

UC Riverside

UC Riverside Previously Published Works

Title

Plant water status and hydraulic conductance during flowering in the southern California coastal sage shrub *Salvia mellifera* (Lamiaceae)

Permalink

<https://escholarship.org/uc/item/98z939pk>

Journal

American Journal of Botany, 98(8)

ISSN

0002-9122

Authors

Lambrecht, Susan C
Santiago, Louis S
DeVan, Caroline M
[et al.](#)

Publication Date

2011-08-01

DOI

10.3732/ajb.1000514

Peer reviewed

**PLANT WATER STATUS AND HYDRAULIC CONDUCTANCE DURING
 FLOWERING IN THE SOUTHERN CALIFORNIA COASTAL SAGE
 SHRUB *SALVIA MELLIFERA* (LAMIACEAE)¹**

SUSAN C. LAMBRECHT², LOUIS S. SANTIAGO^{3,6}, CAROLINE M. DEVAN^{3,4}, J. CARLOS CERVERA^{3,5},
 CARA M. STRIPE³, LEE A. BUCKINGHAM³, AND SARAH C. PASQUINI³

²Department of Biological Sciences, San Jose State University, San Jose, California 95192, USA; and ³Department of Botany and Plant Sciences, University of California, 2150 Batchelor Hall, Riverside, California 92521, USA

- *Premise of the Study:* Plant water status during flowering is important for plant reproduction, but the physiology of floral water use is not well understood. We investigated plant water status in relation to leaf and floral physiology in naturally occurring individuals of a semiarid shrub, *Salvia mellifera* E. Greene.
- *Methods:* We measured stomatal (g_s) and corolla (g_c) conductance to water vapor, transpiration from leaves (E_{leaf}) and corollas ($E_{corolla}$), leaf-specific hydraulic conductance (K_H), bulk shoot water potential (Ψ_{shoot}), and shoot water content on irrigated and control plants to analyze whether water was limiting to leaf and floral water use.
- *Key Results:* Experimental irrigation caused a 203% increase in soil moisture content, a 20% increase in predawn Ψ_{shoot} , a 29% increase in midday Ψ_{shoot} , and a 92% increase in K_H . Floral and leaf gas exchange did not respond significantly to water addition, indicating that rates were at seasonal maxima and not limited by water availability. Total daily water use by corollas was ~20% of total shoot water use. There were no significant differences in total daily shoot water use with water addition. Mean shoot water content (5.07 g) was close to mean daily shoot water use (6.71 g), indicating that the equivalent of total shoot water content turned over every 0.76 d.
- *Conclusions:* These results demonstrate that although irrigation improved whole-plant hydraulic conductance, gas exchange was not limited by water availability. Additionally, the high water use of flowers in this species might limit future flowering and reproductive success during dry years.

Key words: coastal sage scrub; corolla conductance; floral physiology; hydraulic conductance; plant reproduction; *Salvia mellifera*; soil water content; stomatal conductance; transpiration; water potential.

Considering the vital role of water in plant physiological function, its limitation has undoubtedly been a powerful basis for natural selection. Water loss via transpiration is an expensive yet necessary tradeoff associated with carbon gain. The various adaptations that maintain plant water balance in spite of transpirational losses are essential to support photosynthesis and growth (Meinzer et al., 2001). Stomatal closure is the primary mechanism by which plants regulate water loss and reduce the probability of xylem cavitation. Although details of the signaling that induces stomatal closure are unclear, it is widely observed that plants reduce stomatal conductance (g_s) of their leaves in response to declining bulk leaf water potential (Ψ_{shoot}) or to increasing vapor pressure deficit (VPD) (Monteith, 1995;

Saliendra et al., 1995; Oren et al., 1999). The sensitivity of stomata to these environmental cues depends on g_s at low VPD (Oren et al., 1999) and on the range of soil water potential experienced by the plant (Saliendra et al., 1995). Shedding leaves, and thus reducing evaporative surface area, is another mechanism by which plants maintain water balance (Pataki et al., 1998). Yet most of these mechanisms for regulating water loss involve foliar responses, and despite the central role of flowering to plant function, floral hydraulics has been substantially less studied than the hydraulics of leaves, stems and roots.

There is growing evidence that flowering imposes significant water costs to plants (Nobel, 1977; Chapotin et al., 2003; de la Barrera and Nobel, 2004; Galen, 2005; Feild et al., 2009) and that these water costs can deleteriously affect leaf physiology and growth (Galen et al., 1999; McDowell and Turner, 2002; Lambrecht and Dawson, 2007). Floral water balance is essential for the opening and expansion of flowers, as well as the maintenance of floral temperatures, pollen viability, and nectar supplies, all of which are significant factors in determining fitness (van Doorn, 1997; Patiño and Grace, 2002; Tsukaguchi et al., 2003; van Doorn and van Meeteren, 2003; Galen, 2005). Furthermore, extensive agricultural research has demonstrated the consequences of drought for crop production, from the flowering through fruiting stages of reproductive development (Boyer and Westgate, 2004; Passioura, 2006). In spite of these important connections between reproductive physiology and water availability, there is much to learn about floral hydraulics. For example, the primary tissue responsible for conducting water to flowers or fruit is the xylem in some species (Feild et al., 2009;

¹Manuscript received 19 December 2010; revision accepted 29 April 2011.

The authors thank S. Strahm for research coordination, the staff of Santa Margarita Ecological Reserve and the San Diego State Field Stations Program for operational support, and the University of California, Riverside, and San Jose State University for logistical support. D. A. Grantz and A. B. Roddy provided extremely insightful comments on an earlier version of the manuscript. Partial funding was provided by National Science Foundation grant 08-17212 to L. Santiago.

⁴Current address: Department of Biological Sciences, New Jersey Institute of Technology, Newark, New Jersey 07102, USA.

⁵Current address: Facultad de Medicina Veterinaria y Zootecnia, Cuerpo Académico de Ecología Tropical, Universidad Autónoma de Yucatán, Mérida, Mexico.

⁶Author for correspondence (e-mail: santiago@ucr.edu)

Windt et al., 2009), the phloem in others (Trolinder et al., 1993; Chapotin et al., 2003; Mingo et al., 2003; de la Barrera and Nobel, 2004), and a combination of the two in others, with the proportion changing between anthesis and fruit development (Ho et al., 1987; van Ieperen et al., 2003). Furthermore, although the petals of some species have stomata (Lipayeva, 1989; Galen et al., 1993; Vemmos and Goldwin, 1993; van Doorn, 1997), these stomata appear to be nonfunctional and, thus, do not contribute to the control of water loss (Watson, 1962; Hew et al., 1980; van Doorn, 1997; Patiño and Grace, 2002). By contrast, Feild et al. (2009) show large diurnal variation in the stomatal conductance of *Magnolia* tepals. Therefore, given the variation in these results, controls over floral water balance are not well characterized.

The Mediterranean climate of southern California has produced plant communities that exhibit distinctive physiological strategies to cope with extended summer drought. The California coastal sage scrub (CSS) community is found along arid slopes of coastal and interior southern California (Mooney, 1977; Westman, 1981), and many CSS plants escape drought by dropping some or all of their leaves during the summer dry season (Westman, 1981). During the rainy winter and spring months, when CSS plants develop new leaves, they exhibit high physiological rates, particularly as compared with evergreen shrubs of nearby chaparral communities (Kolb and Davis, 1994). Along with these high rates of gas exchange during the wet season, CSS plants have low resistance to water loss, little capacity to store water in shoots, and relatively high vulnerability to xylem cavitation (Poole and Miller, 1975; Kolb and Davis, 1994; Jacobsen et al., 2007). Like many desert plants, CSS plants often produce large, showy flowers and/or inflorescences, which function to attract limited and often highly specialized pollinators. However, such reproductive displays may also impose substantial water costs to the plant.

This study was designed to compare floral and leaf physiology and hydraulics of *Salvia mellifera* E. Greene (black sage, Lamiaceae), one of the dominant species of the CSS community. A short-term irrigation treatment was applied at the end of the spring wet season, when *S. mellifera* was in flower, and prior to the onset of leaf shedding. The objectives of the study were (1) to compare floral and leaf physiological responses to water availability, (2) to examine water supply limitations to floral and leaf physiology, (3) to quantify the daily water costs of leaves and inflorescences, and (4) to verify the presence or absence of stomata on flowers. In accordance with water relations of CSS plants and their limited capacity to store water and resist its loss, it was expected that water loss from *S. mellifera* flowers would come from daily water uptake, and not from longer-term stem-water stores. It was also expected that corollas would exhibit less control over water loss than leaves.

MATERIALS AND METHODS

Study site and experimental design—The study was conducted at the Santa Margarita Ecological Reserve (SMER), a 1758-ha reserve located on the border of Riverside and San Diego counties, California, USA (33.4°N, 117.2°W). The site receives ~400 mm of precipitation annually in a Mediterranean climate of cool, wet winters between November and April and hot, dry summers. Mean annual temperature is 16.4°C, and the elevation range of the site is 152–701 m. Soil is a sandy clay loam of the Las Posas Series derived of igneous and weathered Gabbro material (Vourlitis et al., 2009). Vegetation at the site is a mix of evergreen chaparral dominating north-facing slopes, semidrought deciduous CSS covering south-facing slopes, and riparian habitats along drainages.

Salvia mellifera (Fig. 1) is a semideciduous shrub that is codominant in CSS habitats in southern California along with *Artemisia californica* Less. (Asteraceae), or California sagebrush (Mooney, 1977; Westman, 1981). *S. mellifera* is one of two species of *Salvia* that occur at SMER and grows approximately 1–2 m tall with inflorescences that occur on determinate shoots in 1.6–4 cm wide clusters of pale blue to lavender, two-lobed flowers (Hickman, 1993). Individual flowers are receptive for several days and open sequentially, so that only a few flowers per cluster are open at a time.

A flat to gently sloping (<3°) southwest-facing study area approximately 50 × 50 m in size was selected, and the 10 largest *S. mellifera* plants of similar size (~2 m tall) in the study area were marked as experimental individuals. Each plant was then randomly assigned to either the irrigation or control treatment. Irrigated plants received 15.6 L of water at the base of their stem every 24 h through a 6.35-mm-diameter drip line fitted with a flow controller to ensure constant, low flow rates. A minimum of 7 m buffer separated experimental plants so that control plants received no water. Irrigation was initiated on Julian day 99 2008 (8 April), at approximately 1400 hours and continued through day 104 2008 (13 April). This period represents the early flowering period for *S. mellifera*, approximately 2 wk after the last seasonal rains.

Microclimate—Conditions at the study sites were monitored at the Southside Weather Station Observatory, ~1.5 km from the study plot. Photon flux density (PFD) was measured with a quantum sensor (190SB, Li-Cor Biosciences, Lincoln, Nebraska, USA) and relative humidity and air temperature were measured with a shielded temperature/humidity sensor (HMP45C, Vaisala, Helsinki, Finland). Data were recorded every 5 s and averaged every 30 min with a data logger (23X, Campbell Scientific, Logan, Utah, USA). Vapor pressure deficit was calculated as the difference between saturated and actual air vapor pressure at a given temperature based on air temperature and relative humidity measurements (Rosenberg et al., 1983).



Fig. 1. *Salvia mellifera* growing at Santa Margarita Ecological Reserve, California, USA.

Flowering shoot morphology—To determine shoot morphology, 20 terminal flowering shoots from 20 individuals were selected for measurement. The number of open flowers was counted before shoots were cut back to their first branching point, harvested, and transported in plastic bags and a cooler to the laboratory within 1 h. Flowering shoots consisted of terminal branches 30–50 cm long with 3–5 clustered inflorescences, each containing 10–35 (mean = 19.8 ± 2.8 SE) open flowers. Inflorescences were in the earlier stages of flowering, with <10% of flowers past blooming and >50% of flowers unopened. Area of all leaves per shoot was measured with an area meter (3100C; Li-Cor Biosciences). Three fully open corollas from each of three individuals were scanned on a flatbed scanner, and images were analyzed for area using Image Tool version 2.0 (University of Texas Health Science Center, San Antonio, Texas, USA). Total shoot water content was determined by the difference between fresh and dry mass after drying until constant mass for 2–4 d at 65°C.

Gas exchange measurements—Diurnal measurements of transpiration of leaves (E_{leaf}) and entire corollas (E_{corolla}) and diffusive conductance to water vapor of leaves (g_s) and corollas (g_c) were made every 2 h on treatment and control plants of *S. mellifera* between 0630 and 1800 hours for 2 days (Julian days 101 and 102) with an IR gas analyzer (6400; Li-Cor Biosciences) equipped with an *Arabidopsis* chamber (6400-15; Li-Cor Biosciences). Two leaves and corollas per plant were measured during each round. Photon flux density, temperature, and relative humidity varied with ambient conditions while CO_2 concentration within the cuvette was held at approximately ambient levels. The presence of nighttime transpiration from leaves was investigated by three measurements on each study plant on Julian day 100 (9 April) between 0200 and 0400 hours.

Total daily water use ($\text{g H}_2\text{O d}^{-1}$) of leaves (Leaf E_t) and corollas (Corolla E_t) were calculated on the basis of diurnal measurements of transpiration, time between measurements, and leaf and corolla area (see Flowering shoot morphology, above). Area-weighted total water use per shoot (Shoot E_t) was calculated as the sum of Leaf E_t and Corolla E_t . We were not able to account for sepal transpiration because of the sepals' small size and orientation in bunches.

Hydraulic measurements—Bulk shoot water potential (Ψ_{shoot}) was measured on 2–3 shoots per study plant at midday (1300 hours) before the beginning of the experiment and at predawn (0400 hours) and midday (1300 hours) during irrigation, with a pressure chamber (1001; PMS Instrument Company, Albany, Oregon, USA). Terminal shoots approximately 20 cm in length were clipped and immediately placed in the chamber for measurement. Soil volumetric water content to a depth of 12 cm was measured concurrently with predawn and midday plant water potential, using a hand-held time-domain reflectometer (CS620; Campbell Scientific, Logan, Utah, USA).

The leaf area-specific total hydraulic conductance of the soil/root/leaf pathway (K_H) for study plants was estimated as

$$K_H = \frac{E}{\Delta\Psi}$$

where E is the average transpiration rate per leaf area from leaves during midday leaf-water-potential measurements and $\Delta\Psi$ is the difference between predawn and midday leaf water potential. Although transpiration rates determined with gas exchange tend to overestimate *in situ* rates because of a disruption of the boundary layer, usually this inflation is less than 13% on the basis of estimates of minimum boundary layer conductance (McDermitt, 1990; Sperry and Pockman, 1993).

Microscopy methods—To check for the presence of stomata on corollas, an acrylic monomer was applied to fresh flowers and allowed to dry overnight. The following day, the epidermal peels were separated from floral tissue and viewed under an epifluorescence microscope (Zeiss Axio Scope.A1; Carl Zeiss MicroImaging, Thornwood, New York, USA) at 20 \times magnification. Images were acquired with a digital camera (ORCA-R2 Hamamatsu Photonics, Hamamatsu City, Japan), with dual scan at 1344 \times 1024 resolution. A scanning electron microscope (SEM Hitachi TM-1000; Hitachi High Technologies, Pleasanton, California, USA) was used to determine the location and structure of leaf stomata on *S. mellifera* leaf samples. Samples were prepared from leaves collected at the study site. Sections were cut from the approximate center of each leaf, mounted on aluminum sample holders, and attached using nonconductive press-and-lift tabs so that the sample could be viewed in cross section.

Data analysis—Mean g_s , g_c , E_{leaf} , E_{corolla} , and Ψ_{shoot} were compared between treatments by repeated-measures analysis of variance, using irrigation or control

as the between-subject factor and measurement time as the within-subject factor. Comparisons of K_H , Leaf E_t , Corolla E_t , total E_t and nighttime transpiration between irrigated and control plants were performed with general linear models. Relationships of g_s and g_c as a function of natural log-transformed VPD were conducted with linear regression (Oren et al., 1999). Differences in slope and intercept between irrigated and control plants were then tested using analysis of covariance. Statistical analyses were performed in SAS version 9.1 (SAS Institute, Cary, North Carolina, USA).

RESULTS

The irrigation treatment increased soil and plant water status (Fig. 2). Mean soil volumetric water content (VWC) increased to ~10% greater than that of controls following the application of the irrigation treatment and then remained at 12–22% greater than that of controls for the duration of the study (Fig. 2A). The response of VWC in soil around irrigated plants following irrigation represents an increase of 203% above values for soil around control plants ($F_{1,8} = 161.74$, $P \leq 0.0001$). Midday Ψ_{shoot}

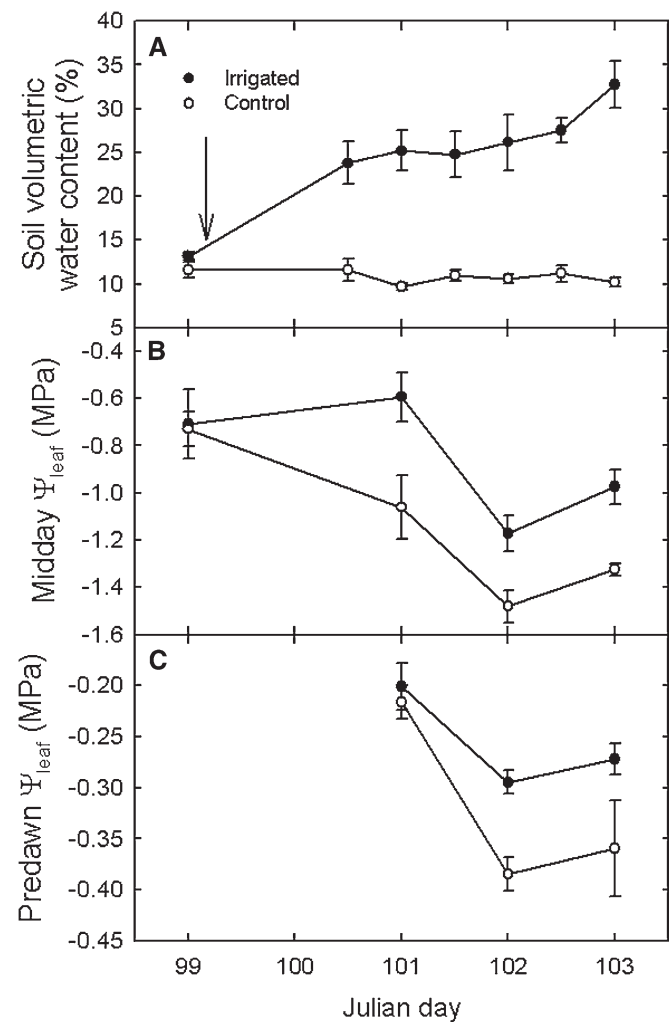


Fig. 2. Soil and plant water status before and during the irrigation treatment: (A) soil volumetric water content, (B) midday, and (C) predawn shoot water potential (Ψ_{shoot}) for control (open circles) and irrigated (closed circles) *Salvia mellifera* plants at Santa Margarita Ecological Reserve, California, USA. Note the difference in y-axis values between B and C. The arrow indicates the application of the irrigation treatment ($n = 5$).

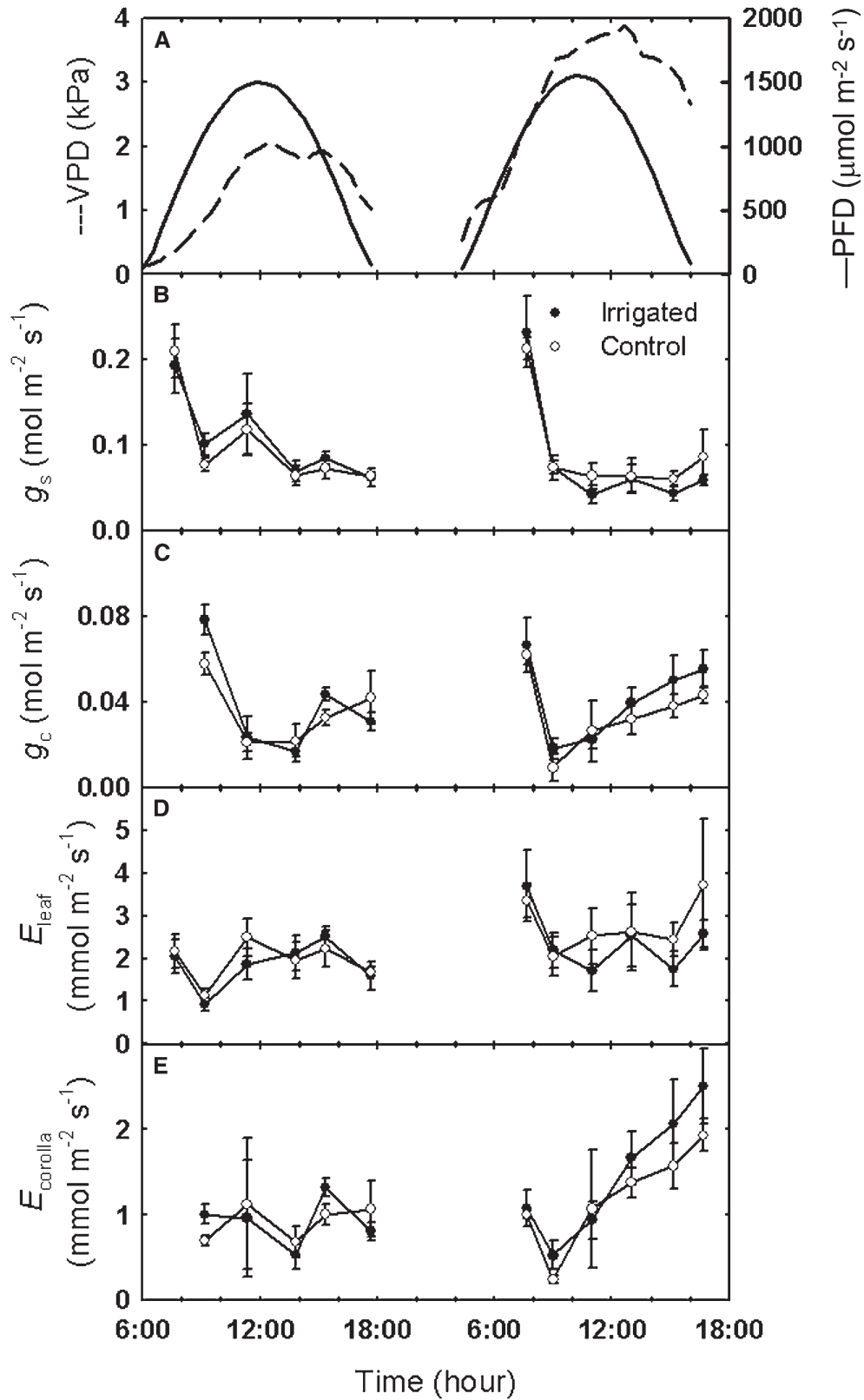


Fig. 3. Gas exchange measurements of *Salvia mellifera* at Santa Margarita Ecological Reserve, California, USA, during two days (Julian days 101 and 102) of experimental irrigation. (A) Vapor pressure deficit (VPD) and photon flux density (PFD) over diurnal measurement periods. (B) Leaf diffusive conductance (g_s) for control (open circles) and irrigated (closed circles) plants. (C) Corolla diffusive conductance (g_c) for control and irrigated plants. (D) Leaf transpiration (E_{leaf}) for control and irrigated plants. (E) Corolla transpiration (E_{corolla}) for control and irrigated plants ($n = 5$).

was similar among plants prior to the irrigation treatment ($F_{1,8} = 0.02$, $P = 0.89$) but was significantly greater for irrigated plants once the irrigation treatment was initiated ($F_{1,8} = 94.68$, $P \leq 0.0001$, Fig. 2B). Predawn Ψ_{shoot} was also significantly greater for irrigated plants than control plants following irrigation ($F_{1,8} = 13.38$, $P \leq 0.01$; Fig. 2C). Predawn and midday Ψ_{shoot} dropped markedly for control and irrigated plants on Julian day 102 (Fig. 2), when VPD was substantially greater than on previous days (Fig. 3A). In spite of differences in soil and plant moisture, the irrigation treatment had no significant effects on diffusive conductance to water vapor of leaf stomata (g_s , $F_{1,8} = 0.00$, $P = 0.99$) or corollas (g_c , $F_{1,8} = 2.33$, $P = 0.22$) (Fig. 3B, C).

Across both treatments, initial measurements of g_s and g_c were high in the morning and then declined with increasing VPD (Fig. 3). However, following this decline, g_s remained fairly constant whereas g_c gradually recovered over the afternoon. Therefore, there were significant relationships between g_s and $\ln(\text{VPD})$ for both irrigated ($r^2 = 0.52$, $df = 11$, $P \leq 0.01$) and control ($r^2 = 0.57$, $df = 11$, $P \leq 0.005$) plants, but relationships between g_c and $\ln(\text{VPD})$ were not significant for either irrigated ($r^2 = 0.20$, $df = 11$, $P = 0.17$) or control ($r^2 = 0.23$, $df = 11$, $P = 0.13$) plants. There were no statistical differences in slopes ($F_{1,22} = 0.143$, $P = 0.68$) or intercepts ($F_{1,22} = 0.039$, $P = 0.85$) for g_s - $\ln(\text{VPD})$ relationships between irrigated and control plants. Nighttime transpiration was not significantly different from zero ($F_{1,8} = 0.722$, $P = 0.42$).

Irrigation treatments did not produce significant differences in E_{leaf} ($F_{1,8} = 0.44$, $P = 0.53$) or E_{corolla} ($F_{1,8} = 0.78$, $P = 0.44$) (Fig. 3D, E). Corolla transpiration rates (E_{corolla}) were approximately half those of the leaves (E_{leaf}) on an area-weighted basis (Table 1). However, when total daily water use (E_t) of each tissue was calculated, Corolla E_t averaged only ~20% of total shoot E_t per day (Table 1), because of the greater evaporative surface area of leaves on each shoot. Mean corolla area was 20.95 cm² per shoot, whereas mean leaf area per shoot was 42.43 cm². There were no significant differences in Leaf E_t ($F_{1,8} = 0.677$, $P = 0.44$), Corolla E_t ($F_{1,8} = 0.27$, $P = 0.62$), or total E_t of the shoot ($F_{1,8} = 0.36$, $P = 0.57$) when compared between treatments (Table 1). However, the irrigation treatment led to significant increases in K_H ($F_{1,18} = 5.58$, $P = 0.03$) (Fig. 4). There were no visible stomata on floral epidermal peels and stomata were not found on the adaxial (upper) surface of leaves but were located on the abaxial (lower) surface of leaves within sunken stomatal crypts (Fig. 5).

TABLE 1. Results of irrigation experiment on leaf and corolla gas exchange for *Salvia mellifera* plants ($n = 5$) from Santa Margarita Ecological Reserve, California, USA. Mean (\pm SE) transpiration per leaf area (E_{leaf}), daily leaf water loss (Leaf E_t), transpiration per corolla area (E_{corolla}), daily corolla water loss (Corolla E_t), area-weighted mean shoot transpiration (E_{shoot}), and sum total daily shoot water loss (E_t).

	Control	Irrigated
Leaf		
E_{leaf} (mmol m ⁻² s ⁻¹)	2.37 \pm 0.20	2.13 \pm 0.20
Leaf E_t (g d ⁻¹)	5.72 \pm 0.87	4.93 \pm 0.63
Corolla		
E_{corolla} (mmol m ⁻² s ⁻¹)	1.07 \pm 0.13	1.21 \pm 0.18
Corolla E_t (g d ⁻¹)	1.32 \pm 0.20	1.45 \pm 0.15
Shoot		
E_{shoot} (mmol m ⁻² s ⁻¹)	1.94 \pm 0.17	1.83 \pm 0.16
E_t (g d ⁻¹)	7.04 \pm 1.01	6.38 \pm 0.72

DISCUSSION

The results indicate that responses of *S. mellifera* to experimental irrigation during the spring flowering season were characterized by increases in leaf water status and total hydraulic conductance of the soil-root-leaf pathway. Gas exchange rates were likely near their seasonal maxima and did not respond to water addition despite improved plant water status. The results also demonstrate that flowers of *S. mellifera* used substantial amounts of water and that floral water loss lacks the regulation provided by stomatal control in leaves. The mean water content of 5.07 \pm 0.36 g in *S. mellifera* shoots was close to the mean daily E_t of 6.71 g H₂O d⁻¹, indicating that the equivalent of total water content of shoots turned over every 0.76 d. These data demonstrate the high water costs of flowers and illustrate the necessity for consistent water supply during reproduction in *S. mellifera*.

The large increase in K_H in response to irrigation, combined with the lack of response in leaf and floral gas exchange, indicates that physiological processes in *S. mellifera* were not limited by water availability during the spring season. Several studies have shown that as water deficit increases, K_H and g_s tend to decrease with minimal changes in Ψ_{shoot} (Meinzer and Grantz, 1990; Saliendra et al., 1995; Hubbard et al., 2001; Santiago et al., 2004). However, in response to water addition, we observed that K_H and Ψ_{shoot} increased with only moderate changes in leaf and floral gas exchange. Large increases in Ψ_{shoot} and K_H have been observed with experimental irrigation in southern California desert shrubs (Meinzer et al., 1988), consistent with our measured responses of Ψ_{shoot} and K_H . Therefore, although transpiration rates were similar between control and irrigated plants, increased whole-plant hydraulic conductance is the major response to irrigation during flowering in *S. mellifera*.

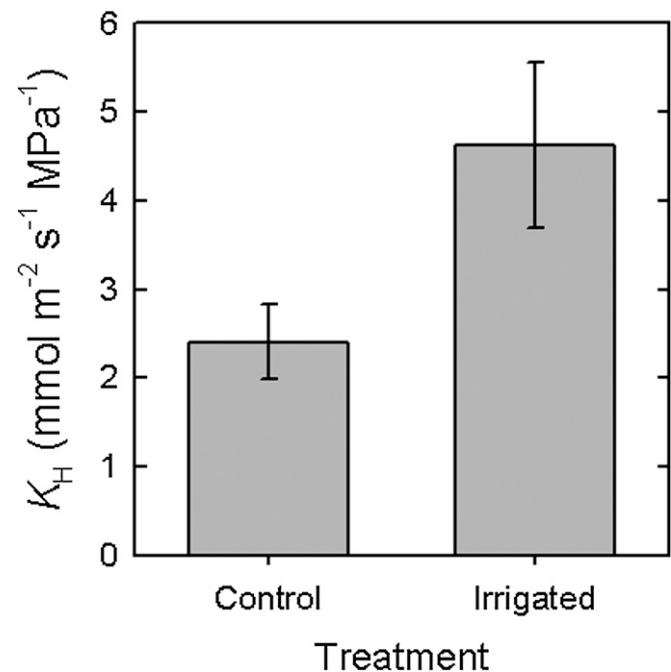


Fig. 4. Area-based midday total hydraulic conductance of the soil-root-leaf pathway (K_H) of irrigated and control plants of *Salvia mellifera* ($n = 5$). K_H was greater in irrigated plants than control plants ($P = 0.03$).

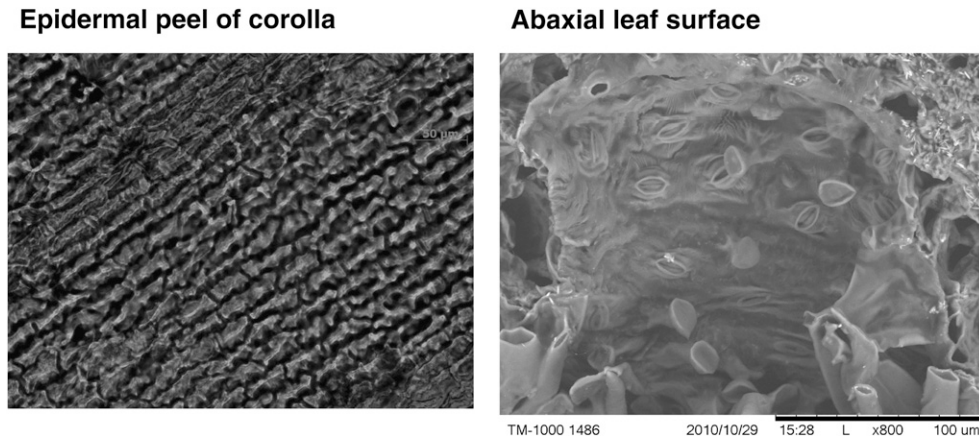


Fig. 5. Epidermal peel of corolla showing absence of stomata (left panel) and stomatal crypt of the abaxial leaf surface showing presence of stomata (right panel) for *Salvia mellifera* plants growing at Santa Margarita Ecological Reserve, California, USA.

The observed patterns of leaf physiological rates of *S. mellifera* are consistent with seasonal hydraulic patterns in CSS plants that include maximizing physiological activity when water is available (Jacobsen et al., 2007). To support high rates of photosynthesis and growth during their short metabolically active season, CSS plants are often highly efficient at transporting water (Kolb and Davis, 1994). However, CSS plants are also semideciduous during summer drought, a characteristic that reduces transpirational surface area and, thus, water loss (Pataki et al., 1998; Santiago et al., 2000). Yet data for *S. mellifera* suggest that leaf shedding does not adequately enable avoidance of seasonal summer drought (Gill and Mahall, 1986; Kolb and Davis, 1994). Instead, it appears that *S. mellifera* sheds its leaves in response to water-stress-induced cavitation, and irrigation applied throughout the summer drought can prevent leaf shedding (Kolb and Davis, 1994). Interestingly, leaf shedding in *S. mellifera* has been reported to occur earlier on flowering shoots than on nonflowering shoots (Gill and Mahall, 1986; Kolb and Davis, 1994). Our data demonstrating the high water costs of flowering in *S. mellifera* suggest two hypotheses for this pattern: (1) when faced with declining water availability, plants shed leaves to favor floral water supply; or (2) the high water costs of flowering cause rapid depletion of water resources as seasonal water availability declines. These hypotheses could be distinguished by bagging flowers to reduce water loss and observing whether leaves are still shed earlier on flowering shoots than on nonflowering shoots.

Rates of water loss increased throughout the afternoon in flowers, but not in leaves, which suggests less control of *S. mellifera* floral water loss compared with that of leaves. Corollas of *S. mellifera* lack stomata (Fig. 5), which is consistent with the other *Salvia* species that has been investigated for the presence of floral stomata (Lipayeva, 1989). Therefore, unlike leaves, only a thin cuticle on the corolla appears to protect *S. mellifera* floral tissues from the evaporative demand of rising VPD, which is consistent with our data showing larger increases in E_{corolla} than E_{leaf} with increasing VPD. However, even though there were no stomata on corollas, g_c responded to VPD, and this suggests that other factors, such as severe tissue dehydration, changes in cuticle permeability, or a decoupling between VPD measured at the climate station and within the microclimate of the corolla, cause diurnal variation in g_c . The large drop in both g_c and g_s in the morning likely reflects the formation of xylem

emboli, consistent with a hydraulic strategy that sacrifices protection for high conductivity (Kolb and Davis, 1994). Yet the large afternoon fluctuations observed in E_{corolla} are consistent with limited control of water loss and the high water costs of flowering.

Our values for E_{corolla} in *S. mellifera* are the highest reported for a floral tissue. The few reports of transpiration rates from flowers range from about 0.006 to 2.2 mmol m⁻² s⁻¹ (Blanke and Lovatt, 1993; Patiño and Grace, 2002; Galen, 2005; Feild et al., 2009). Maximum E_{corolla} of *S. mellifera* was 2.5 mmol m⁻² s⁻¹, a rate that was ~60% of maximum E_{leaf} . This ratio of floral to leaf transpiration is similar to that of *Magnolia grandiflora* L., which has the highest previously reported E_{corolla} (Feild et al., 2009) but has a lower ratio of floral to leaf transpiration than *Persea americana* Mill. (Blanke and Lovatt, 1993). The highest rates of E_{corolla} for *S. mellifera* were observed on Julian day 102, when VPD was highest (Fig. 3A). High rates of E_{corolla} offer a critical floral cooling mechanism (Patiño and Grace, 2002) and may have protected flowers from high temperatures experienced during our study.

Our data showing that daily water use by corollas during flowering constitutes ~20% of shoot water use demonstrate that the hydraulic costs of reproduction in this species are substantial and should be incorporated into models of plant water balance. Current estimates of climate change in California predict increased frequency of drought in association with warmer temperatures (IPCC, 2007). Although changes in species distribution are predicted to occur with changing climate (Lenihan et al., 2003), plant reproduction under declining environmental water availability would be necessary to support such species migration. Our data demonstrate the importance of water supply to floral physiology and suggest that a complete understanding of plant water balance and its susceptibility to alterations in water supply are critical for determining the future of natural vegetation in California.

LITERATURE CITED

- BLANKE, M. M., AND C. J. LOVATT. 1993. Anatomy and transpiration of the avocado inflorescence. *Annals of Botany* 71: 543–547.
- BOYER, J. S., AND M. E. WESTGATE. 2004. Grain yields with limited water. *Journal of Experimental Botany* 55: 2385–2394.
- CHAPOTIN, S. M., N. M. HOLBROOK, S. R. MORSE, AND M. V. GUTIERREZ. 2003. Water relations of tropical dry forest flowers: Pathways for

- water entry and the role of extracellular polysaccharides. *Plant, Cell & Environment* 26: 623–630.
- DE LA BARRERA, E., AND P. S. NOBEL. 2004. Nectar: properties, floral aspects, and speculations on origin. *Trends in Plant Science* 9: 65–69.
- FEILD, T. S., D. S. CHATELET, AND T. J. BRODRIBB. 2009. Giant flowers of southern magnolia are hydrated by the xylem. *Plant Physiology* 150: 1587–1597.
- GALEN, C. 2005. It never rains but then it pours: The diverse effects of water on flower integrity and function. In E. G. Reekie and F. A. Bazzaz [eds.], *Reproductive allocation in plants*, 77–95. Elsevier Academic Press, Burlington, Vermont, USA.
- GALEN, C., T. E. DAWSON, AND M. L. STANTON. 1993. Carpels as leaves: Meeting the carbon cost of reproduction in an alpine buttercup. *Oecologia* 95: 187–193.
- GALEN, C., R. A. SHERRY, AND A. B. CARROLL. 1999. Are flowers physiological sinks or faucets? Costs and correlates of water use by flowers of *Polemonium viscosum*. *Oecologia* 118: 461–470.
- GILL, D. S., AND B. E. MAHALL. 1986. Quantitative phenology and water relations of an evergreen and a deciduous chaparral shrub. *Ecological Monographs* 56: 127–143.
- HEW, C. S., G. L. LEE, AND S. C. WONG. 1980. Occurrence of non-functional stomata in the flowers of tropical orchids. *Annals of Botany* 46: 195–201.
- HICKMAN, J. C. 1993. *The Jepson manual: Higher plants of California*. University of California Press, Berkeley, California, USA.
- HO, L. C., R. I. GRANGE, AND A. J. PICKEN. 1987. An analysis of the accumulation of water and dry-matter in tomato fruit. *Plant, Cell & Environment* 10: 157–162.
- HUBBARD, R. M., M. G. RYAN, V. STILLER, AND J. S. SPERRY. 2001. Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine. *Plant, Cell & Environment* 24: 113–121.
- IPCC. 2007. *Climatic Change 2007: The Physical Science Basis*. Contribution of Working Group I to the Forth Assessment. Report of the Intergovernmental Panel on Climate Change, Cambridge, United Kingdom.
- JACOBSEN, A. L., R. B. PRATT, S. D. DAVIS, AND F. W. EWERS. 2007. Cavitation resistance and seasonal hydraulics differ among three arid Californian plant communities. *Plant, Cell & Environment* 30: 1599–1609.
- KOLB, K. J., AND S. D. DAVIS. 1994. Drought tolerance and xylem embolism in co-occurring species of coastal sage and chaparral. *Ecology* 75: 648–659.
- LAMBRECHT, S. C., AND T. E. DAWSON. 2007. Correlated variation of floral and leaf traits along a moisture availability gradient. *Oecologia* 151: 574–583.
- LENIHAN, J. M., R. DRAPEK, D. BACHELET, AND R. P. NEILSON. 2003. Climate change effects on vegetation distribution, carbon, and fire in California. *Ecological Applications* 13: 1667–1681.
- LIPAYEVA, L. 1989. On the anatomy of petals in angiosperms. *Botanicheskii Zhurnal* 74: 826–830.
- MCDERMITT, D. K. 1990. Sources of error in the estimation of stomatal conductance and transpiration from porometer data. *HortScience* 25: 1538–1548.
- MCDOWELL, S. C. L., AND D. P. TURNER. 2002. Reproductive effort in invasive and non-invasive *Rubus*. *Oecologia* 133: 102–111.
- MEINZER, F. C., M. J. CLEARWATER, AND G. GOLDSTEIN. 2001. Water transport in trees: Current perspectives, new insights and some controversies. *Environmental and Experimental Botany* 45: 239–262.
- MEINZER, F. C., AND D. A. GRANTZ. 1990. Stomatal and hydraulic conductance in growing sugarcane: Stomatal adjustment to water transport capacity. *Plant, Cell & Environment* 13: 383–388.
- MEINZER, F. C., M. R. SHARIFI, E. T. NILSEN, AND P. W. RUNDEL. 1988. Effects of manipulation of water and nitrogen regime on the water relations of the desert shrub *Larrea tridentata*. *Oecologia* 77: 480–486.
- MINGO, D. M., M. A. BACON, AND W. J. DAVIES. 2003. Non-hydraulic regulation of fruit growth in tomato plants (*Lycopersicon esculentum* cv. Solairo) growing in drying soil. *Journal of Experimental Botany* 54: 1205–1212.
- MONTEITH, J. L. 1995. A reinterpretation of stomatal responses to humidity. *Plant, Cell & Environment* 18: 357–364.
- MOONEY, H. A. 1977. Southern coastal scrub. In M. G. Barbour and J. Major [eds.], *Terrestrial vegetation of California*, 471–489. Wiley Interscience, New York, New York, USA.
- NOBEL, P. S. 1977. Water relations of flowering of *Agave deserti*. *Botanical Gazette (Chicago, Illinois)* 138: 1–6.
- OREN, R., J. S. SPERRY, G. KATUL, D. E. PATAKI, B. E. EWERS, N. PHILLIPS, AND J. P. MEGONIGAL. 1999. Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapor pressure deficit. *Plant, Cell & Environment* 22: 1515–1526.
- PASSIOURA, J. 2006. Increasing crop productivity when water is scarce—from breeding to field management. *Agricultural Water Management* 80: 176–196.
- PATAKI, D. E., R. OREN, AND N. PHILLIPS. 1998. Responses of sap flux and stomatal conductance of *Pinus taeda* L. trees to stepwise reductions in leaf area. *Journal of Experimental Botany* 49: 871–876.
- PATIÑO, S., AND J. GRACE. 2002. The cooling of convolvulaceous flowers in a tropical environment. *Plant, Cell & Environment* 25: 41–51.
- POOLE, D. K., AND P. C. MILLER. 1975. Water relations of selected species of chaparral and coastal sage communities. *Ecology* 56: 1118–1128.
- ROSENBERG, N. J., B. L. BLAD, AND S. B. VERMA. 1983. *Microclimate: The biological environment*. John Wiley and Sons, New York, New York, USA.
- SALIENDRA, N. Z., J. S. SPERRY, AND J. P. COMSTOCK. 1995. Influence of leaf atmospheric drought, and soil drought in *Betula occidentalis*. *Planta* 196: 357–366.
- SANTIAGO, L. S., G. GOLDSTEIN, F. C. MEINZER, J. B. FISHER, K. MACHADO, D. WOODRUFF, AND T. JONES. 2004. Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia* 140: 543–550.
- SANTIAGO, L. S., G. GOLDSTEIN, F. C. MEINZER, J. FOWNES, AND D. MUELLER-DOMBOIS. 2000. Transpiration and forest structure in relation to soil waterlogging in a Hawaiian montane cloud forest. *Tree Physiology* 20: 673–681.
- SPERRY, J. S., AND W. T. POCKMAN. 1993. Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis*. *Plant, Cell & Environment* 16: 279–287.
- TROLINDER, N. L., B. L. MCMICHAEL, AND D. R. UPCHURCH. 1993. Water relations of cotton flower petals and fruit. *Plant, Cell & Environment* 16: 755–760.
- TSUKAGUCHI, T., Y. KAWAMITSU, H. TAKEDA, K. SUZUKI, AND Y. EGAWA. 2003. Water status of flower buds and leaves as affected by high temperature in heat-tolerant and heat-sensitive cultivars of snap bean (*Phaseolus vulgaris* L.). *Plant Production Science* 6: 24–27.
- VAN DOORN, W. G. 1997. Water relations of cut flowers. *Horticultural Reviews* 18: 1–85.
- VAN DOORN, W. G., AND U. VAN MEETEREN. 2003. Flower opening and closure: A review. *Journal of Experimental Botany* 54: 1801–1812.
- VAN IEPEREN, W., V. S. VOLKOV, AND U. VAN MEETEREN. 2003. Distribution of xylem hydraulic resistance in fruiting truss of tomato influenced by water stress. *Journal of Experimental Botany* 54: 317–324.
- VEMMOS, S. N., AND G. K. GOLDWIN. 1993. Stomatal and chlorophyll distribution of Cox's orange pippin apple flowers relative to other cluster parts. *Annals of Botany* 71: 245–250.
- VOURLITIS, G. L., S. C. PASQUINI, AND R. MUSTARD. 2009. Effects of dry-season N input on the productivity and N storage of Mediterranean-type shrublands. *Ecosystems (New York)* 12: 473–488.
- WATSON, L. 1962. The taxonomic significance of stomatal distribution and morphology in *Epacridaceae*. *New Phytologist* 61: 36–40.
- WESTMAN, W. E. 1981. Factors influencing the distribution of species of Californian coastal sage scrub. *Ecology* 62: 439–455.
- WINDT, C. W., E. GERKEMA, AND H. VAN AS. 2009. Most water in the tomato truss is imported through the xylem, not the phloem: A nuclear magnetic resonance flow imaging study. *Plant Physiology* 151: 830–842.