

SHOOT DIEBACK DURING PROLONGED DROUGHT IN *CEANOOTHUS* (RHAMNACEAE) CHAPARRAL OF CALIFORNIA: A POSSIBLE CASE OF HYDRAULIC FAILURE¹

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Progressive diebacks of outer canopy branchlets of *Ceanothus crassifolius* were repeatedly observed after rainless periods up to 9 mo in duration in the Santa Monica Mountains of southern California. Mean xylem pressures of branchlets near the end of drought were as low as -11.2 MPa ($N = 22$) with a mean of about 60 dead branchlets per shrub. Inoculation ($N = 15$) with three species of fungi previously isolated from the same population of *C. crassifolius* did not promote dieback, suggesting that the observed decline was not fungal induced, as had been proposed. Further, at least 50% of healthy-appearing twigs, without symptoms of dieback, contained isolatable endophytic fungi. We used a centrifugal force method to determine the range of xylem pressure causing cavitation (vulnerability curves) for branchlets ($N = 12$) and roots ($N = 16$). We combined vulnerability curves with soil texture data ($N = 6$) into a water transport model that estimated the critical values (P_{Lcrit}) of leaf xylem pressure associated with the loss of water from soil to foliage. Maximum P_{Lcrit} was between -10 and -11 MPa and within the range of minimum measured xylem pressures of branchlets during drought and dieback. Branchlet dieback correlated with seasonal declines in xylem pressure in concert with declining safety margins from hydraulic failure. Symptoms of dieback were duplicated in the field by partially severing stem xylem that normally supplied branchlets with water. Taken together, these results indicate that loss of hydraulic conductance to foliage was the probable cause of the observed dieback in *C. crassifolius*. Partial dieback of peripheral branchlets, and its attendant reduction in evaporative surface area, may be a last-resort mechanism for whole-plant water conservation and drought survival in this species.

Key words: *Ceanothus*; chaparral; water relations; xylem cavitation.

In the fall of 1995, after a protracted summer drought, we observed a progressive increase in branchlet death in the outer canopy of *Ceanothus crassifolius* growing in the Santa Monica Mountains of southern California (Fig. 1A, B). We initially assumed the dieback was fungal related, as previously proposed (Riggan et al., 1994). However, there were no external symptoms of fungal disease, dieback occurred after nearly 9 mo without rain, and mean midday xylem pressure was as low as -11.2 MPa. This suggested an alternate possibility, that branchlet death was caused by water-stress-induced failure of water transport via xylem cavitation and soil drying (Tyree and Sperry, 1988; Sperry et al., 1998). In chaparral shrubs, to maintain the evergreen habit, it is particularly vital that water is continuously delivered to the evergreen foliage. This is especially true for shallow rooted, nonsprouting species, such as *C. crassifolius* (Davis et al., 1999). Such species do not have a root crown or a mechanism of shoot replacement after damage by drought and other disturbances such as wildfire (Thomas and Davis, 1989) or wind (Wagner, Ewers, and Davis, 1998).

We hypothesized that the observed dieback in *C. crassifolius* was caused by water-stress-induced loss of hydraulic conductance in the soil-to-canopy continuum, which blocked the normal flow of water to terminal branchlets. If this were the case, then inoculation of healthy branches with endogenous fungi would not promote the observed symptoms (color change in leaves) or dieback of peripheral branchlets. In contrast, reduction of hydraulic supply by partially cutting through xylem would generate typical symptoms and branchlet death. Furthermore, estimates of the critical leaf xylem pressure required to cause hydraulic failure during drought should be within the range of actual leaf xylem pressure during dieback episodes. Estimates of the critical xylem pressure and associated critical transpiration rate were predicted using a water transport model of the soil-leaf continuum (Sperry et al., 1998; Hacke et al., 2000). The model determined the steady-state carrying capacity of the continuum based on measurements of the vulnerability of roots and stems to xylem cavitation, soil texture, and bulk soil water potential.

MATERIALS AND METHODS

Study site—Our study site was located on or adjacent to the Malibu Forestry Unit of Los Angeles County, California, USA (Fig. 1A, B), along Malibu Canyon Road, across from Tapia Park, at an elevation of 180 m ($34^{\circ}5' N$, $118^{\circ}42' W$). In addition to *Ceanothus crassifolius* (Torrey), the mixed chaparral community was composed of *C. oliganthus* (Nutt.), *Adenostoma fasciculatum* (Hook. & Arn.), *Cercocarpus betuloides* (Torrey & A. Gray), *Malosma laurina* (Nutt.), *Rhus ovata* (S. Watson), and *Quercus berberidifolia*

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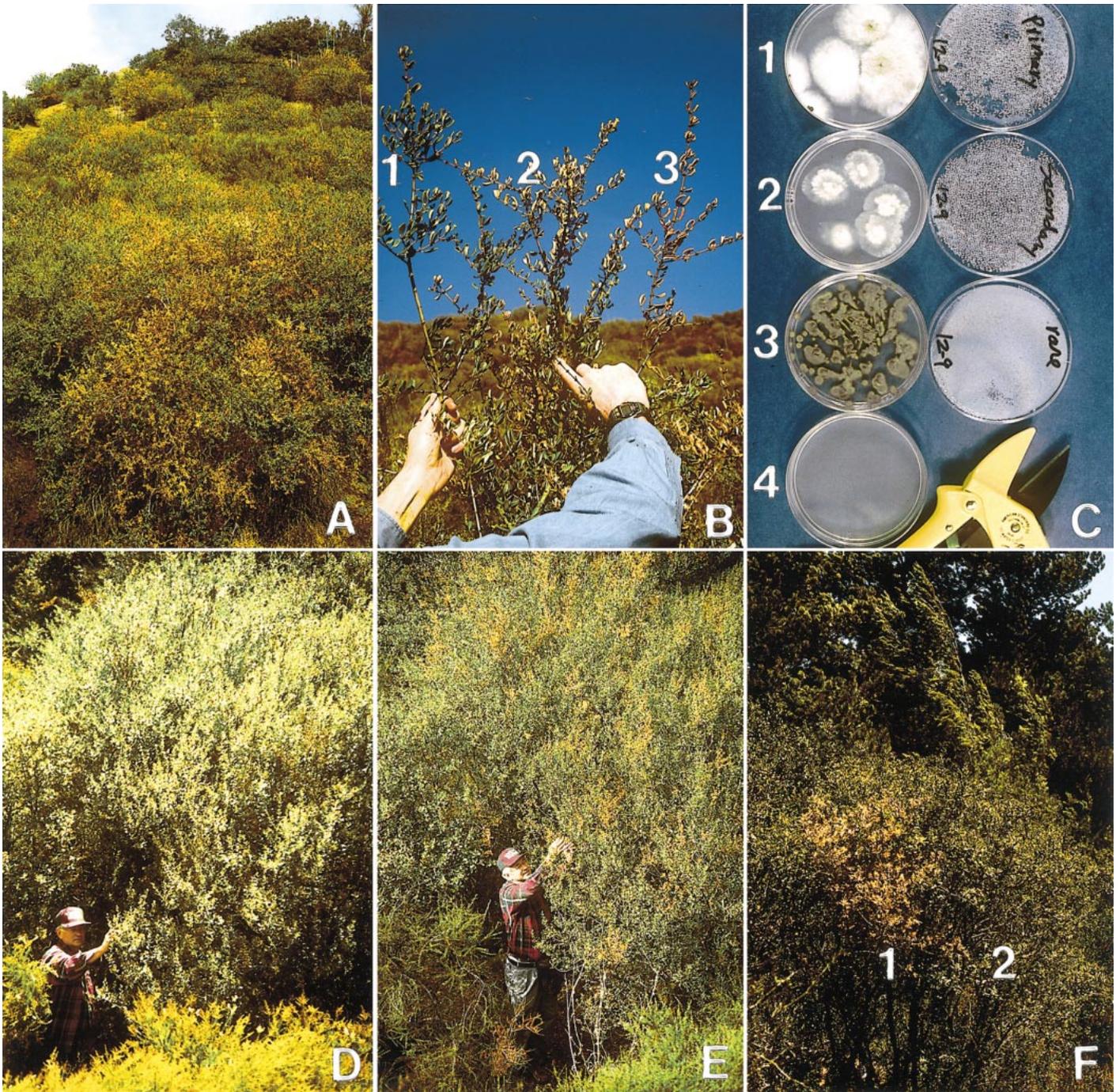


Fig. 1. (A) Mixed stand of *Ceanothus crassifolius* growing at the Malibu Forestry Unit of Los Angeles County in the Santa Monica Mountains of southern California, USA. Note dieback, predominately among terminal, outer canopy branchlets. (B) Individual *C. crassifolius* shrub in November of 1997, at the peak of seasonal drought with close-up view of outer canopy branchlets: (1) healthy, (2) recently dead, and (3) month-old dead. (C) Three species of fungi isolated from *C. crassifolius* growing at our study site and used for inoculation treatments: (1) *Botryosphaeria dothidea*, (2) *Botryosphaeria* sp., (3) *Sclerophoma* sp., and (4) control—agar only. (D) Healthy *C. crassifolius* canopy in midsummer: (E) Same view as in panel D but in late fall after the onset of branchlet dieback. (F) Example of a healthy shrub in midsummer 15 d after the basal stem of one branch was notched (1) adjacent to remaining branches and (2) that were not notched (control).

(Liebm.). Nomenclature follows Hickman (1993). Annual precipitation was recorded at a meteorological station 4 km from our study site (Malibu Beach-Dunne Station, Number 1025, Los Angeles Flood Control District). Precipitation in the rain season of 1995–1996 was 305 mm and in 1996–1997, 329 mm. This was 76% and 82%, respectively, of the 100-yr mean.

Seasonal changes in xylem pressure and assessment of branchlet dieback—We estimated seasonal changes in predawn and midday leaf xylem pressure (P_L) on 12 *C. crassifolius* individuals between November 1995 and June 1998, using a pressure chamber (model 1001, PMS Instrument Company, Corvallis, Oregon, USA), on terminal branchlets, following the methods of

Scholander et al. (1965). Our pressure chamber was custom designed to measure water potentials down to -14 MPa. A wildfire in October of 1996 consumed our 12 original plants, at which time we switched to 12 auxiliary plants within 100 m of the original stand. In November of 1997, we sampled 22 additional plants that suffered extreme dehydration and branchlet dieback, about 200 m from the original stand. On the 12 individuals plus the 22 new individuals in November, we counted the number of recently discolored branchlets (leaves yellow in color; Fig. 1B) between 8 August and 9 December 1997, before the onset of winter rains.

Fungal isolation experiments—In October of 1995, 100 peripheral branchlets, 30–50 cm in length, one from each of 100 individuals of *C. crassifolius*, were collected in the field. Samples were selected that had some, but not all, of their twigs containing discolored leaves. They were individually wrapped in wax paper to avoid moisture condensation or contamination and shipped by overnight mail to the Plant Pathology Laboratory at Michigan State University, where they were processed within 24 h. There were no signs of fruiting bodies, symptoms of necrosis on young leaves or petioles, nor evidence of canker on stems. From these samples, stem segments were taken both from healthy-appearing tissue within 1 cm of discolored (brown) tissue and also from discolored tissue. In July of 1997, 280 peripheral, green, healthy-appearing branchlets were sampled, one from each of 280 individual shrubs. These were processed in the same manner as for the discolored samples mentioned above. For each branchlet, a segment 2 cm in length was surface sterilized for 1 min in 70% ethanol and then for 10 min in 10% chlorine bleach (0.05% sodium hyperchlorite). Excess bleach on stem surfaces was blotted dry between sterile paper towels. The stem segments were subdivided by cutting with a flame-sterilized scalpel both transversely and longitudinally to achieve segments that included both xylem and phloem tissues, of final dimensions $0.5 \times 0.25 \times 0.25$ cm. Petri plates were filled with 20 mL Difco PDA (potato dextrose agar) plus one drop of 25% lactic acid. The final stem segments were pushed into the agar with sterile forceps and incubated in the dark at room temperature for 9 d.

Three species of fungi isolated from discolored branchlets were: (1) *Botryosphaeria dothidea*, which was found in all 100 branchlets (primary fungus), (2) *Botryosphaeria* sp. (undetermined species, secondary fungus) isolated from about ten branchlets, (3) *Sclerophoma* sp. (rare undetermined species, tertiary fungus) isolated from only a few branchlets. The three isolates (Fig. 1C) were then used for inoculation experiments into healthy-appearing branches in the field (see below).

Inoculation experiments—The three cultures isolated above were inoculated on 3 January 1997 into three branches of 15 individuals of *C. crassifolius* growing at our study site. The inoculum consisted of a 0.5 cm diameter agar plug from the margin on a 10–15-d culture on PDA. The culture plug was held in place on the stem and protected from drying with parafilm wrap. Also a fourth branch was inoculated with sterile agar (sterile control) and a fifth was not inoculated but sawed through near its base (severed control) and supported in its normal position in the canopy with duct tape. Subsequently, xylem pressure, variable fluorescence (F_v/F_m , after a 15-min dark adaptation; Model OS5-FL, Modulated Fluorometer, Opti-Science, Tyngsboro, Massachusetts, USA), and a color index of leaves were measured every few days at first, then at progressively longer intervals until 27 July 1997 (204 d). Our color index ranged from 1 to 9 with low values representing green leaves, intermediate values representing yellow leaves, and high values representing brown leaves (Fig. 1B). These numbers corresponded to Munsell Color Standards for Plant Tissues (Munsell Color, Kollmorgen Instruments, Baltimore, Maryland, USA). Our numbers with their corresponding Munsell Colors are as follows: 1 = 5 GY 3/4; 2 = 5 GY 4/4; 3 = 5 GY 5/8; 4 = 2.5 GY 5/6; 5 = 2.5 GY 7/8; 6 = 5 Y 6/8; 7 = 7.5 YR 6/8; 8 = 5 YR 5/8; 9 = 5 YR 3/4.

Xylem-notching experiments—During the summer of 1997, we greatly reduced hydraulic supply by basal stems to terminal branchlets by using a saw to aseptically cut stems (surface disinfected with 70% ETOH) about halfway through, five times, at a 1-cm spacing, spiraling at 90° angles with each suc-

cessive cut (Fig. 1F). Sawed branches were reinforced with a metal splint (two aluminum scapulas held together around the sawed portion of the stem with duct tape). Uncut branches on the same individuals served as a control. Xylem pressure and color index (Munsell Color Standards for Plant Tissues) were measured periodically over a 25-d period.

Vulnerability curves—We determined the susceptibility of stem and root xylem to water-stress-induced embolism using the centrifuge method of Alder et al. (1997). Bowen (1999) has established that the centrifuge method of constructing vulnerability curves matches closely the dehydration and air injection methods of constructing vulnerability curves for chaparral shrubs (cf. Jarbeau, Ewers, and Davis, 1995). Stems were measured in the spring of 1997. One stem segment was cut from each of 12 individuals in our *C. crassifolius* population. Branches were wrapped in plastic and sent by overnight mail to the University of Utah. Branch segments were trimmed underwater to produce an unbranched length of 257 mm with a diameter of 4–7 mm. Segments were inserted in a tubing manifold and flushed for 1 h at 100 kPa with a 0.1 mol/L solution of HCl in distilled water, which had been degassed and passed through a 0.1- μ m mesh diameter filter. We found that HCl or water or KCl produced the same curves (Alder, Sperry, and Pockman, 1996). Now we use water plus 10 mmol KCl. After flushing to remove embolism, the hydraulic conductivity (K_h , in meters to the fourth power per megaPascal per second) was measured with the aid of an analytical balance connected to a computer that calculated K_h as

$$K_h = q/(\Delta P/\Delta x) \quad (1)$$

where $\Delta P/\Delta x$ is the pressure gradient (in megaPascals per meter) and q the net volume flow rate (in cubic meters per second) caused by the applied pressure (background flow at $\Delta P/\Delta x = 0$ subtracted). The applied pressure (ΔP) was kept below 5 kPa to avoid the displacement of embolism during the conductivity measurements. Following the initial flush and measurement of K_h , segments were then removed and spun in a centrifuge rotor designed to accommodate woody stems and roots (cf. Alder, Sperry, and Pockman, 1997). The spinning induces a negative pressure profile in the segment that is a function of segment length and the rotation rate. The duration of the spin treatment was 5 min, after which K_h was measured, and the percentage loss from the initial K_h was calculated (percentage of embolism). The procedure was repeated using progressively higher rotation rates (corresponding to decreasing xylem pressure). The relationship between percentage of embolism and xylem pressure gave the vulnerability curve to water-stress-induced embolism.

Root segments were measured during the summer of 1999 at Pepperdine University using the same technique as above. Lateral roots of 5–12 mm diameter were collected at 20–40 cm depth from the same population sampled for the stem measurements. One root segment was collected from each of 16 individual plants.

Estimation of critical xylem pressure (P_{Lcrit}) and maximum transpiration rate (E_{crit})—We used a water transport model (Sperry et al., 1998; Hacke et al., 2000) to estimate the most negative leaf xylem pressure (P_{Lcrit}) associated with the maximum possible steady-state transpiration rate (E_{crit}) for the canopy. The model calculated the relationship between E and P_x at any bulk soil water potential, taking into account the decreases in hydraulic conductance in the rhizosphere and xylem associated with transpiration. Any leaf xylem pressure more negative than P_{Lcrit} (or E greater than E_{crit}) would cause essentially the complete loss of hydraulic conductance from soil to leaf by the drying of soil in the rhizosphere and the cavitation of the xylem.

The major inputs for the model were (a) the vulnerability curves of root and stem xylem, (b) soil texture in terms of percentage of sand, silt, and clay particles, (c) bulk soil water potential, and (d) the ratio of absorbing root area to transpiring leaf area (A_R/A_L). Stem and root vulnerability curves were used to predict how the hydraulic conductance (k_p) of plant components declined with xylem pressure (P_x) based on a Weibull function curve fit to vulnerability data (Neufeld et al., 1992)

$$k_p = k_{sat} e^{-(P_x/d)^c} \quad (2)$$

TABLE 1. Soil-texture and soil-hydraulic parameters at 15–20 cm depth taken beneath the main *Ceanothus crassifolius* population. This population was on a slope, and soil texture varied with position. Soil A ($N = 3$) was taken from a downslope position relative to soil B ($N = 3$) which came from just below the ridgeline. Air entry potential (Ψ_e , kPa), saturated conductivity (k_{sat} , $\text{mol} \cdot \text{s}^{-1} \cdot \text{MPa}^{-1} \cdot \text{m}^{-1}$), and b values (Eq. 4) were calculated from texture parameters as described in Campbell (1985), assuming a bulk density of 1.3 Mg/m^3 .

Soil	% sand	% silt	% clay	Ψ_e	k_{sat}	b	Soil type
A	76.7 ± 6.1	13.7 ± 2.5	9.7 ± 3.8	-0.91	68.5	4.13	Sandy loam
B	53.7 ± 4.0	29.3 ± 4.0	17.0 ± 0.0	-1.51	23.3	5.62	Sandy loam
Mean	65.2 ± 13.4	21.5 ± 9.1	13.3 ± 4.7	-1.12	40.1	4.54	Sandy loam

where k_{sat} was the saturated hydraulic conductance of the component, and d and c are (positive) curve fitting parameters of the Weibull function. While the k_{sat} can be assigned from measurements of maximum plant hydraulic conductance (e.g., Hacke et al., 2000), in the present analysis we were only interested in relative changes in k_p and we assigned k_{sat} to give a maximum whole-plant conductance of $1 \text{ mmol} \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$. The arbitrary assignment for k_{sat} does not affect the model predictions of P_x , but causes the corresponding predictions of E to be valid in relative, rather than absolute, units. We also expressed E on a plant, rather than leaf area basis, to avoid complications of changing leaf area per plant during the season. The whole-plant k_{sat} was divided equally between root and shoot components as is typical of many woody plants (Sperry et al., 1998). The root component was divided equally into minor vs. major roots, and the shoot component into minor vs. major stems, with each being given the same $k_p(P_x)$ function. A sensitivity analysis indicated that $\pm 20\%$ variation in k_{sat} assignments had little influence on predictions. The model was most sensitive to the $k_p(P_x)$ function.

The hydraulic conductance of the rhizosphere (k_r), as a function of soil water potential (Ψ_s , assuming a negligible osmotic component), was calculated as

$$k_r = Xk_{sat} (\Psi_d/\Psi_s)^{(2+3/b)} \quad (3)$$

where k_{sat} is the saturated hydraulic conductivity of the soil, Ψ_e is the soil air entry potential, b is the exponent of the moisture release equation, and X is a "conductance factor," which converts soil conductivity to rhizosphere conductance based on the cylindrical geometry of water uptake by a root (Sperry et al., 1998). Equation 3 was discretized to represent concentric rhizosphere

layers as explained in Sperry et al. (1998). The soil parameters k_{sat} , Ψ_e , and b were estimated from the percentage of sand, silt, and clay particles measured at the site according to Campbell (1985). Six soil samples were taken at 15–20 cm depth from the study site and analyzed by the hydrometer method (Soil Analytical Laboratory, Logan, Utah, USA). Soil texture and derived parameters are given in Table 1. *Ceanothus crassifolius* is a relatively shallow-rooted shrub, so we represented the bulk soil water potential of the rooting zone by a single value equal to the predawn leaf xylem pressure.

The root-to-leaf area ratio (A_R/A_L) is required to convert rhizosphere and plant conductances to a leaf area basis. We did not attempt to measure this difficult parameter, but instead set it to 10 because values at or above this proved to have a negligible influence on P_{Lcrit} . Lower values gave less negative P_{Lcrit} estimates, so our setting of A_R/A_L was chosen to give minimum (most negative) possible P_{Lcrit} for this parameter. An A_R/A_L of 10 is within the range measured for trees in coarse soils (Hacke et al., 2000) and estimated for a desert shrub (Kolb and Sperry, 1999).

For any given bulk soil Ψ_s and transpiration rate E , the model calculated the corresponding leaf xylem pressure for steady-state conditions. By incrementing E until there was no longer any significant hydraulic conductance in the continuum, the critical values of E and P_L were estimated. We used an E increment equal to 1% of the maximum predicted E under wet soil conditions. The k in Eqs. 2 and 3 closely approach but never reach zero for any finite P_x , and in actuality there should always be some limited hydraulic conductance associated with molecular films of water on soil particles and within cell wall nanopores, regardless of how negative P_x or Ψ_s may become. For this reason, the predictions of E_{crit} and P_{Lcrit} are not points of complete hydraulic failure, but rather conservative estimates of the limits to transport capacity necessary to sustain any biologically meaningful gas exchange (Sperry et al., 1998).

Statistical tests—Statistical comparisons between paired treatments were made by unpaired Student's t tests at $P < 0.05$.

RESULTS

On 6 December 1995 (day 341; Fig. 2A), the plants at the original study site were at the peak of drought stress, prior to the first winter rains (Fig. 2B). For green, healthy-appearing branchlets, the mean water potential was -8.4 MPa (Fig. 2A). However, when adjacent branchlets with discolored leaves were sampled from the same branch of the same 12 individuals, all 12 had water potentials below the limits that the pressure chamber could measure (-14.0 MPa), suggesting that by the time the leaves were discolored, the stems were completely air blocked. Midday leaf xylem pressure (P_L) varied between -1.3 MPa in winter of 1996 and -8.6 MPa in the fall of 1997. A mean P_L of -11.2 MPa was measured in a population 200 m from the main study site on 8 November 1997 after 273 d without significant ($< 0.3 \text{ mm}$) rainfall (square symbol in Fig. 2A). Midday P_L is not reported for the fall of 1996 due to a wildfire that swept the area in October 1996. Midday P_L returned to predrought values with the onset of winter rains. During the peak of the drought, dieback of terminal branches was observed in a patchy distribution within a given crown

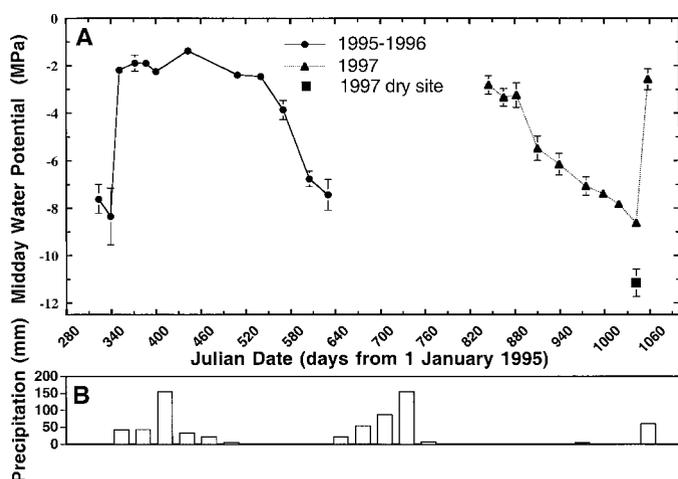


Fig. 2. (A) Seasonal changes in midday leaf xylem pressure (P_L) for *Ceanothus crassifolius* growing in a mixed chaparral stand at the Malibu Forestry Unit of Los Angeles County in the Santa Monica Mountains of California from late fall 1995 to late fall 1997. Due to a wildfire at our site in October 1996, which burned the 12 individuals tagged in 1995, 12 new plants, within 100 m of the original 12, were monitored for 1997. Also shown for the fall of 1997 is the mean P_L for $N = 22$ individuals from an adjacent, dry site where dieback was particularly extensive (square symbol). (B) Monthly accumulative precipitation measured at the Malibu Beach-Dunne Station, Number 1025, by the Flood Control District of Los Angeles County.

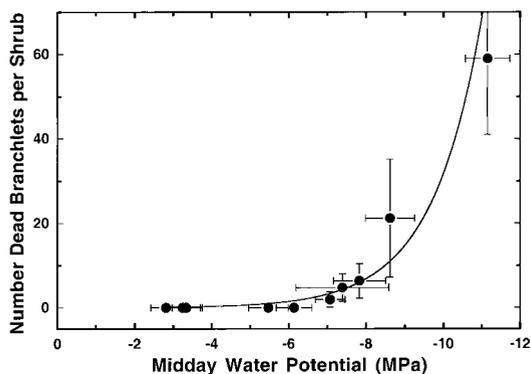


Fig. 3. Relationship between midday leaf xylem pressure (P_L) and the number of dead branchlets per shrub for *Ceanothus crassifolius* during the summer/fall drought of 1997 (9 mo without significant rainfall; see Fig. 2B). Individuals were growing in a mixed chaparral stand at the Malibu Forestry Unit of Los Angeles County in the Santa Monica Mountains of California. The datum for the lowest mean water potential of -11.2 MPa ($N = 22$) was taken from an adjacent stand 200 m away from the original 12 individuals.

(Fig. 1E). The number of dead, terminal branchlets increased abruptly as midday P_L fell below -8 MPa during the fall of 1997 (Fig. 3). Although there was some variation in the incidence of dieback between plants (Fig. 1A), no plant showed complete dieback.

For the green, healthy-appearing branchlets collected in late June, before the severe drought conditions, 49.6% of the branchlets had endophytic fungi. Of the isolated fungi, 71% were *Botryosphaeria dothidea*, 14% were an undetermined species of *Botryosphaeria*, and the remaining 14% were a *Sclerophoma* species and other miscellaneous fungi.

Ceanothus crassifolius inoculated with three species of indigenous fungi (Fig. 1C) in January 1996 did not decline in P_L , experience branchlet dieback, or show a decline in variable fluorescence (F_v/F_m) over a 30-d period (Fig. 4A, B); the opposite was the case for branches detached from the plant to show the effect of dehydration on these parameters. Furthermore, inoculated branches did not increase in their Munsell Color Index over a 204-d period, unlike detached branches (Fig. 4C). Branches that remained on the plant, but whose hydraulic conductance was diminished by the xylem-notching treatment, showed a decrease in P_L to a minimum mean value of -14 MPa and increased in Munsell Color Index to a maximum mean value of 5 over a 15-d period (Figs. 1F, 5).

Vulnerability curves of roots and shoots showed no significant increase in percentage of embolism until P_x reached -8 MPa and below (Fig. 6). For values below -8 MPa, roots were not significantly more vulnerable to embolism than shoots. At water potentials below -11 MPa, loss in hydraulic conductivity exceeded 90%. Thus, the increased frequency of branch dieback at $P_x < -8$ MPa (Fig. 3) paralleled the increase in xylem embolism.

The soil at the site was a sandy loam (Table 1), averaging 65% sand. However, the site was on a slope, and soil texture at 15–20 cm depth varied with position. The downslope soil "A" was significantly coarser (77% sand) than soil "B" taken just below the ridgeline (54% sand). Although both soils A and B fell into the sandy loam classification, their hydraulic properties as estimated from texture data were different (Table 1).

The soil texture data and vulnerability curves were used in

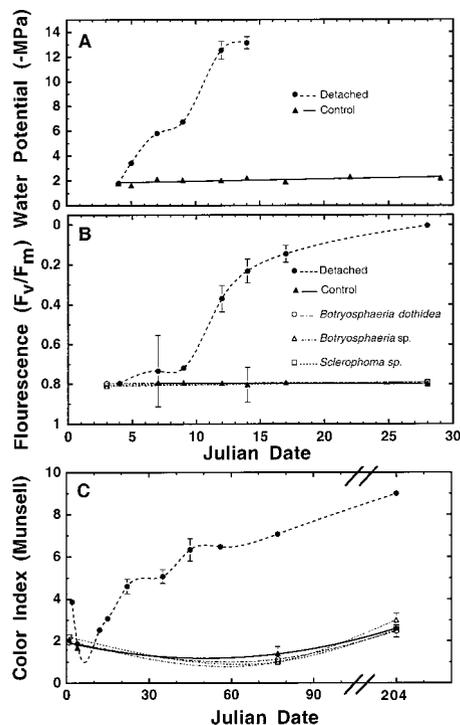


Fig. 4. Changes in (A) leaf xylem pressure (P_L), (B) variable fluorescence (F_v/F_m), and (C) Munsell Color Index in *Ceanothus crassifolius* for detached branches, control branches, and branches inoculated with three indigenous species of fungi. Mean ± 1 SE, $N = 15$. Shrubs were growing in a mixed chaparral stand at the Malibu Forestry Unit of Los Angeles County in the Santa Monica Mountains of California.

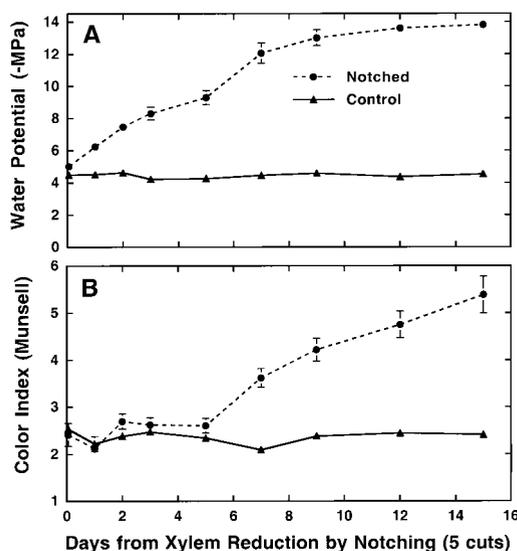


Fig. 5. Changes in leaf xylem pressure (P_L) and Munsell Color Index in *Ceanothus crassifolius* for branches cut about halfway through five times (notched) and uncut branches (control) on 16 individuals. Shrubs were growing in a mixed chaparral stand at the Malibu Forestry Unit of Los Angeles County in the Santa Monica Mountains of California.

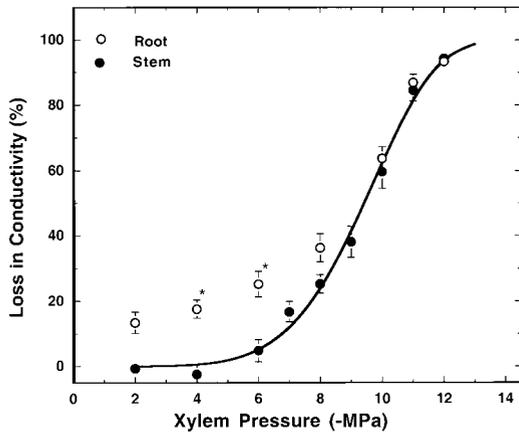


Fig. 6. Vulnerability-to-embolism curve for root and stem segments of *Ceanothus crassifolius* using the centrifuge method (Alder et al., 1997). Open circles represent roots ($N = 16$), and closed circles represent stems ($N = 12$). Bars on symbols represent ± 1 SE. An asterisk indicates significant difference by an unpaired Student's t test at $P < 0.05$.

the transport model to predict P_{Lcrit} over a range of bulk Ψ_s for the *C. crassifolius* population. Using mean soil texture and mean vulnerability curves, the corresponding average P_{Lcrit} was near -12 MPa, varying only slightly with bulk soil Ψ_s (Fig. 7A). The corresponding values of mean E_{crit} vs. Ψ_s show E_{crit} declining to near zero as Ψ_s approaches P_{Lcrit} (Fig. 7B). Recall that the modeled E values were arbitrary (because of the arbitrary choice of k_{sat} in Eqs. 2) and expressed on a per plant basis. Plotting them shows the relative decline in allowable plant water use as Ψ_s declines.

To estimate the maximum possible range in P_{Lcrit} around the mean we ran the model using extremes of soil and vulnerability data. The coarse soil (A) in combination with the most vulnerable stem and root xylem gave the most hydraulically limiting combination and the least negative P_{Lcrit} . These maximum P_{Lcrit} values were near -10 MPa, again showing little trend with bulk Ψ_s (Fig. 7A). The corresponding minimum E_{crit} shows a decline to near zero as Ψ_s declines to -10 MPa and beyond (Fig. 7B, dotted curve). Conversely, minimum P_{Lcrit} based on the finer soil (B) and the most resistant vulnerability curves was near -13 MPa (Fig. 7A).

Safety margins from hydraulic failure were evaluated by comparing actual midday P_L with P_{Lcrit} as predawn P_L (a proxy for Ψ_s) became more negative during drought (Fig. 7A). As can be seen from the convergence of midday P_L to within the P_{Lcrit} range, safety margins were predicted to reach zero for worst-case scenarios where the most vulnerable xylem is combined with the coarsest soils. This indicates that hydraulic failure was a distinct possibility within the population and was likely a contributing cause of the observed dieback.

As the drought progressed, midday and predawn P_L converged to a 1 : 1 correspondence (Fig. 7A: dashed line vs. solid line) showing the progressive reduction in midday ΔP_x from bulk soil to leaf to zero as E per plant was reduced to zero. The predicted reduction in E with soil drought is plotted along with E_{crit} in Fig. 7B (E_{pred}), which allows safety margins to be viewed in terms of E rather than P_x as in Fig. 7A. There is no new information contained in such a plot, because the E_{pred} values were deduced from the P_L data. However, a more realistic view of the safety margin from hydraulic failure is obtained. It can be seen that safety margins from E_{crit} are dimin-

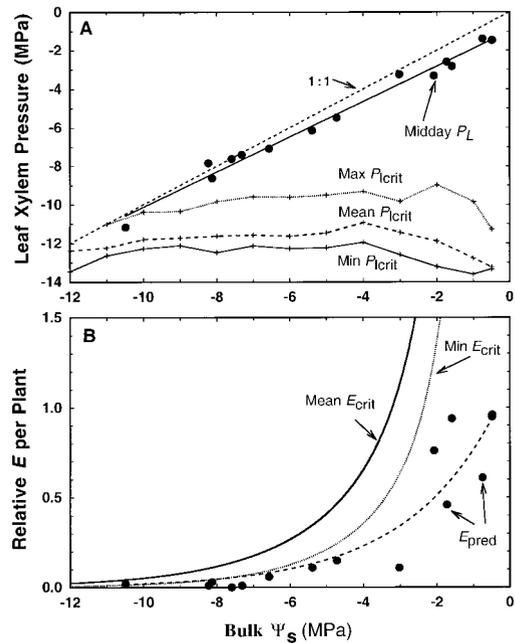


Fig. 7. (A) Leaf xylem pressure (P_L) vs. soil water potential (Ψ_s) for *Ceanothus crassifolius*. Solid circles are measured mean midday P_L where Ψ_s was assumed equal to mean predawn P_L . The solid line is a linear regression through these points, and the dotted line is the 1 : 1 relationship. Crosses are model predictions of P_{Lcrit} as a function of Ψ_s . The mean P_{Lcrit} line is for mean values of soil texture and xylem vulnerability, the maximum P_{Lcrit} line is for the coarse soil "A" (Table 1) in combination with the most vulnerable stem and root xylem in the population, and the minimum P_{Lcrit} line is for the fine soil "B" (Table 1) with the most resistant xylem in the population. (B) Relative transpiration rate (E) per plant vs. soil water potential (Ψ_s). The E_{crit} is the modeled steady-state E associated with P_{Lcrit} , with the mean and minimum E_{crit} lines corresponding to mean and maximum P_{Lcrit} values, respectively. The circles represent the predicted E (E_{pred}) from the model based on predawn and midday P_L measurements through three seasons.

ished more rapidly with drought than safety margins from P_{Lcrit} . For example, plants at -8 MPa have what appears to be a comfortable 2-MPa safety margin from a P_{Lcrit} of -10 MPa (Fig. 7A). However, at the same time their E_{pred} is very close to E_{crit} (Fig. 7B). The difference in safety margins occurs because when P_x in the continuum is approaching negative values near the tail ends of the soil drying or xylem vulnerability curve, a small increment in E translates into a disproportionately large drop in P_x . Thus, as hydraulic failure is approached, P_x would be expected to drop rather abruptly prior to dieback. This may be the explanation for the relative scarcity of data below -8 MPa for green shoots: plants or branches in this range are close to hydraulic failure and could be in a rapid transition to dieback.

The model predicted which component of the soil-root-shoot system, i.e., rhizosphere, minor and major roots, or major and minor branches, was most hydraulically limiting at the critical point where $P_x = P_{Lcrit}$ and $E = E_{crit}$ (Fig. 8). When soil was either very wet ($\Psi_s > -2$) or very dry ($\Psi_s < -10$), the greatest resistance was in the minor branch component as a result of xylem cavitation. However, at intermediate Ψ_s , the greatest resistance was within the rhizosphere as a result of soil drying around the root during transpirational uptake (Fig. 8). This basic pattern was obtained regardless of whether mean or extreme values of soil texture and xylem vulnerability were used in the model, or if A_R/A_L was doubled from 10 to 20. It

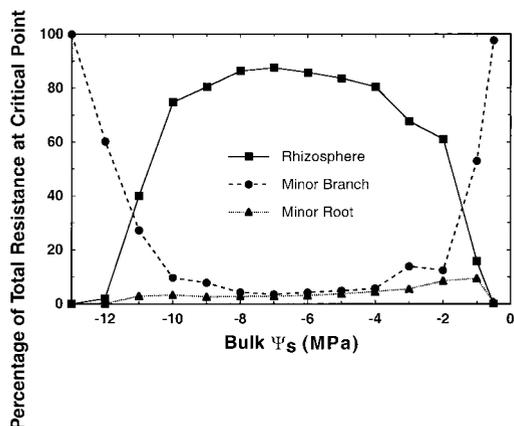


Fig. 8. Model predictions of the percentage of total soil-to-canopy hydraulic resistance residing in minor branch, minor root, and rhizosphere components of the flow path when *Ceanothus crassifolius* is at P_{crit} and E_{crit} . Percentages are shown as a function of bulk soil water potential (Ψ_s). The model results correspond to maximum P_{Lcrit} conditions under which hydraulic failure was predicted for the *Ceanothus crassifolius* population.

was also not sensitive to $\pm 20\%$ changes in how the maximum soil-canopy conductance was partitioned between the four plant components. In the relevant Ψ_s range below -8 MPa, where hydraulic failure was likely to have occurred for our population (Fig. 7), the limiting component was transitional between rhizosphere and minor branch xylem. Predicted percentage of embolism in branches at P_{Lcrit} under these circumstances was $>95\%$.

DISCUSSION

The results suggest that the observed dieback in *Ceanothus crassifolius* (Fig. 1) was not caused by a fungal pathogen, but was consistent with insufficient water transport to foliage caused by extremely negative xylem pressures and soil water potentials associated with prolonged drought. The model predicted that a combination of soil drying and extensive xylem cavitation was responsible for insufficient hydraulic connection between soil and leaves to sustain transpiration. The pattern of dieback supports this explanation, increasing for $P_L < -8$ MPa (Fig. 3) in accordance with the onset of xylem cavitation (Fig. 6) and shrinking safety margins from P_{Lcrit} and E_{crit} (Fig. 7). Simulated reductions in hydraulic conductance to foliage caused by xylem notching or severing caused similar dieback symptoms in foliage to those caused by the natural drought (Figs. 4, 5).

Apparently endophytic fungi were widely present, occurring in at least half of the healthy stems. However, upon death of the branchlets, they proliferated and were present in 100% of dead branchlets. By Occam's razor, drought-induced embolism of branchlets is sufficient to explain all the dieback symptoms. Therefore, contrary to interpretations by Brooks and Ferrin (1991) and Riggan et al. (1994), perhaps the endophytic fungi should be viewed in this case as well-positioned saprophytes rather than latent parasites.

During the peak of drought, the green, healthy-appearing branchlets had water potentials of about -8.4 MPa, whereas adjacent branchlets on the same branch, but with discolored leaves, always had measured water potentials below the limits of our pressure chamber (less than -14.0 MPa). This is consistent with air blockage as the cause of branchlet dieback.

Once branchlets are 100% embolized, it would be difficult to force water out of the severed end of branchlets with a pressure chamber.

The patchy nature of the dieback within single plants (Fig. 1A, E) suggests that the reduction in hydraulic conductance by water stress was not equal to all branchlets. This would result from intraplant variation in the parameters that determine the point of hydraulic failure. These parameters include the predrought soil-to-leaf hydraulic conductance, the vulnerability of individual leaves, branchlets, and rootlets to cavitation, the depth of the roots that preferentially supply different zones of the crown, and the soil properties in their rooting zones. While we only assessed interplant variation in this study and thus analyzed hydraulic limitations implicitly on a whole-plant basis, the range of intraplant variation is likely to be similar if previous work on other species is representative (Zimmermann, 1978; Tyree and Sperry, 1988; Sperry and Saliendra, 1994; Cochard et al., 1997). As recognized and demonstrated previously (Zimmermann, 1983; Tyree and Sperry, 1988), patchy dieback within the crown under water-stressed conditions would act to improve the hydraulic conductance and water status to remaining foliage, acting as a last-ditch mechanism to avoid whole-plant mortality (Rood et al., 2000).

The patchy nature of the dieback also implies that the point of greatest hydraulic restriction was not in the major transport arteries—otherwise the whole crown would be equally affected. Consistent with this observation, the model indicated that the greatest restrictions were in the peripheral parts of the flow path—in the rhizosphere component and in the minor branches (Fig. 8). Importantly, even if failure was initiated belowground in the rhizosphere, it would also trigger failure in the distal branches downstream. In addition to promoting a patchy dieback pattern, localizing hydraulic restrictions to peripheral units also facilitates recovery from the drought. In the case of the rhizosphere restriction, rewetting of soil would be the only requirement for restoring conductivity. Dead branchlets could be replaced by axillary buds on the surviving stems.

If whole branches were to die back to ground level, which was not observed for any individual in our population, replacement would be improbable. This is because *C. crassifolius* is a nonsprouter after wildfire and does not produce a root crown (lignotuber) with adventitious buds and carbon stores to facilitate whole-branch regrowth (James, 1984; Davis et al., 1999). This is in contrast to chaparral species that are sprouters after wildfire. Such species are known to undergo whole-branch replacement after dieback by wildfire (DeSouza, Silka, and Davis, 1986; Thomas and Davis, 1989; Stoddard and Davis, 1990), dieback by freezing (Langan, Ewers, and Davis, 1997), and breakage by wind (Wagner, Ewers, and Davis, 1998).

It should be noted that the branchlet death in the outer canopy of our shrubs was not due to natural pruning as reported in the literature (Mahall and Wilson, 1986; Keeley, 1975, 1992, 1999). Natural pruning is associated with low light levels in combination with water stress. In our study, peripheral branchlet dieback was associated with drought, not shade. Furthermore, we did not observe whole-plant mortality during our investigation, only dieback of outer canopy branchlets.

Our results are consistent with the findings of Schlesinger and his colleagues for the closely related non-sprouting species, *Ceanothus megacarpus* (Schlesinger and Gill, 1978, 1980; Schlesinger et al., 1982). They found whole-plant mortality to be restricted to a thinning stage between years 5 and 15 with little mortality thereafter. The primary cause of plant

death was attributed to water stress. The lowest seasonal water potential that they observed was -12 MPa, in 6-yr-old pure stands of *C. megacarpus*. Mortality approximated 50% of the individuals by year 15 and did not significantly increase in stands up to at least 54 yr old. Our stands of *C. crassifolius* were 25 yr old at the initiation of our study. Therefore, whole-plant death due to thinning would not be expected.

Specht (1969) estimated the percentage of dead to live biomass in stands of *C. crassifolius* to be 58% at 9 yr, 64% at 18 yr, and 70% at 37 yr. If one included natural pruning of lower branches in deep shade (Mahall and Wilson, 1986) and water-stress-induced dieback of small peripheral branchlets observed in this study, the 12% increase in dead biomass between years 9 and 37 would be expected. Likewise, Hanes (1971) found the number of live to dead shrubs of *C. crassifolius* in a 40-yr stand to be a little over 50%. Taken together, it appears that the percentage of dead to live biomass in mature *Ceanothus* stands frequently achieves 50%, with whole-plant mortality restricted to a thinning stage. However, the age of thinning probably depends on extreme drought events, which may occur later in stand development as recorded by Horton and Kraebel (1955). They found nearly 50% mortality of *C. crassifolius* shrubs between the 20th and 25th yr as a result of severe drought.

It is possible that the branchlet dieback we observed in this study represents a mechanism to reduce overall transpiration rate, conserving water and reducing the incidence of whole-plant mortality. This process would be adaptive considering the relatively shallow rooting depth of *C. crassifolius* and the inability of these species to sprout from a root crown after major branch death. This is in contrast to sprouting species of chaparral that have been shown to continue major branch replacement throughout their life span (Keeley, 1992).

Our results differ from previous analyses of hydraulic limitations in some other species that have predicted the major hydraulic restriction developing in the minor roots as a result of extensive root cavitation (Alder, Sperry, and Pockman [1996] for *Acer grandidentatum*; Kolb and Sperry [1999] for *Artemisia tridentata*; Hacke et al. [2000] for *Pinus taeda*; Mencuccini and Comstock [1997] for *Hymenoclea salsola* and *Ambrosia dumosa*). There were three reasons why cavitation in *C. crassifolius* roots was not a limiting factor in our study, whereas rhizosphere drying was important (Fig. 8). First, the vulnerability of roots to cavitation was not significantly different from shoots (Fig. 6) in *C. crassifolius*, whereas in the other study species, roots were considerably more vulnerable than shoots. Equal vulnerability of roots and shoots ensures that hydraulic restrictions will develop either in the rhizosphere or peripheral branches. Second, the overall resistance of *C. crassifolius* xylem to cavitation was much greater than previous study species. In fact, the vulnerability curves in Fig. 6 are among the most resistant known, together with curves for *Juniperus monosperma*, *Larrea tridentata*, and *Ambrosia dumosa* of the Sonoran and Mojave deserts (Mencuccini and Comstock, 1997; Pockman and Sperry, 2000). The more resistant the xylem is to cavitation, the more likely hydraulic failure will occur in the rhizosphere rather than in the xylem unless the greater cavitation resistance is accompanied by an A_R/A_L large enough to avoid a rhizosphere restriction (Hacke et al., 2000). Third, significant rhizosphere restriction is unavoidable when cavitation-resistant xylem is combined with a relatively coarse soil as was the case for our *C. crassifolius* population. In this circumstance, significant hydraulic resis-

tance will be predicted in the rhizosphere regardless of how high the A_R/A_L (Sperry et al., 1998).

Aside from the obvious advantage of protecting the major transport arteries, the adaptive significance of localizing the peripheral hydraulic restrictions specifically to rhizosphere vs. minor roots vs. minor branch components is unknown. A better understanding would require analysis of the costs of cavitation resistance and investment in roots vs. the benefits of enhanced water extraction in a given life-history, environmental, and competitive context. It may be that plants where roots are significantly more vulnerable than shoots are also plants with relatively deep root systems such that failure in vulnerable (= cheap) shallow roots acts to shift water use to progressively deeper layers. *Ceanothus crassifolius* is relatively shallowly rooted, and it may require very cavitation-resistant roots to more effectively mine the shallow soil water. It is known that within the chaparral community, deeper rooted plants are correspondingly more vulnerable to shoot cavitation at particular xylem pressures (Jarbeau, Ewers, and Davis, 1995; Davis, Kolb, and Barton, 1998; Davis et al., 1999), and there is some recent evidence that deep-rooted species have much lower cavitation resistance of roots than stems (Crocker, 1999; McElwain, 2001).

The natural dieback we observed in *C. crassifolius* is one of the few examples of mortality in a natural setting that can be linked to hydraulic limitations on plant gas exchange. While a variety of studies have demonstrated how an observed reduction of gas exchange during drought protects plants from hydraulic failure (e.g., Cochard, Breda, and Granier, 1996; Lu et al., 1996; Hacke et al., 2000), it is rare to observe extreme natural drought events where plants have been forced to their limits. This is presumably more common at the vulnerable seedling stage, where previous studies in the chaparral have shown a correlation between increasing embolism and seedling mortality (Williams, Davis, and Portwood, 1997). Thomas and Davis (1989) reported a minimum water potential less than -10 MPa (the limit of their pressure chamber) for seedlings of *Ceanothus megacarpus*, about 4 km from our study site, and Schlesinger et al. (1982) recorded water potentials as low as -12.0 MPa for seedlings of *C. megacarpus* in the Santa Ynez Mountains near Santa Barbara, California. The lowering of water tables in riparian areas as a result of altered stream flows has been linked to cavitation and branch dieback in adult cottonwood (*Populus deltoides*, *P. fremontii*) trees (Tyree et al., 1994; Rood et al., 2000). It seems likely that future work will provide more examples of hydraulic limits "in action" as they are more widely recognized as a potential cause of mortality (cf. Sparks and Black, 1999).

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