

Kristofer R. Wagner · Frank W. Ewers · Stephen D. Davis

Tradeoffs between hydraulic efficiency and mechanical strength in the stems of four co-occurring species of chaparral shrubs

Abstract Possible tradeoffs between efficiency of water transport and mechanical strength were examined in stems of two congeneric pairs of co-occurring chaparral shrubs. First, since previously published results indicated that *Adenostoma sparsifolium* (Rosaceae) had greater specific conductivity (k_s or hydraulic conductivity per xylem transverse area) than *A. fasciculatum*, it was hypothesized that *A. sparsifolium* would have greater vessel lumen area per square millimeter of xylem area, and less mechanical strength, than *A. fasciculatum*. Secondly, since *Ceanothus megacarpus* (Rhamnaceae) is a non-sprouter (unable to sprout from the root crown following fire or other major disturbance) whereas *C. spinosus* is a sprouter and thus able to form new stems following disturbance, it was hypothesized that *C. megacarpus* would have greater mechanical strength, but lower k_s , than *C. spinosus*. Both hypotheses were supported. Based upon computer-aided image analyses, *A. sparsifolium* had significantly higher mean and maximum vessel diameters (16.4, 40.5 vs. 14.6, 35.7 μm), a 34% greater percent vessel lumen area, and a two-fold greater measured and theoretical k_s than *A. fasciculatum*. This corresponded to 14% lower stem density (wet weight/volume) and less mechanical strength, with a 37% lower modulus of elasticity (MOE) and a 30% lower modulus of rupture (MOR) than *A. fasciculatum*. Similarly, *C. spinosus* had a significantly higher maximum vessel diameter (52.7 vs. 41.8 μm) and a 92% higher theoretical k_s (and 43% higher measured k_s) than *C. megacarpus*. This corresponded to a 9% lower stem density and 20% lower MOR than for *C. megacarpus*. Thus, at least within these two congeneric pairs of chaparral shrubs growing together in the same habitat, there may be

tradeoffs between mechanical strength and conductive efficiency of the stem xylem which correspond to differences in transport physiology and life history traits of sprouter versus non-sprouter species.

Key words Mechanical strength · Modulus of elasticity · Modulus of rupture · Specific conductivity · Vessel diameter

Introduction

Although the wood (secondary xylem) of plants is widely known to have dual functions of mechanical support and water transport, there has been little study of the possible tradeoffs between these functions. In the xylem of angiosperms, the vessels are specialized conduits composed of cells that are stacked end-to-end, with wide lumens for efficient water transport and thin secondary walls. Vessels are non-living at functional maturity, with water transport occurring through the otherwise empty cell lumens. Fibers, with narrow lumens and thick secondary walls, are the cells that are specialized for mechanical support in angiosperm xylem (Esau 1977).

Vessel lumen diameter and vessel frequency per cross-sectional area of xylem are heritable traits that are extremely variable from species to species. However, the field of ecological wood anatomy has, to date, centered on the relationship of xylem anatomy to drought tolerance and water transport efficiency (Carlquist 1975; Zimmermann 1983; Baas 1986; Tyree et al. 1994). Effects of vessel number and diameter on mechanical properties of the xylem has received little consideration from an ecological/evolutionary perspective. Is wood that is highly efficient in water transport likely to have low density (weight per volume), relatively few fibers and little mechanical strength?

Possible tradeoffs between mechanical strength and water transport efficiency are complex due, in part, to exponential relationships between geometry and physical

K.R. Wagner · S.D. Davis (✉)
Natural Science Division, Pepperdine University,
Malibu, CA 90263, USA
e-mail: davis@pepperdine.edu, Fax: +1-310-4564785

F.W. Ewers
Department of Botany and Plant Pathology, Michigan State
University, East Lansing, MI 48824, USA

properties. For instance, assuming homogeneous structural material, the stiffness of a cylinder (e.g., a stem) is proportional to the stem radius to the fourth power. Thus a small increase in stem diameter could dramatically alter its mechanical properties (Niklas 1992). Similarly, a small increase in vessel diameter can greatly alter xylem conductivity since the efficiency of transport of water through a capillary (e.g., a vessel) is proportional to the capillary diameter to the fourth power (Tyree et al. 1994).

By Poiseuille's law for ideal capillaries, hydraulic conductivity, or the hydraulic conductance per pressure gradient (k_h) will be proportional to the summation of the fourth power of the capillary diameters (Calkin et al. 1986). Thus, to determine the theoretical k_h of an angiosperm stem, one needs to account for the diameter of all of the stem vessels, not just the average vessel diameter. The wider vessels in a stem contribute a disproportionate amount to the k_h (Hargrave et al. 1994).

The specific conductivity (k_s) is equal to the k_h divided by the xylem transverse area (Tyree and Ewers 1991). Increasing vessel diameter should increase k_s but it might result in weaker wood if the vessel lumen area per transverse xylem area were also increased. With wider vessels there might be less room for fibers and, as a result, less lignified wall area per transverse area. If vessel frequency per square millimeter xylem transverse area were kept constant, increasing vessel diameter would increase theoretical (k_s) to the fourth power, while it would increase the vessel lumen area per square millimeter to the second power of vessel diameter. Thus doubling the vessel diameter would increase k_s by 16 times while increasing vessel lumen area by only 4 times.

Tyree et al. (1994) suggested that, considering the "cost" of carbon investment, there should be natural selection for stems that are just strong enough to provide static support, yet able to provide adequate water transport for the environmental conditions in which the plant is found. It seems intuitive that if all else were held constant, increased lumen area should increase k_s , but weaken the wood. However, when comparisons are made across genera, multiple changes in stem anatomy (differences in pith diameter, cortical width, differences in the width of vascular rays, thickness of fiber walls, or the presence/absence of tracheids), or chemical changes in the amount or type of lignin, would probably confound the influence of vessel size and frequency on mechanical strength. Furthermore, amongst different growth forms (e.g., trees versus climbing plants) and across different habitats, the selective pressures for "optimum" stem structure might vary considerably. Therefore, in this study, we make comparisons only between congeneric species, reducing possible phyletic bias, and only between shrub species growing side by side in the same habitat, reducing possible differences in the environmental factors affecting species evolution. All four species in this study commonly grow together in

mixed chaparral communities of the Santa Monica Mountains of southern California (Beatty 1987; Redtfeldt and Davis 1996).

Redtfeldt and Davis (1996) found that stems of *Adenostoma sparsifolium* had a two-fold greater k_s than stems of the co-occurring chaparral shrub, *A. fasciculatum*. This led to our first hypothesis, that stems of *A. sparsifolium* would have greater vessel lumen area per square millimeter xylem area, and less mechanical strength, than *A. fasciculatum*.

Secondly, the shrub *Ceanothus megacarpus* is a non-sprouter (unable to sprout from the root crown following fire or other major disturbance) whereas the co-occurring *C. spinosus* is a sprouter. Following wild-fire, severe wind-storms, or other major disturbance, sprouting members of the chaparral community are able to replace lost stems with new growth from the root crown. Since non-sprouters have no mechanism for stem replacement following loss, they might be exposed to greater selective pressure for mechanically resilient stems. Thus, our second hypothesis was that *C. megacarpus* would have greater mechanical strength, but lower k_s , than *C. spinosus*.

Materials and methods

Study sites

For determination of hydraulic conductivity of *A. sparsifolium* (Rosaceae) and *A. fasciculatum*, branches were collected at a site (site 1) in the Santa Monica Mountains of southern California, just below Murphy Ranch (now called the Cold Creek Canyon Preserve), immediately west of Stunt Road, at an elevation of 375 m (34°05'30"N, 118°38'30"W).

For determination of hydraulic conductivity of *C. megacarpus* (Rhamnaceae) and *C. spinosus*, branches were collected at a site (site 2) in the Santa Monica Mountains, located in Puerco Canyon, 1.5 km north of Highway 1, at an elevation of 370 m (34°02'30"N, 118°43'30"W).

For measurement of mechanical strength of *A. sparsifolium*, *A. fasciculatum*, *C. megacarpus*, and *C. spinosus*, branches were collected at a site (site 3) in the Santa Monica Mountains, 0.5 km south of Encinal Canyon Road, at an elevation of 480 m (34°05'00" N, 118°50'30" W). This site was chosen as representative of a mature, mixed stand of chaparral with all four species co-occurring at an elevation and coastal exposure similar to that used in previous studies. This site was also used to examine naturally occurring stem breakage, as described below. Site 3 was used since site 1 had burned in November 1993, thus, mature plants were unavailable there. In addition, all four species do not co-occur at site 2.

Hydraulic conductivity

For determination of hydraulic conductivity, in June 1991, branches were collected from 20 individuals of *A. sparsifolium* and *A. fasciculatum* at site 1 (Redtfeldt and Davis 1996). Branches were recut under water to produce stem segments 10 cm in length and from 3.5–8.5 mm in diameter. In June 1992, similar branches were collected from 20 individuals of *C. megacarpus* and *C. spinosus* at site 2. Maximum k_h was measured following removal of embolisms via high pressure perfusions as described by Sperry et al. (1988). Subsamples of the stems used for hydraulic conductivity measurements ($n = 6$) were used to calculate theoretical conductivity as described below.

Xylem anatomy and theoretical k_s

To determine how to distinguish narrow vessels from fibers or tracheids, wood macerations were prepared from some of the stems used for conductivity measurements. As described elsewhere in detail (Hargrave et al. 1994), the bark was removed from three stem segments per species, the wood was shaved down to the pith and placed in separate vials with Jeffrey's solution for 4 days, sonicated for 30 min, rinsed in water, stained in safranin, suspended in 50% ethanol, and placed on glass slides for observation with a compound microscope. For each species, lumen diameters of 100 each of vessel elements, tracheids, and fibers were measured at the longitudinal midpoint of each element. This allowed for determination of the extent of overlap, if any, between diameters of the different cell types, which might be confused in transverse sectional view.

Transverse stem sections were then used for comparisons between species, using computer-aided image analysis, which allowed for large sample sizes (about 1000 vessels per stem). For each species, six of the stem segments that had previously been used for hydraulic conductivity determination were placed in boiling water for 5–10 s to rehydrate the tissue. Several 10- to 30- μm transverse sections were made of each stem with a sliding microtome. We stained the sections in a 0.1% solution of crystal violet for 1 min, rinsed the sections in distilled water to remove any residual stain, and mounted eight sections from each individual on a single microscope slide in a 70% glycerol/30% water solution and examined them at 200 \times magnification (Nikon microscope, Model MicrophotFX and Javelin Chromachip II camera, Model JE3462RGB). Images were imported into a computer (Apple Macintosh IICI) and captured using image analysis software (Image v1.55, National Institutes of Health). Lumens smaller than the largest known fiber/tracheid lumen diameter for that species (determined from wood macerations, above) were excluded. All measurements were recorded and imported into a statistics software package (StatView 4.0, Abacus Concepts, Inc., Berkeley, Calif., USA) for further manipulation and analysis. For each vessel, the major and minor axes were averaged to obtain the vessel diameter. In addition, for calculation of theoretical k_s , for each vessel the lumen area was measured and used to calculate the diameter of a circle with equivalent area. Those diameters were then used to calculate theoretical k_h as described in Calkin et al. (1986).

While the stems were more or less circular in outline, our microscopic subsamples, captured by image analysis, consisted of four belt transects, each made up of a series of rectangular fields of view starting at the outermost edge of the xylem. In order to correctly weight each field of view according to the transectional area each occupied in the stem (inner views represented less area than outer views), numbers for each field of view were multiplied by the fractional area of the xylem that each subsample represented. After applying this weighted correction factor, for each stem the mean and maximum vessel diameters were estimated, as were vessel frequency per square millimeter, percent xylem vessel lumen area, and theoretical k_s .

Mechanical strength

In June 1995, at site 3, branches were collected and placed in plastic bags, from 20 individuals of *A. sparsifolium*, *A. fasciculatum*, *C. megacarpus*, and *C. spinosus*. Immediately prior to cantilever mechanical strength tests, the water potential of the shoot was measured with a pressure chamber (Scholander et al. 1965). For each branch, a 20 cm long unbranched stem segment was cut that was within the range of diameters (3.5–8.5 mm) used in determination of hydraulic conductance and vessel diameter. The stem was oriented horizontally and perpendicular to the edge of a table, with the basal half of the stem taped and clamped to the table while the distal half projected over the edge (Fig. 1). The clamp was made of wood and entirely covered the basal 10 cm of the stem. The clamp allowed up to 9 mm space for the stem (stems were 3.5–8.5 mm in diameter) and was held in place with a weight of 25 kg. The edge of the table was rounded (3 mm radius) such that it did not dig into

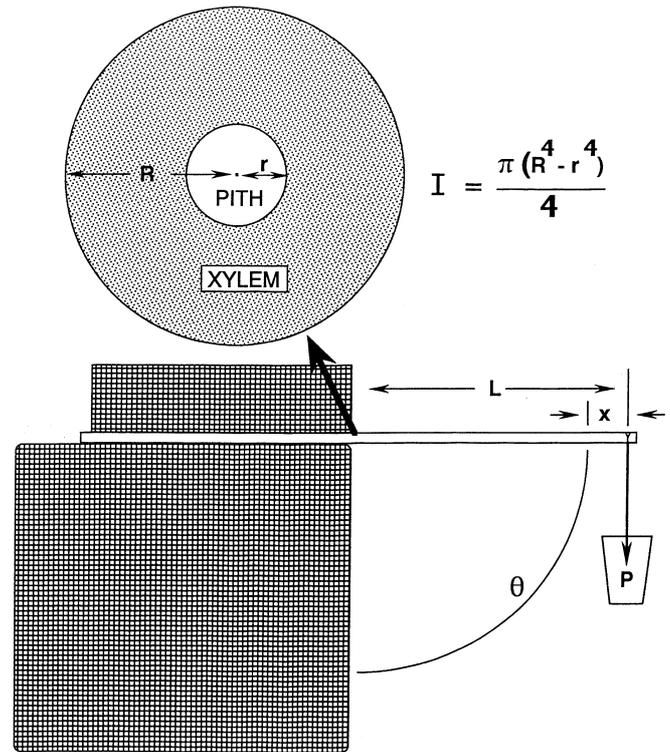


Fig. 1 The apparatus and some of the measurement parameters for cantilever strength tests of woody stems. The deflection angle (θ) was measured with a protractor and the point load (P) was steadily increased throughout the test. The length of the cantilever arm (L) and the distance from the point load to the measurement position (x) were 0.1 and 0.018 m. The stem geometry, used for calculation of the second moment of xylem area (I), is shown at the base of the cantilever arm, where breakage occurred

the stem as the stem was bent (Fig. 1). To continuously add weight to the end of the stem, a small notch was made 1 cm from the distal end of the stem segment, which allowed attachment of a container (point load or P in Fig. 1) into which water was added at a constant flow rate of $3 \times 10^{-3} \text{ m}^3 \text{ min}^{-1}$. The distance from the notch to the edge of the bench (L in Fig. 1) was 10 cm. As water was added to the container, the change in angle of deflection of the stem (θ in Fig. 1) was recorded over time on a protractor with a video camera (Panasonic Omnimovie VHS camera, Model PV-940). The protractor measurements were 1.8 cm inwards (x in Fig. 1) from the point of attachment of the load. The point load (P), measured in $\text{kg} \times 9.8 \text{ m s}^{-2}$ (to derive Newtons), was continuously increased until stem failure, which was signaled by the rapid collapse of the stem and usually a sharp cracking noise. After breakage, the clamped as well as free portions of the stem were examined by eye. No evidence of deformation nor crushing of the clamped stem portion was observed. In each case the stem broke at the base of the cantilever, which was the plane at which the second moment of xylem area (I in Fig. 1) was measured.

Flexural stiffness (MOE-I) was calculated based upon an equation derived from Niklas (1992) for cantilevered beams with a point load at the free end:

$$\text{MOE} \cdot I = P \cdot (2L^3 - 3L^2x + x^3) / 6d_x$$

with d_x equal to the deflection (in meters) at the distance x from the point load. Considering that the deflection distance equals the product of $\sin \theta$ and $(L - x)$, and inserting values of 0.1 m and 0.018 m for L and x , respectively, the equation simplifies in our case to:

$$\text{MOE} \cdot I = 0.005P / \sin \theta$$

As noted by Niklas (1992), the above equation is accurate only when used for small deflections, less than 10% of the length of the cantilever, which would correspond to θ values of less than 5.8° . Since in our case the initial deflection from attaching the bucket to the cantilever (θ in Fig. 2) resulted in mean and median deflections of 3.51 and 2.25° , respectively, and since subsequent readings often corresponded with deflections greater than 5.8° , only the initial reading, made about 5 s after placing the initial point load on the cantilever, was used for the flexural stiffness calculation on each stem.

The modulus of elasticity (MOE), was calculated from the flexural stiffness divided by the second moment of xylem area for each stem (I). To calculate I , transverse sections were taken at the base of the cantilever, and the pith radius (r) and xylem radius (R) were measured with an ocular micrometer on a compound microscope in each of the four cardinal directions, to derive an average r and R value for the stem. The value of I was then calculated as $\pi(R^4 - r^4)/4$ (Niklas 1992).

The modulus of rupture (MOR) was determined from the formula (Ugural 1991):

$$\text{MOR} = (P \cdot L \cdot R) / I$$

with P equal to the load at stem failure (f in Fig. 2).

Torque (T) refers to the force that is perpendicular to the stem axis. Torque at stem failure was calculated as $T = (P \cdot \cos \phi L)$.

Stem taper and density

Stem taper was measured (mm m^{-1}) for each stem used in the breakage experiments. This was calculated as the diameter (mm, electronic caliper measurements) at the stem "tip" (adjacent the notch where weight was attached in breakage experiments) minus the diameter at the stem "base" (adjacent the plane of stem breakage), divided by the distance between the base and tip (m).

Stem density was measured (kg dry weight/volume) based both upon the water saturated volume of the stems (stems were held in degassed citric acid solution until maximum wet weight was achieved) and upon the dry volume of the stems (70°C oven till constant weight). Volume was measured by displacement of water in a narrow graduated cylinder. For a parameter of "stem cost", stem dry weight per length was also calculated.

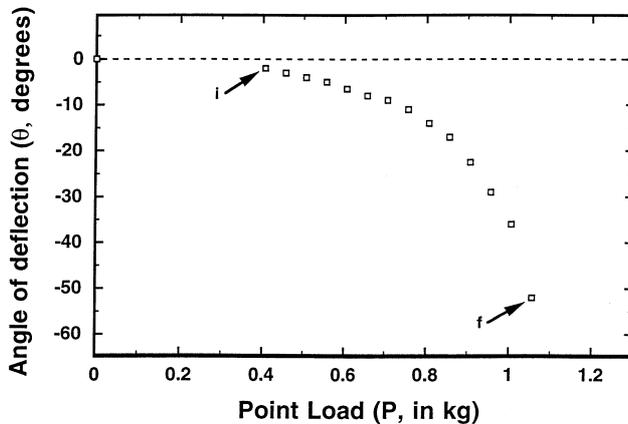


Fig. 2 Representative plot of the measured angle of deflection (θ , as in Fig. 1) as a function of the applied point load (P). The initial deflection angle/point load, i , measured to the nearest 0.25° , was used to calculate flexural stiffness and the modulus of elasticity (MOE). Exactly 5 s elapsed between each point on the graph. The final deflection angle/point load, f , measured immediately prior to stem failure, was used to calculate the modulus of rupture (MOR)

Natural breakage

Natural stem breakage was recorded at site 3 on 23 June 1998. Ten individuals per species were sampled, all of which could be accessed from all sides, to assess stem breakage on the entire individual. Previous observations on marked stems of chaparral shrubs indicated that after 3 months, leaves on broken stems were often abscised and were always nearly black in color (Portwood et al. 1997). Such stems were ignored in this study since broken stems with abscised or blackened leaves often fall from the plant, making the counts of such stem breakage unreliable. Thus, in this study, only recent stem breaks (slight or no leaf discoloration) were recorded, and only for stems of the size range used in the mechanical strength experiments (3.5–8.5 mm diameter).

Statistical analysis

In all cases, statistical comparisons between species in a genus were performed using an unpaired, two-tailed Student's t -test at $P < 0.05$.

Results

Measured and theoretical k_s

A. sparsifolium had a measured k_s that was 2.7 times greater than in *A. fasciculatum* (Table 1). In the subsample that was used for anatomical measurements ($n = 6$ individuals), the measured k_s was 1.9 times greater ($P < 0.01$), and a theoretical k_s , based upon anatomical measurements, was 1.8 times greater ($P < 0.005$) than in *A. fasciculatum* (Table 1). The ratio of measured to theoretical k_s was quite similar in the two species, with the measured k_s equal to 62% (in *A. sparsifolium*) and 58% (in *A. fasciculatum*) of the theoretical k_s .

C. spinosus had a measured k_s that was 1.4 times greater than in *C. megacarpus* (Table 1). In the subsample that was used for anatomical measurements, the measured k_s was 1.2 times greater ($P > 0.1$) and the theoretical k_s that was 1.9 times greater ($P < 0.03$) than in *C. megacarpus*. The ratio of measured to theoretical k_s was quite different in the two species, with the measured k_s equal to 58% (in *C. spinosus*) and 92% (in *C. megacarpus*) of the theoretical k_s (Table 1).

Vessel diameter, frequency per square millimeter, lumen area

Representative stem transverse sections are shown in Fig. 3. Comparing *A. sparsifolium* to *A. fasciculatum*, on average the former species had maximum vessel diameters that were 13% larger ($P < 0.02$), mean vessel diameters 12% larger ($P < 0.002$), and lumen areas per square millimeter that were 34% greater ($P < 0.04$) than for *A. fasciculatum* (Table 2). *Adenostoma sparsifolium* also had an 8% greater mean value for vessel frequency per square millimeter than for *A. fasciculatum*. However, the differences between these two species in vessel frequency were not statistically significant ($P > 0.05$).

Table 1 Mean values (\pm SE) for specific conductivity (k_s or hydraulic conductivity per xylem area) in $10^{-3} \text{ m}^2 \text{ MPa}^{-1} \text{ s}^{-1}$ for four species of chaparral shrubs growing adjacent to each other in the Santa Monica Mountains of southern California. Measured k_s was determined after all air emboli were removed. A subsample of in-

dividuals ($n = 6$) was used for the vessel measurements in Table 2 and to calculate the theoretical k_s values below. An asterisk indicates a significant difference between congeneric species at $P < 0.05$ (Student's t -test)

	n	<i>Adenostoma</i>		<i>Ceanothus</i>	
		<i>A. fasciculatum</i>	<i>A. sparsifolium</i>	<i>C. megacarpus</i>	<i>C. spinosus</i>
Measured k_s	20	0.69 \pm 0.09	1.84 \pm 0.15*	1.06 \pm 0.10	1.52 \pm 0.13*
Measured k_s (subsample)	6	0.64 \pm 0.06	1.23 \pm 0.13*	1.46 \pm 0.09	1.77 \pm 0.46
Theoretical k_s	6	1.11 \pm 0.19	1.96 \pm 0.14*	1.58 \pm 0.13	3.04 \pm 0.53*

Fig. 3 Micrographs of xylem transverse-sections of **A** *Adenostoma fasciculatum*, **B** *A. sparsifolium*, **C** *Ceanothus megacarpus* and **D** *C. spinosus*, stained with 0.1% crystal violet. Such sections were used for image analysis of vessel number, vessel diameter, and theoretical specific conductivity (k_s). The scale bar in **C** indicates the magnification for all four micrographs

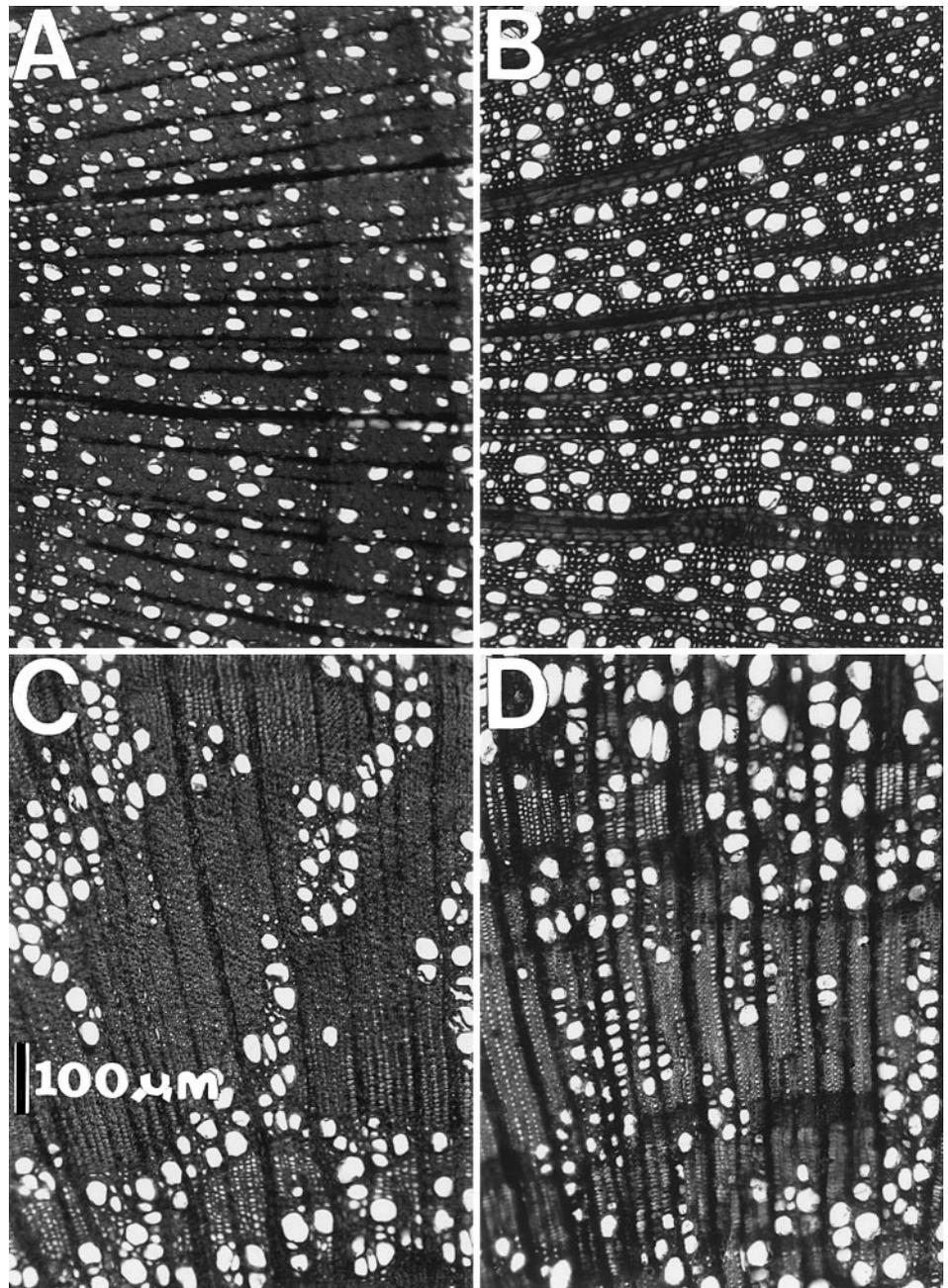


Table 2 Mean values (\pm SE) for stem vessel anatomy, stem physical properties, and natural stem breakage for four species of chaparral shrubs growing adjacent to each other in the Santa Monica Mountains of southern California. Anatomical values were determined from transverse sections of stem segments using bright field microscopy and computer-aided image analysis. Stem

	<i>Adenostoma</i>		<i>Ceanothus</i>	
	<i>A. fasciculatum</i>	<i>A. sparsifolium</i>	<i>C. megacarpus</i>	<i>C. spinosus</i>
Maximum vessel diameter (μm)	35.7 \pm 1.2	40.5 \pm 1.1*	41.8 \pm 0.6	52.7 \pm 2.3*
Mean vessel diameter (μm)	14.6 \pm 0.2	16.4 \pm 0.4*	23.3 \pm 0.1	25.1 \pm 1.1
Vessel frequency per square millimeter	505 \pm 52	545 \pm 27	141 \pm 11	158 \pm 12
Percent vessel lumen area	10.2 \pm 1.2	13.7 \pm 0.7*	6.47 \pm 0.49	8.79 \pm 0.90*
Stem taper (mm m^{-1})	1.47 \pm 0.73	0.56 \pm 1.55	4.05 \pm 1.08	2.79 \pm 0.87
Dry weight/stem length (g m^{-1})	27.0 \pm 1.36	26.2 \pm 1.79	27.6 \pm 1.58	24.8 \pm 1.16
volume (kg m^{-3})	847 \pm 9	722 \pm 14*	841 \pm 9	806 \pm 9*
Stem density, wet volume (kg m^{-3})	708 \pm 5	608 \pm 8*	664 \pm 5	601 \pm 7*
Natural breakage (stems per plant)	0.20 \pm 0.13	1.00 \pm 0.33*	0.40 \pm 0.31	0.50 \pm 0.22

Comparing *C. spinosus* to *C. megacarpus*, on average the former species had a maximum vessel diameter that was 26% greater ($P < 0.01$), a mean vessel diameter that was 8% greater, vessel frequency per square millimeter that was 12% greater and lumen areas per square millimeter that were 36% greater ($P < 0.05$). However, the differences between these two species in mean vessel diameter ($P > 0.1$) and in vessel frequency ($P > 0.1$) were not statistically significant (Table 2).

Mechanical strength

Water potentials of stems used in mechanical strength experiments ranged from -1 to -6 MPa. However, for each of the four species, regardless of the strength parameter, there was no correlation between water potential and mechanical strength (data not shown).

The mean flexural stiffness (MOE·I) was 7.7% lower in *A. sparsifolium* than in *A. fasciculatum* ($0.516 \pm \text{SE } 0.100$ vs. $0.559 \pm 0.061 \text{ N m}^2$) and 8.4% lower in *C. spinosus* than in *C. megacarpus* ($0.553 \pm \text{SE } 0.089$ vs. $0.604 \pm 0.077 \text{ N m}^2$). However, mean values were not significantly different because a range of stem diameters were used (3.5–8.5 mm) such that variation within a species in flexural stiffness was greater than differences between species. However, when the size and geometry of the stems were accounted for, by dividing the mechanical properties of a stem by the second moment of area, significant differences were evident (Figs. 4, 5).

Comparing *A. sparsifolium* to *A. fasciculatum*, on average the former species had significantly less mechanical strength in its xylem. The MOE was 37% lower in *A. sparsifolium* than in *A. fasciculatum* (Fig. 5). When divided by the second moment of xylem area, mean torque at stem failure was also significantly less in *A. sparsifolium* than in *A. fasciculatum* ($P < 0.0001$). Furthermore, as stems increased in the second moment of area of the xylem, differences between these species were accentuated (Fig. 4). The MOR, which incorpo-

rates the second moment of area, was 30% lower in *A. sparsifolium* than in *A. fasciculatum* (Fig. 5). Comparing *C. spinosus* to *C. megacarpus*, on average the former species had significantly less mechanical strength in its xylem. When divided by the second moment of xylem area, mean torque at stem failure was significantly lower in *C. spinosus* than in *C. megacarpus* ($P < 0.01$) and, as stems increased in moment of area, differences between species were accentuated (Fig. 4).

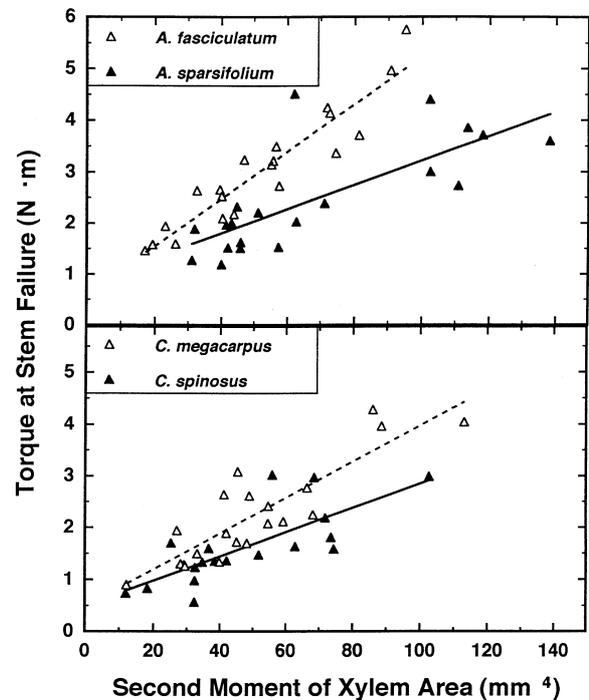


Fig. 4 Torque applied at stem failure as a function of the second moment of xylem area for congeneric, co-occurring species of *Adenostoma* and *Ceanothus* growing in the Santa Monica Mountains of southern California. Solid and dashed lines indicate linear regression; for *A. f.* $y = 0.46x + 0.64$, $r^2 = 0.88$; for *A. s.* $y = 0.24x + 0.86$, $r^2 = 0.57$; for *C. m.* $y = 0.35x + 0.50$, $r^2 = 0.75$; for *C. s.* $y = 0.24x + 0.50$, $r^2 = 0.57$

rates the second moment of area, was 30% lower in *A. sparsifolium* than in *A. fasciculatum* (Fig. 5).

Comparing *C. spinosus* to *C. megacarpus*, on average the former species had significantly less mechanical strength in its xylem. When divided by the second moment of xylem area, mean torque at stem failure was significantly lower in *C. spinosus* than in *C. megacarpus* ($P < 0.01$) and, as stems increased in moment of area, differences between species were accentuated (Fig. 4).

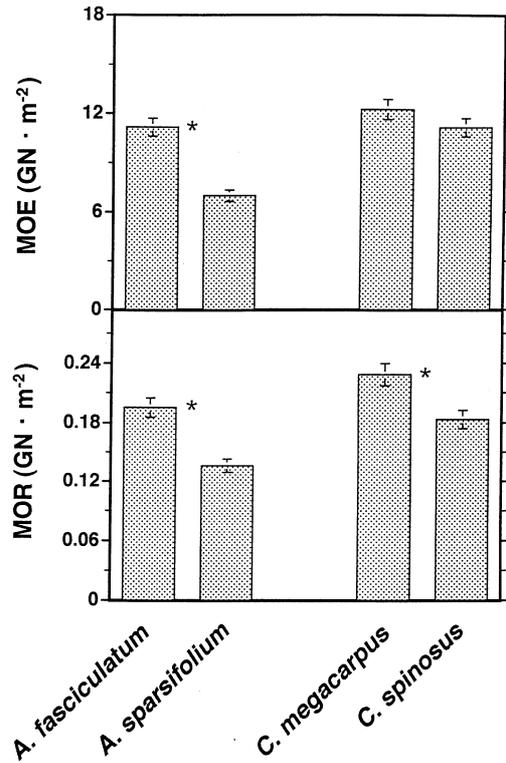


Fig. 5 Mean \pm 1 SE modulus of elasticity (MOE) and modulus of rupture (MOR) for stems of congeneric, co-occurring species of *Adenostoma* and *Ceanothus*, $n = 20$. An asterisk indicates significant difference between congeneric species by a Student's t -test ($P < 0.05$)

The mean MOR was 20% lower in *C. spinosus* than in *C. megacarpus* ($P < 0.01$). The mean value for MOE was 9% lower in *C. spinosus* than in *C. megacarpus*, but was not significantly different ($P > 0.1$; Fig. 5).

There was a large difference between genera in the deflection angle, θ , at stem failure. Mean \pm SE values, in degrees, for *A. fasciculatum* and *A. sparsifolium* were 29 ± 2 and 30 ± 2 , respectively. In contrast, the θ values for *C. megacarpus* and *C. spinosus* were 52 ± 4 and 55 ± 3 . The values were not significantly different between species within a genus.

Stem taper and density

Stem taper, as well as dry weight per stem length, were not significantly different between *A. sparsifolium* versus *A. fasciculatum*, nor between *C. spinosus* versus *C. megacarpus* (Table 2). Dry weight per stem length was used as a cost estimate parameter for each species. Mean torque at stem failure, divided by dry weight per stem length, was 20.1% higher in *A. fasciculatum* than in *A. sparsifolium* ($P < 0.01$), and 23.3% higher in *C. megacarpus* than in *C. spinosus* ($P < 0.01$), as indicated by Fig. 6.

Based upon dry weight per dry stem volume, or upon dry weight per saturated (wet) volume, mean stem densities were significantly lower in *A. sparsifolium* than in

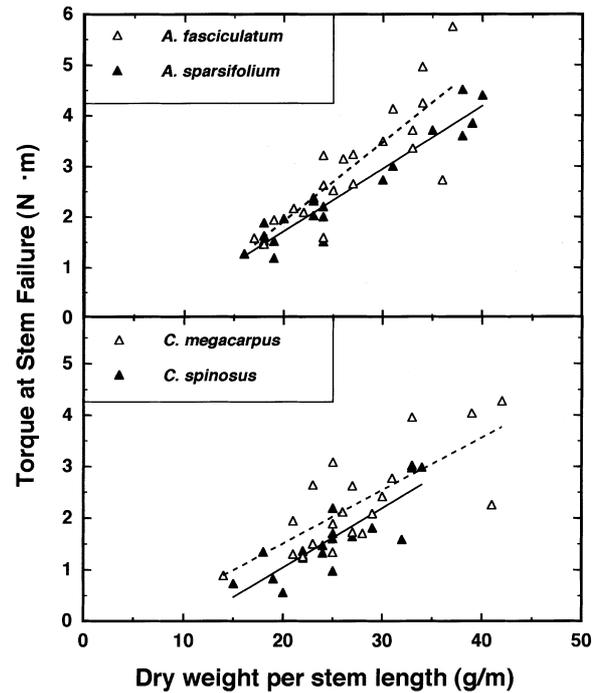


Fig. 6 Torque applied at stem failure as a function of dry weight per stem length for congeneric, co-occurring species of *Adenostoma* and *Ceanothus* growing in the Santa Monica Mountains of southern California. Mean \pm SE values of torque at stem failure divided by dry weight per stem length were, for *A. f.* 0.110 ± 0.005 ; for *A. s.* 0.0915 ± 0.0033 ; for *C. m.* 0.0816 ± 0.0049 ; for *C. s.* 0.0626 ± 0.0041 . The mean differences were statistically significant between species within each congeneric pair ($P < 0.01$)

A. fasciculatum (Table 2). Similarly, stem densities were significantly lower in *C. spinosus* than in *C. megacarpus* (Table 2).

Discussion

The range of values for the MOE for the four shrubby species in the present study, with species means from 7.0 to 12 GN m⁻² for MOE, are within the range of values reported for angiosperm trees and shrubs (Gartner 1991; Niklas 1992). In contrast, the values we reported for the MOR, from 0.13 to 0.23 GN m⁻², overlap with, but range somewhat higher than, values reported for angiosperm trees (Niklas 1992). In this study we used intact stem segments, with pith and cortex, for the mechanical strength studies. However, our calculated MOE and MOR values were based only upon the xylem (not the entire stem) second moment of area. We reasoned that the hardened, lignified tissue (the xylem) was of overriding importance to the mechanical strength of the stems, with the non-lignified areas (the phloem and pith) of little direct importance in this regard. This assumption becomes more accurate as the stems increase in girth, because as stems enlarge the cross-sectional area of the xylem tends to dwarf that of the other tissues. When the MOR values were computed based upon the

entire stem areas, the MOR values were 20–35% lower than shown here, but with the same, statistically significant trends.

Within each of the congeneric pairs of species in this study, the species with greater theoretical xylem conductivity tended to have weaker and less dense stems. This might be expected since those factors known to increase k_s , namely, increased number of vessels per transverse area and increased diameters of vessels, would both tend to result in less dense and, presumably, weaker wood. Recall that k_s is linearly proportional to vessel frequency but proportional to the fourth power of vessel diameter. Therefore a slight increase in vessel diameter could result in a dramatic increase in k_s while perhaps only slightly weakening the wood. In contrast, increasing vessel frequency in wood might result in a linear increase in k_s but perhaps also a linear decrease in wood strength. In both examples in the present study, enhanced k_s within a congeneric pair was clearly associated with increased vessel diameter and with increased vessel lumen area, but increases in vessel frequency were not statistically significant.

From an ecological perspective, a possible tradeoff between strength and conductive efficiency might consider not just strength relative to volume, but also strength relative to biomass utilized. It is important to note that, even when controlled for dry weight per stem length, which was our cost parameter, the species in each pair with the greater theoretical xylem conductivity still had significantly weaker stems. This suggests the size and number of vessels within the stem can have strength and conductivity tradeoffs independent of the biomass allocated to a stem. Presumably, the wider vessels in the stem represent the “weak links” in the mechanical system, that could override the importance of total biomass in determining strength. Such weak links could even override the importance of variation in fiber anatomy/lignification, but such assertions would require future study.

In the case of *Adenostoma*, the 34% greater lumen area in *A. sparsifolium* versus *A. fasciculatum* can be accounted for by considering that the mean and maximum vessel diameters were about 12% greater and vessel frequency was 8% greater in *A. sparsifolium*. Given the second power relationship between lumen diameter and area, the increased vessel diameter would result in a 25% ($1.12^2 = 1.25$) increase in lumen area, which, when factoring in vessel frequency, would by itself result in a predicted 35% increase in lumen area ($1.25 \times 1.08 = 1.35$) almost identical to the 34% measured increase. A similar analysis can be applied to explain the 36% greater lumen area in *C. spinosus* versus *C. megacarpus*, with the complication that mean vessel diameters were only 8% larger (would result in a 17% increase in lumen area), whereas maximum vessel diameter was 26% larger (59% increase in lumen area); larger vessels tending to skew results. Thus, vessel diameter appears to be more important than vessel frequency for explaining the greater lumen areas in the species with weaker, less dense stems.

Vessel diameter is also the factor that is most responsible for the 77% greater theoretical k_s in *A. sparsifolium* versus *A. fasciculatum*. In *A. sparsifolium* the mean and maximum vessel diameters were 12 and 13% greater, which would correspond to a 57% ($1.12^4 = 1.57$) and 63% ($1.13^4 = 1.63$) greater theoretical k_s . Factoring in the 8% higher vessel frequency would then account for a 70% ($1.57 \times 1.08 = 1.70$) to 76% ($1.76 \times 1.08 = 1.91$) increase in theoretical k_s , close to the actual 77% greater theoretical k_s in *A. sparsifolium*. A similar analysis could explain the 92% greater theoretical k_s in *C. spinosus* versus *C. megacarpus*, but as with the analysis of lumen area, the analysis of theoretical k_s is made complex by the fact that mean vessel diameter was 8% larger in *C. spinosus* (would result in a 36% greater theoretical k_s), whereas maximum vessel diameter was 26% larger (would result in a 152% greater theoretical k_s).

Measured k_s , determined by measuring flow rates at known applied pressure gradients, was 58–92% of the theoretical k_s calculated from image analysis of vessels in the stems. This is very similar to the range of results reported for woody dicotyledonous plants in the literature (Ewers and Cruiziat 1991; Tyree and Ewers 1991). The theoretical k_s tends to be higher than measured k_s because theoretical k_s considers only theoretical vessel lumen resistance, not the total resistance to axial flow in the system. Some of the factors which may add to the total resistance, and thus decrease measured k_s relative to theoretical values, are vessel perforation plates, pit membranes between adjacent vessels, vessel taper, and the hydrophilicity of cellulose.

The cantilever strength test that we used would be ecologically relevant to the situation where fruit production near the tips of branches, such as occurs in each of the four species in the present study, results in a “point load” at the free end of the beam (i.e., the distal end of the shoot). The response to the load varied with the size of the stem within a species, with differences between species accentuated in larger stems. The fact that the stems always broke at the base suggests that our measurements of the second moment of stem area were done at the correct spot, and that the damping of our stems in the apparatus was effective. Breaks never occurred in the clamped portion. The natural breakage data should be considered preliminary since the data were collected in June following new growth. We would expect many more stem breaks per stem following the seasonally strong Santa Ana winds, which normally occur in the autumn in the Santa Monica Mountains. At such times stems also often have a heavy fruit load at their tips. Future studies will consider the combined impact of wind and fruit load on stem breakage.

Between species, differences in the MOE, which incorporates the second moment of xylem area and thus corrects for the size and geometry of the stem, reflect differences in the stiffness of the stem xylem. A higher MOE value indicates that, for a particular second moment of area, a greater load is required to achieve a

particular deflection angle. The MOR values reflect the total strength of the xylem; higher MOR values indicate that, for a particular second moment of area, a greater load is required to achieve stem breakage.

Within *Ceanothus*, there was considerably more deflection before final breakage than for *Adenostoma*. The deflection angle affects the distribution of the load. As an example, it may be more difficult to hold a weight in one's hand when one's arm is horizontal ($\theta = 0^\circ$) than when it is vertical ($\theta = 90^\circ$). The much greater tolerance of deflection without breakage that occurred in *Ceanothus* could reflect tissue distributions. In *Adenostoma* the vessels appeared to be rather evenly distributed amongst the fibers in transverse view, whereas, in *Ceanothus*, the vessels tended to be clumped, resulting perhaps in a cable-like fiber system that could tolerate more bending without stem failure.

Moisture content is known to affect mechanical properties of wood (Nildas 1992). Unlike many cases, especially those in the field of wood technology, in the present study the stems were kept at a moisture content well within the range of water potentials that these species experience in nature (Redtfeldt and Davis 1996; Davis et al. 1998). Within the range of water potentials used, water potential was not correlated with mechanical strength.

Could natural selection favor stronger wood, with less conductive efficiency, in *C. megacarpus* than in the co-occurring *C. spinosus*? Considering that *C. megacarpus* is a nonsprouter, breakage of the stem would more likely result in plant death than in the sprouter, *C. spinosus*, which very readily resprouts from the root crown following shoot die-back. Furthermore, *C. spinosus* is more deeply rooted, and is less tolerant of low water potentials than *C. megacarpus* (Thomas and Davis 1989; Saruwatari and Davis 1989). *C. spinosus* may thus be more dependent on efficient water transport, and less dependent on stem longevity, than *C. megacarpus*.

Could natural selection favor weaker wood, with more efficient water conduction, in *A. sparsifolium* than in the co-occurring *A. fasciculatum*? *Adenostoma sparsifolium* is a taller, more deeply rooted plant than *A. fasciculatum*, it has higher rates of water use, and it is less tolerant of low water potentials (Hanes 1965; Beatty 1987; Redtfeldt and Davis 1996). These factors might select for enhanced conductive efficiency, perhaps at the expense of weaker wood.

The possible tradeoffs between xylem conductive efficiency and safety from stem mechanical failure has been little studied in the past. One extreme situation that has been examined involves climbing plants. Lianas (woody vines) are dependent on external objects or host plants for mechanical support, thus they are said to be "mechanical parasites" (Gartner 1991a; Ewers and Fisher 1991). Presumably because they have considerably reduced mechanical demands on their stems, they have evolved narrow stems that are highly efficient in water transport, with extremely wide vessels and high

vessel frequency. Liana stems are typically capable of being variously twisted without damage to the transport system, but they are usually incapable of self-support (Gartner 1991b; Putz and Holbrook 1991). In this study, possible tradeoffs between transport efficiency and mechanical strength were explored in some co-occurring chaparral shrubs. There could be many other examples of tradeoffs between conductivity and mechanical strength in terrestrial plants that have, to date, gone unnoticed.

Acknowledgements We would like to thank Mike Feltner, Terence Kite, Jerel Davis, Ben Ewers III, Frank Telewski, Tammy North, Brian Godines, Graham Boorse, Raymond Sauvajot and the National Park Service for their assistance in this study. This project was funded by a grant from the National Science Foundation (BSR-9225034) and a grant from the University Research Council of Pepperdine University.

References

- Baas P (1986) Ecological patterns in xylem anatomy. In: Givnish TJ (ed) On the economy of plant form and function. Cambridge University Press, Cambridge, pp 327–352
- Beatty SW (1987) Spatial distributions of *Adenostoma* species in southern California chaparral: An analysis of niche separation. *Ann Assoc Am Geogr* 77:255–264
- Calkin HW, Gibson AC, Nobel PS (1986) Biophysical model of xylem conductance in tracheids of the fern *Pteris vittata*. *J Exp Bot* 37:1054–1064
- Carlquist S (1975) Ecological strategies of xylem evolution. University of California Press, Berkeley
- Davis SD, Kolb KJ, Barton KP (1998) Ecophysiological processes and demographic patterns in the structuring of California chaparral. In: Rundel PW, Montenegro G, Jasic F (eds) Landscape disturbance and biodiversity in Mediterranean-type ecosystems. Springer, Berlin Heidelberg New York, (in press)
- Esau K (1977) Anatomy of seed plants, 2nd edn. Wiley, New York
- Ewers FW, Cruiziat P (1991) Measuring water transport and storage. In: Lassoje JP, Hinckley TM (eds) Techniques and approaches in forest tree ecophysiology. CRC, Boca Raton, pp 91–115
- Ewers FW, Fisher JB (1991) Why vines have narrow stems: Histological trends in *Bauhinia*. *Oecologia* 88:233–237
- Gartner BL (1991a) Structural stability and architecture of vines vs. shrubs of poison oak, *Toxicodendron diversilobum*. *Ecology* 72:2005–2015
- Gartner BL (1991b) Stem hydraulic properties of vines vs. shrubs of western poison oak, *Toxicodendron diversilobum*. *Oecologia* 87:180–189
- Hanes TL (1965) Ecological studies on two closely related chaparral shrubs in southern California. *Ecol Monogr* 35:213–235
- Hargrave KR, Kolb KJ, Ewers FW, Davis SD (1994) Conduit diameter and drought-induced embolism in *Salvia mellifera* Greene (Labiatae). *New Phytol* 126:695–705
- Niklas KJ (1992) Plant biomechanics: an engineering approach to plant form and function. The University of Chicago Press, Chicago
- Portwood KS, Ewers FW, Davis SD, Sperry JS, Adams GC (1997) Shoot dieback in *Ceanothus* chaparral during prolonged drought – a possible case of catastrophic xylem cavitation. *Bull Ecol Soc Am* 78:298
- Putz FE, Holbrook NM (1991) Biomechanical studies of vines. In: Putz FE, Mooney HA (eds) The biology of vines. Cambridge University Press, Cambridge, pp 73–97

- Redtfeldt RA, Davis SD (1996) Physiological evidence of niche segregation between two co-occurring species of *Adenostoma* in California chaparral. *Ecoscience* 3:290–296
- Saruwatari MW, Davis SD (1989) Tissue and water relations of three chaparral shrub species after wildfire. *Oecologia* 80:303–308
- Scholander PF, Hammel HT, Bradstreet ED, Hemmingsen EA (1965) Sap pressures in vascular plants. *Science* 148:339–346
- Sperry JS, Donnelly JR, Tyree MT (1988) A method for measuring hydraulic conductivity and embolism in xylem. *Plant Cell Environ* 11:35–40
- Thomas CM, Davis SD (1989) Recovery patterns of three chaparral shrub species after wildfire. *Oecologia* 80:309–320
- Tyree MT, Ewers FW (1991) The hydraulic architecture of trees and other woody plants. *New Phytol* 119:345–360
- Tyree MT, Davis SD, Cochard H (1994) Biophysical perspectives of xylem evolution: is there a tradeoff to hydraulic efficiency for vulnerability to dysfunction? *Int Assoc Wood Anat J* 15:335–360
- Ugural AC (1991) *Mechanics of materials*. McGraw-Hill, New York
- Zimmermann MH (1983) *Xylem structure and the ascent of sap*. Springer, Berlin Heidelberg New York