Standard Time, PST) because previous data indicated that maximum transpiration rates generally occur be-

tween 1000 and 1100 for chaparral shrubs at our study sites (DeSouza et al. 1986, Thomas and Davis 1989). We measured two fully expanded, mature leaves from each of six individuals of each species ($n = 6$). We selected neighboring shrubs that had leaves of each species adjacent to each other allowing us to alternate the sequence of measurements between the two species. Measurements of photosynthesis and transpiration were accompanied by measurements of percent leaf nitrogen (dry mass basis) using a micro-Kjeldahl digestion and titration method (Nutritional Analysis Laboratory, Range Science Department, Colorado State University, Fort Collins, Colorado, USA) and leaf specific mass (in grams per square metre). The same two leaves from each individual shrub used for photosynthesis/transpiration measurements were also used for leaf area, leaf dry mass (dried at 70°C for 48 h), and percent leaf nitrogen determination. We used percent leaf nitrogen and leaf specific mass to calculate nitrogen contents on a leaf area basis (in millimoles per square metre) and divided these values into photosynthetic rates to compute the potential photosynthetic nitrogen-use efficiency (PPNUE) in micromoles of CO_2 fixed per mole of N per second. PPNUE is an estimate of instantaneous nitrogen-use efficiency under conditions of maximum photosynthetic rates (cf. Field and Mooney 1986).

We bulked 10 leaves for *S. mellifera* and 30 leaves for *C. megacarpus* from the same six individuals of each species used for photosynthesis/transpiration measurements ($n = 6$), for determination of carbon isotope ratios ($\delta^{13}\text{C}$) relative to the Peedee belemnite standard (Stable Isotope Laboratory, Boston University, Boston, Massachusetts, USA), which we converted to carbon isotope discrimination values (Δ) in parts per thousand using an atmospheric CO_2 composition of -8‰ (Farquhar et al. 1989). We used Δ to estimate the time-integrated CO_2 -flux-weighted ratio of the CO_2 concentration inside the leaf to the CO_2 concentration in the atmosphere (integrated C_i/C_a) by the relationship $C_i/C_a = (\Delta - a/b - a)$, where a is the discrimination factor due to stomatal diffusion of CO_2 (4.4 ‰), and b is the discrimination factor associated with carboxylation by C_3 plants (27 ‰), as fully discussed by Farquhar et al. (1989).

Integrated C_i/C_a was used to estimate the integrated water-use efficiency (integrated A/E) for leaves of each species by the relationship $A/E = C_a(1 - C_i/C_a)/(1.6 \times V)$, where C_a is the ambient CO_2 concentration (0.015 mol/m³), 1.6 is the diffusivity of CO_2 relative to water vapor, and V is the leaf-air vapor concentration difference measured by gas exchange (in moles per cubic metre) at our study site between 1000 and 1100 PST on 22 April 1992.

Root pressures

We measured root pressures on six individuals of *S. mellifera* after heavy rainfall on 22 and 23 March 1991 (Fig. 1) using an Ashcroft pressure transducer (Model

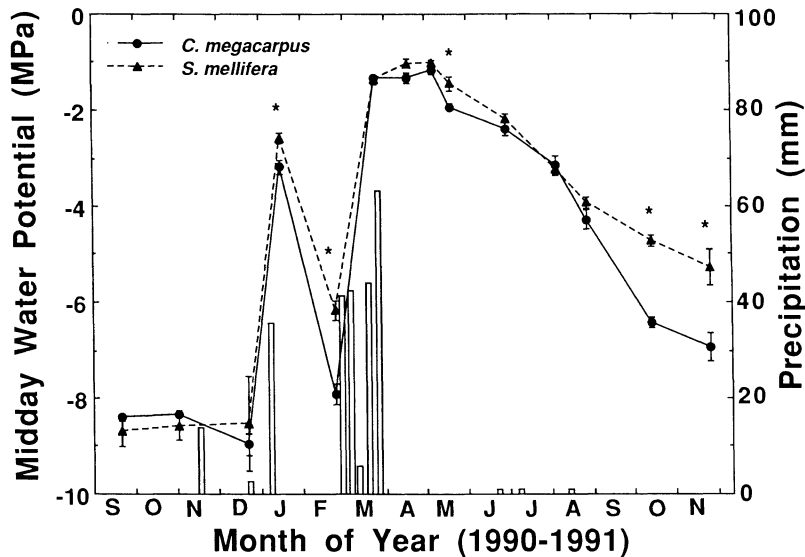


FIG. 1. Seasonal precipitation and seasonal change in midday water potential for the stem tissues of *Ceanothus megacarpus* and *Salvia mellifera* growing adjacent to each other in the Santa Monica Mountains of southern California, USA. Vertical bars on symbols represent ± 1 SE, $n = 10$. An asterisk above symbols indicates a significant difference in midday water potential between the two species by an unpaired Student's t test at $P < .05$.

7356, Dresser Industries, Stratford, Connecticut, USA). The accuracy of our pressure transducer was ± 0.5 kPa. Plants were double bagged with Space Emergency Blankets (Outdoor Safety Products, Winchester, Massachusetts, USA) 1 d before measurements were made to insure they were fully hydrated and had adequate time for their root systems to come into equilibrium with moisture in the soil. Small plants that forked into two major branches just above the soil surface were selected for measurements. This allowed one-half of the plant to remain bagged while the other half could be severed ≈ 10 cm above the soil surface, trimmed with a fresh razor blade, and attached to the pressure transducer to measure positive root pressure. All measurements were made prior to sunrise. We also measured water potentials with a pressure chamber at the same time root pressures were determined.

Stem growth

At the Corral Canyon site we attempted to document the construction of new xylem tissue for our *S. mellifera* plants between fall and spring 1992. We did this by permanently marking one branch from each of 12 individuals on 6 November 1991, measuring their stem diameter with a digital caliper, and remeasuring the stems on 5 May 1992. The initial stem diameters, 6.86 ± 0.14 mm (mean ± 1 SE, $n = 12$), approximated the mean diameter of stems used in our embolism studies. In May 1992 we also assessed the number of dead branches in each of the 12 *S. mellifera* examined.

Statistical analysis

We determined if mean values of measured parameters were significantly different between *S. mellifera*

and *C. megacarpus* at the Corral Canyon site and between irrigated and nonirrigated *S. mellifera* at the Pepperdine site using an unpaired Student's t test.

RESULTS

Seasonal change in water potential

The seasonal change in midday water potentials for *S. mellifera* and *C. megacarpus* showed similar patterns, but *S. mellifera* had substantially higher water potentials in February, October, and November 1991 (Fig. 1). For most of the season the two species had identical water potentials, indicating that *S. mellifera* and *C. megacarpus* experienced similar xylem water tensions. Midday water potentials in October 1990 were much more negative than in October 1991. This difference probably resulted from the 4 yr of below-average rainfall prior to the fall of 1990 followed by a year when most of the rainfall came late in the season (Fig. 1).

Vulnerability of xylem to water stress-induced embolism

S. mellifera was more susceptible to water stress-induced embolism of its xylem than was *C. megacarpus* (Fig. 2). *S. mellifera* had a 50% loss in k_h at a xylem tension of ≈ -4.5 MPa whereas *C. megacarpus* had a 50% loss in k_h at -11 MPa. Neither species had 0% embolism when fully hydrated (midday water potential ≈ -1.5 MPa). In October 1989 we found midday water potential and percent loss in k_h for continuously irrigated individuals to be $\Psi = -1.42 \pm 0.12$ MPa (mean ± 1 SE, $n = 10$), loss in $k_h = 10.2 \pm 0.9\%$ for *S. mellifera* and $\Psi = -1.62 \pm 0.12$ MPa, loss in $k_h = 11.4 \pm 1.4\%$

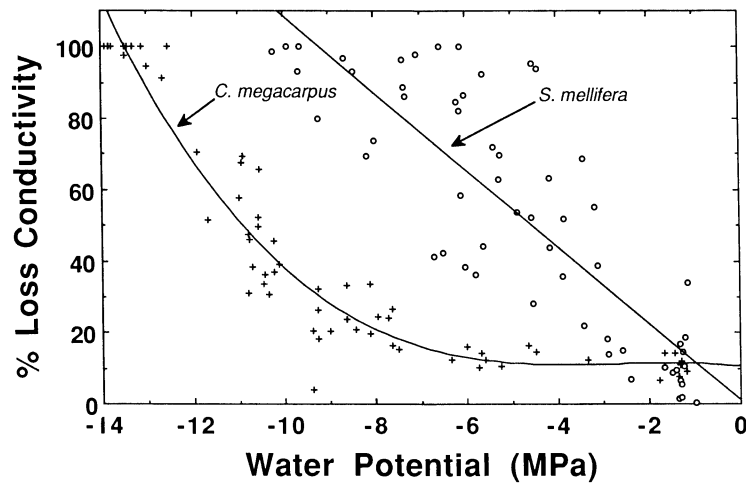


FIG. 2. Comparison of the vulnerabilities of *Ceanothus megacarpus* and *Salvia mellifera* to water stress-induced embolism of their xylem tissues. Branches were collected from irrigated individuals in the field, returned to an air-conditioned laboratory, and allowed to dehydrate for various lengths of time in order to induce increasing levels of water stress (more negative water potentials) and higher levels of xylem embolism (percent loss in hydraulic conductivity due to embolism). The data were fitted by a third-degree polynomial for *C. megacarpus* ($y = -7.246X^3 - 0.574X^2 - 1.251X + 10.491$, $r^2 = 0.92$) and a linear regression for *S. mellifera* ($y = -10.741X + 1.237$, $r^2 = 0.71$).

for *C. megacarpus*. These nonzero embolism values are thought to represent the native embolism level at the time of sampling and reflect a background level of embolized vessels that are nonrepairable by coastal sage and chaparral under field conditions (cf. Tyree and Sperry 1989). According to Tyree and Ewers (1991), native embolism levels for trees normally range between 5 and 20%.

Hydraulic transport properties of xylem

The seasonal extremes in hydraulic transport properties for *S. mellifera* and *C. megacarpus* during our study are represented by fall and spring values taken in October 1990 and June 1991 (Table 1). In October *S. mellifera* and *C. megacarpus* had the same active xylem area ($df = 38$, $t = 0.90$, $P > .37$) and the same

TABLE 1. Seasonal extremes in hydraulic transport properties for xylem tissue of *Salvia mellifera* and *Ceanothus megacarpus* growing adjacent to each other in the Santa Monica Mountains of southern California, USA. † Sample size = 20 shrubs.

Properties	October 1990		June 1991		
		<i>Salvia</i>	<i>Ceanothus</i>	<i>Salvia</i>	<i>Ceanothus</i>
Xylem diameter (mm)	Mean	6.40	6.53	6.28	6.26
	SE	0.11	0.47	0.18	0.08
Leaf area (m ²)	Mean	2.42×10^{-2}	3.02×10^{-2}	8.32×10^{-2}	8.36×10^{-2}
	SE	0.31	0.47	1.06	0.65
Midday water potential (MPa)	Mean	-8.65	-8.43	-2.40	-2.18
	SE	0.22	0.06	0.13	0.09
Loss in hydraulic conductivity (%)	Mean	78.1	17.3*	47.7	12.2*
	SE	3.4	2.0	4.7	1.4
Hydraulic conductivity (m ⁴ ·MPa ⁻¹ ·s ⁻¹)	Mean	1.21×10^{-8}	2.50×10^{-8} *	3.10×10^{-8}	3.87×10^{-8}
	SE	0.22	0.33	0.36	0.28
Leaf specific conductivity (m ² ·MPa ⁻¹ ·s ⁻¹)	Mean	0.55×10^{-6}	0.96×10^{-6} *	0.38×10^{-6}	0.49×10^{-6}
	SE	0.09	0.14	0.04	0.04
Specific conductivity (m ² ·MPa ⁻¹ ·s ⁻¹)	Mean	2.42×10^{-3}	1.06×10^{-3} *	4.14×10^{-3}	2.16×10^{-3} *
	SE	0.26	0.10	0.39	0.17
Huber value	Mean	1.15×10^{-3}	1.22×10^{-3}	0.37×10^{-3}	0.28×10^{-3}
	SE	0.17	0.18	0.14	0.03

* $P < .05$ by Student's t test comparing the two species.

† Values taken in October 1990 represent severe water stress conditions resulting from the immediate effects of summer drought plus 4 yr of below average rainfall. The June 1991 values were collected following a winter of normal precipitation. Between October 1990 and June 1991 *C. megacarpus* had significantly different leaf area, midday water potential, percent loss in hydraulic conductivity, specific conductivity, leaf specific conductivity, and Huber value (Student's t test at $P < .05$). The same was true for *S. mellifera* except there was no significant difference in leaf specific conductivity.

leaf area ($t = 1.09$, $P > .28$). Consequently, the Huber values were also the same ($t = 0.30$, $P > .77$). However, a loss in k_h of 78% for *S. mellifera* was nearly fivefold greater than the loss in k_h for *C. megacarpus* ($t = 15.5$, $P < .0001$). *S. mellifera* also had a higher specific conductivity ($t = 4.9$, $P < .0001$) but a lower leaf specific conductivity ($t = 2.5$, $P < .02$) than *C. megacarpus*.

In June 1991 the only significant differences in hydraulic transport properties between the species were in percent loss in k_h ($t = 7.32$, $P > .0001$) and specific conductivity ($t = 4.67$, $P < .0001$). In both instances, *S. mellifera* had higher values than *C. megacarpus*.

Seasonal changes in embolism of irrigated and nonirrigated *S. mellifera*

Percent loss in k_h for the xylem of nonirrigated *S. mellifera* increased during the summer drought, between spring 1990 and fall 1990 ($df = 37$, $t = 2.5$, $P < .02$), whereas percent loss in k_h of irrigated specimens decreased ($t = 2.9$, $P < .01$) (Fig. 3). After the winter rains of 1991 (Fig. 1), the nonirrigated plants decreased in percent loss in k_h ($t = 3.8$, $P < .001$), but the percent loss in k_h for summer irrigated plants remained constant ($t = 0.37$, $P > .7$). The percent loss in k_h for continuously irrigated *S. mellifera* (irrigated for ≈ 10 yr, adjacent the lawn at the Pepperdine site) was not significantly different from the percent loss in k_h for *S. mellifera* receiving only 6 mo of irrigation during the summer and fall of 1990 ($t = 1.9$, $P > .07$).

Hydraulic transport properties of irrigated and nonirrigated *S. mellifera*

After one summer of irrigation treatment, in October 1990 *S. mellifera* had much higher leaf area ($df = 35$, $t = 8.2$, $P < .0001$) and midday water potential ($t = 30.8$, $P < .0001$) than nonirrigated individuals (Table

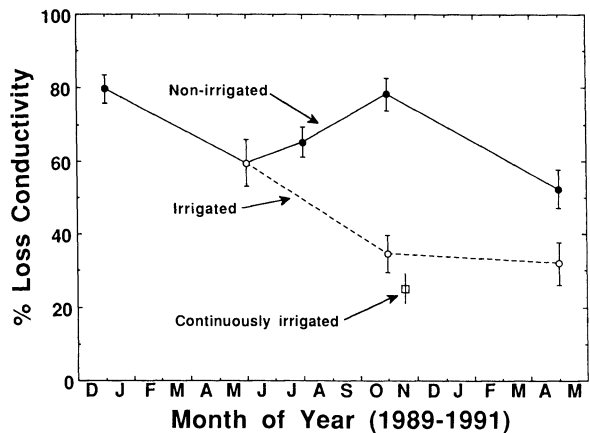


FIG. 3. Seasonal changes in xylem embolism (percent loss in hydraulic conductivity due to embolism) for nonirrigated *Salvia mellifera* in comparison to neighboring *S. mellifera* that were irrigated between May and November 1990. In November 1990, we also measured xylem embolism on continuously irrigated individuals that had received summer watering for ≈ 10 yr.

2). Also, irrigated *S. mellifera* had a lower percent loss in k_h ($t = 6.2$, $P < .0001$), leaf specific conductivity ($t = 2.6$, $P < .014$) and Huber value ($t = 6.6$, $P < .0001$) than the nonirrigated treatment. Irrigated *S. mellifera* shrubs at the Pepperdine site were similar to *S. mellifera* shrubs growing at Corral Canyon in the spring (compare Table 2 to Table 1), whereas nonirrigated individuals were similar to *S. mellifera* growing at Corral Canyon in the fall.

Transpiration and photosynthetic rates

At the same light level (photosynthetic photon flux density [PPFD]) and leaf temperature, the photosynthetic rates and transpiration rates were significantly

TABLE 2. Hydraulic transport properties of stem segments from irrigated and nonirrigated *Salvia mellifera*. The irrigated treatment consisted of a previously nonirrigated stand of native coastal sage scrub which was subjected to one summer of irrigation beginning in May 1990. Nonirrigated individuals grew ≈ 50 m from the irrigation treatment. Specimens were collected on the Pepperdine University's campus in Malibu, California, USA in October 1990. Sample size = 20 shrubs.

Properties		Summer irrigated	Nonirrigated
Xylem diameter (mm)	Mean	6.22	6.42
	SE	0.14	0.16
Leaf area (m ²)	Mean	11.37×10^{-2}	1.19×10^{-2} *
	SE	1.23	0.16
Midday water potential (MPa)	Mean	-1.53	-9.09*
	SE	0.09	0.13
Loss in hydraulic conductivity (%)	Mean	38.4	78.3*
	SE	4.9	4.3
Hydraulic conductivity (m ⁴ ·MPa ⁻¹ ·s ⁻¹)	Mean	2.87×10^{-8}	0.87×10^{-8} *
	SE	0.36	0.23
Leaf specific conductivity (m ² ·MPa ⁻¹ ·s ⁻¹)	Mean	0.24×10^{-6}	0.79×10^{-6} *
	SE	0.14	0.09
Specific conductivity (m ² ·MPa ⁻¹ ·s ⁻¹)	Mean	2.52×10^{-3}	1.87×10^{-3}
	SE	0.30	0.23
Huber value	Mean	0.18×10^{-3}	2.35×10^{-3} *
	SE	0.02	0.30

* $P < .05$ by an unpaired Student's t test.

TABLE 3. Comparison of the physiological performance between leaves of *Salvia mellifera* and *Ceanothus megacarpus* growing adjacent to each other at Corral Canyon in the Santa Monica Mountains of southern California, USA. Data (given as Mean \pm 1 SE) were taken on fully illuminated, mature leaves between 1000 and 1100 (PST), 22 April 1992.

Measurements†	<i>S. mellifera</i>	<i>C. megacarpus</i>	P
PPFD ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	1536 \pm 62	1463 \pm 86	>.5
Leaf temperature ($^{\circ}\text{C}$)	26.7 \pm 0.3	26.3 \pm 0.1	>.2
Midday water potential (MPa)	-1.35 \pm 0.02	-1.50 \pm 0.04	<.01
Stomatal conductance ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	527 \pm 22	298 \pm 18	<.0001
Photosynthesis ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	24.9 \pm 0.9	16.9 \pm 1.0	<.0001
Transpiration ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	6.72 \pm 0.28	3.82 \pm 0.13	<.0001
Instantaneous A/E ($\mu\text{mol}/\text{mmol}$)	3.72 \pm 0.07	4.48 \pm 0.26	<.02
Instantaneous C_i/C_a	0.69 \pm 0.02	0.61 \pm 0.02	<.02
Carbon isotope discrimination, Δ (‰)	21.5 \pm 0.20	19.5 \pm 0.19	<.0001
Integrated A/E ($\mu\text{mol}/\text{mmol}$)	3.60 \pm 0.17	5.40 \pm 0.22	<.0001
Integrated C_i/C_a	0.76 \pm 0.01	0.67 \pm 0.01	<.0001
Leaf specific mass (g/m^2)	83 \pm 4	212 \pm 15	<.0001
Leaf nitrogen (mmol/g)	1.99 \pm 0.04	1.48 \pm 0.11	<.002
Leaf nitrogen (mmol/m^2)	165 \pm 6	311 \pm 24	<.0001
PPNUE ($\mu\text{mol}\cdot\text{mol}^{-1}\cdot\text{s}^{-1}$)	151 \pm 4	57 \pm 6	<.0001

† Abbreviations are defined in Methods: transpiration and photosynthetic rates. Mean values were compared by an unpaired Student's *t* test. The sample size (*n*) for all parameters was 6 individuals of each species except for midday water potential where *n* = 10.

higher for *S. mellifera* than for *C. megacarpus* at the Corral Canyon site during the spring of 1992 (Table 3). *S. mellifera* also had lower water-use efficiency (instantaneous A/E) but higher CO₂ internal to external ratio (instantaneous C_i/C_a). This pattern was consistent with estimates of integrated A/E and integrated C_i/C_a based on measurements of carbon isotope discrimination (Δ). Even though leaf nitrogen per unit dry mass was greater for *S. mellifera* than *C. megacarpus*, the lower specific mass of *S. mellifera* leaves resulted in a much lower leaf nitrogen content when expressed on an area basis. This lower leaf nitrogen for *S. mellifera*, in combination with its higher photosynthetic rate, led to a threefold greater estimate of potential photosynthetic nitrogen-use efficiency (PPNUE), consistent with predictions by Field and Mooney (1986) for comparisons of coastal sage to chaparral.

We used the leaf specific conductivities (Table 1) and the transpiration values collected on 22 April 1992 (Table 3) to calculate water potential gradients ($\Delta P/\Delta x$) along the shoot of *S. mellifera* and *C. megacarpus*. The estimated gradient for branches of *S. mellifera* was 0.32 MPa/m whereas the gradient for *C. megacarpus* was 0.14 MPa/m. Since the mean height for our population of *S. mellifera* and *C. megacarpus* was 1.43 and 4.05 m, respectively, the overall water potential drop from the stem at the soil surface to the top of each species would be 0.46 MPa for *S. mellifera* and 0.61 MPa for *C. megacarpus*, taking into account gravitational effects. If the additional drop in water potential due to the root system is calculated at one-half the mean rooting depth of *S. mellifera* (0.75 m, cf. Hellmers et al. 1955) and one-half the mean rooting depth of *C. megacarpus* (1.1 m, Thomas and Davis 1989), the overall water potential drop from the roots to the top of each species would be 0.58 MPa for *S. mellifera* and 0.76 MPa for *C. megacarpus*. The actual values, based on measured differences between predawn and midday

water potentials on this same date and at the same height were 0.48 \pm 0.02 MPa (mean \pm 1 SE, *n* = 10) for *S. mellifera* and 0.74 \pm 0.06 MPa for *C. megacarpus*.

Stem diameters

The average diameter of eight stems, one from each of eight individuals of *S. mellifera*, increased by 1.99 \pm 0.31 mm (mean \pm 1 SE) between 6 November 1991 and 5 May 1992. We initially tagged 12 stems on 6 November 1991 for assessing changes in stem diameter but 4 of the 12 were dead by the time of our second sampling on 5 May 1992.

Root pressures

We only detected positive root pressures when one-half of our *S. mellifera* specimens were tightly covered with a double bag and the pressure transducer was on the cut stump of the other half of the plant. When the bag was removed from *S. mellifera*, the positive root pressures measured on the other half of each specimen dropped to zero within 1 or 2 min. This indicated that positive root pressures were unlikely events at our study site. Even with bagged plants, the mean root pressures were only 7.5 \pm 0.9 kPa (mean \pm 1 SE, *n* = 6).

DISCUSSION

Our results demonstrate that there can be large differences in the degree of xylem embolism between the coastal sage species *Salvia mellifera* and the chaparral species *Ceanothus megacarpus* when they are found growing together at the same microsite (Table 1). Because both species experienced similar degrees of seasonal water stress (Fig. 1, cf. Gill and Mahall 1986), yet had very different levels of xylem embolism (Table 1), it was not surprising that artificial dehydration experiments showed that the xylem of *S. mellifera* was more susceptible to water stress-induced embolism (Fig.

2). The artificial dehydration curve predicted a loss in k_h of 87% for *S. mellifera* at a xylem tension of -8 MPa, within 10% of the actual loss in k_h obtained for specimens at the Corral Canyon site (compare Fig. 2 to Table 1). The same curve for *C. megacarpus* predicted a loss in k_h of 20%, within 3% of the observed.

Irrigation of *S. mellifera* during the summer drought period reduced embolism levels from 78 to 38% (Fig. 2), consistent with the hypothesis that the high levels of xylem dysfunction observed for this species was primarily caused by water stress. The most probable mechanism for the partial recovery of xylem function in *S. mellifera* after irrigation or after overwintering was the construction of new xylem tissue. This view is supported by at least three observations: (1) the recovery of xylem function was gradual and not complete in response to irrigation or overwintering (Fig. 2), (2) positive root pressures were only obtained under very artificial conditions (bagged plants), and (3) the average diameter of eight stems increased by 1.99 ± 0.31 mm between fall and spring months indicating a substantial construction of new xylem (cf. Sperry et al. 1987).

C. megacarpus appears to be more resistant to water stress-induced embolism than any other species of woody plant thus far examined (Fig. 2, cf. Tyree and Ewers 1991). The species most resistant to embolism reported by Tyree and Ewers were 50% embolized at -6 MPa, whereas we found that *C. megacarpus* was not 50% embolized until ≈ -11 MPa. Such extreme resistance to xylem embolism by *C. megacarpus* may be facilitated by a number of anatomical features, the most important of which is extremely small diameter pores in the pit membranes of vessels and tracheids that prevent the drawing of air into these conduits via high tensions on xylem water (Sperry and Tyree 1988). It is unlikely that differences in vessel diameters can account for differences in vulnerability to embolism observed for *S. mellifera* and *C. megacarpus* because (1) we are not aware of any empirical data that indicate that differences in vessel diameter between species is correlated with susceptibility to water stress-induced embolism (Tyree and Sperry 1989), and (2) the mean vessel diameter for *S. mellifera* (22.3 ± 1.9 μm , [mean ± 1 SE], $n = 100$) was not significantly different from that of *C. megacarpus* (20.8 ± 0.76 μm , $n = 198$; $t = 0.89$, $P > .3$).

Zimmermann (1983) proposed that there may be a trade-off between xylem efficiency and xylem safety in woody plants. That is, those plants having xylem with high specific conductivity (high efficiency in water transport) may inherently be more susceptible to water stress-induced embolism. This notion is consistent with our results for *S. mellifera* and *C. megacarpus*. Even though *S. mellifera* underwent 50% loss in k_h at a much higher water potential (-4.5 MPa) than *C. megacarpus* (-11 MPa), the xylem of *S. mellifera* had twice the specific conductivity as *C. megacarpus*, both in the fall of 1990 and in the spring of 1991 (Table 1). The greater

efficiency in hydraulic transport by the xylem of *S. mellifera* may permit higher transpiration rates during spring months, thus facilitating rapid growth and higher rates of photosynthesis (Table 3). More efficient xylem may be a prerequisite for sustaining the relatively short-lived, metabolically more active leaves of drought deciduous scrubs (coastal sage) in comparison to the long-lived, metabolically more conservative leaves of evergreen, sclerophyllous shrubs (chaparral) (cf. Harrison et al. 1971, Gill and Mahall 1986, Mooney 1989).

The decrease in specific conductivity for both *S. mellifera* and *C. megacarpus* between spring and fall months possibly resulted from a greater proportion of wide vessels embolizing as compared to narrow vessels in response to summer drought. Since a doubling of vessel diameter causes a 16-fold increase in hydraulic conductivity as predicted by the Hagen-Poiseuille equation for ideal capillaries (Ewers and Cruiziat 1989), any preferential dysfunction of wide vessels over narrow vessels would cause an overall decrease in specific conductivity (Table 1). Preferential dysfunction of wide vessels over narrow vessels in response to water stress has been documented for other woody species (Tyree and Dixon 1986, Sperry and Tyree 1990) and for *S. mellifera* (Hargrave et al. 1993), but has not yet been examined for *C. megacarpus*.

Gill and Mahall (1986) argue that leaf shedding in *S. mellifera* is not an effective water stress-avoiding mechanism because, in their studies, *S. mellifera* experienced an extremely low seasonal water potential of -9 MPa, almost identical to that of co-occurring *C. megacarpus*. Our results are consistent with these findings and further demonstrate that *S. mellifera* does not effectively avoid embolism under extremely low water potentials. It may be that the facultative deciduous habit of *S. mellifera* occurs in response to progressive increases in water stress-induced embolism during summer drought (Fig. 2). Our supplemental irrigation of *S. mellifera* documents that the removal of water stress during summer months not only halts leaf shedding and xylem embolism but enhances leaf area (Table 2) and reduces embolism levels (Fig. 2). Our results are consistent with Gill and Mahall's (1986) observation that the timing of leaf shedding in *S. mellifera* may be related to photoperiod and flowering but the degree of leaf shedding is correlated with low water potentials.

We were surprised to find such a large increase in leaf area for *C. megacarpus* between the fall of 1990 and the spring of 1991 (Table 1) for two reasons: (1) *C. megacarpus* is considered an evergreen species, and (2) the magnitude of change in leaf area was similar to that of the facultative deciduous species *S. mellifera*. One possible explanation for this unexpected result is that our study was initiated in the fall of 1990 after 4 yr of severe drought that may have caused leaf areas of *C. megacarpus* to be unusually low. After two seasons of average rainfall, Gill and Mahall (1986) found during spring months that new leaves comprised 84%

of *S. mellifera*'s total leaf area while new leaves comprised only 55% of *C. megacarpus*'s total leaf area. In comparison, our data (Table 1) indicate that the contribution of new leaves to total leaf area was $\approx 77\%$ for *S. mellifera* and 73% for *C. megacarpus*.

We were also surprised to find 30% of the stems we tagged for diameter measurements in November 1991 to be dead by May 1992. This suggests that a significant proportion of the branches of *S. mellifera* die each season, possibly due to high embolism levels. This may explain how *S. mellifera* has a twofold greater shoot elongation rate than *C. megacarpus* each season (Gill and Mahall 1986) yet only achieves about one-third the total height of *C. megacarpus*. A similar high frequency of branch death for *C. megacarpus* is unlikely because: (1) it is less vulnerable to shoot dieback via water stress-induced embolism; (2) unlike *S. mellifera*, it has a central trunk with no mechanism for crown sprouting (nonsprouter); and (3) it has relatively slow rates of shoot elongation (cf. Thomas and Davis 1989).

We found that *C. megacarpus* had a lower Δ and C_e/C_a than *S. mellifera* which corresponds to a higher water-use efficiency (WUE) (integrated A/E , Table 3). Ehleringer and Cook (1988) discovered among perennial plants in the Sonoran Desert of California that high WUE plants tended to be longer lived and have lower productivity under high soil moisture conditions than low WUE plants. They argued that when soil water is limiting, low WUE plants are more susceptible to decreases in growth rate and mortality. This is consistent with our results that indicate that the lower WUE plant (*S. mellifera*) has a higher photosynthetic rate in the spring, but is more vulnerable to water stress-induced embolism and shoot dieback during summer drought.

Harrison et al. (1971) reported that transpiration rates were twofold greater for coastal sage species (*S. mellifera*, *S. leucophylla*, *Artemisia californica*, *Encelia californica*, *Eriogonum cinereum*) than for chaparral species (*Cercocarpus betuloides*, *Heteromeles arbutifolia*, *Prunus ilicifolia*, *Rhus ovata*, *R. laurina*) in the Santa Monica Mountains. They also found that the rate of desiccation for detached leaves of coastal sage was about twice that of chaparral. They concluded that leaves of coastal sage, in contrast to chaparral, are more mesomorphic, having less ability to control water loss, and thus the leaves of coastal sage undergo desiccation, death, and abscission during summer drought. They speculated that this apparent disadvantage among coastal sage species is compensated by high assimilation rates during short periods of available moisture, allowing for rapid growth, flowering, and fruiting prior to the onset of summer drought. Gill and Mahall (1986) have reported that shoot elongation rates are at least twofold greater for *S. mellifera* than for *C. megacarpus* and also the initiation of shoot elongation begins 2–3 wk earlier for *S. mellifera*.

Our results extend the observations of Harrison et

al. (1971) and Gill and Mahall (1986) in suggesting that the xylem of coastal sage is also more mesomorphic and ephemeral than that of chaparral. It may also be true that the high assimilation rates reported for coastal sage facilitate the rapid construction of new xylem, allowing for a quick recovery from xylem embolism incurred during summer drought. It is attractive to speculate that drought deciduousness is in response to xylem dysfunction and that rapid leaf growth is facilitated by the construction of new xylem. Our results show no significant change in leaf specific conductivity with season, documenting that leaf loss and recovery are matched by hydraulic supply of the xylem (Table 1). It may be that the greater susceptibility of *S. mellifera* to water stress-induced embolism is tightly coupled to the drought deciduous habit of coastal sage.

CONCLUSION

The ability of *S. mellifera* to occupy drier microsites than *C. megacarpus*, even though its xylem and spring leaves appear more mesophytic, probably results from a suite of factors, the most important of which is the early, rapid growth of new tissue during spring months with the preferential dysfunction or loss of these same tissues (wide vessels and spring leaves) during summer drought. Narrow vessels (Carlquist 1985, 1989, Hargrave et al. 1993) and summer leaves (Westman 1981, Mooney 1989) sustain *S. mellifera* even through the driest of periods, when water potentials may plummet as low as -9 MPa (Gill and Mahall 1986). By comparison, *C. megacarpus* has slower photosynthetic and growth capabilities but xylem vessels that are extremely resistant to water stress-induced embolism.

Our results demonstrate that both *S. mellifera* and *C. megacarpus* are extremely tolerant of water stress and tissue dehydration in comparison to other woody plants (cf. Tyree and Ewers 1991). Even though *C. megacarpus* appears to have the advantage in being more resistant to water stress-induced embolism than *S. mellifera*, its life history pattern makes this a prerequisite for survival. *C. megacarpus* is a nonsprouter with a central trunk, which must achieve heights two- to threefold that of *S. mellifera* in order to compete for light in dense chaparral stands (McPherson and Muller 1967, Gray 1983). Irreversible xylem dysfunction in the central trunk would lead to total shoot dieback with no mechanism for recovery (cf. Thomas and Davis 1989). In contrast, xylem dysfunction in *S. mellifera* is not as critical for survival because this species is a resprouter, with multiple branches near the base, having high growth rates, but reaching only a fraction of the height of *C. megacarpus*. These traits in conjunction with drought deciduousness presumably allow *S. mellifera* to grow in drier microsites than *C. megacarpus*, despite *S. mellifera*'s greater vulnerability to water stress-induced embolism.

It is obvious from these results that susceptibility to xylem embolism cannot be used as a sole index of water

stress tolerance but must be evaluated in conjunction with other traits that also impart drought resistance. It appears that plant adaptation to severe tissue dehydration is a highly coordinated, whole-plant process that maintains both the functional integrity of the symplast as well as the functional integrity of the apoplastic water transport system (xylem vessels and tracheids).

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