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Stem hydraulic properties of vines vs. shrubs of western poison oak, *Toxicodendron diversilobum**

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Summary. This study investigated the effect of mechanical support on water transport properties and wood anatomy of stems of western poison oak, *Toxicodendron diversilobum* (T. & G.) Greene. This plant grows as a vine when support is present but as a shrub when support is absent. I compared vines and shrubs growing naturally in the field and those produced from cuttings of 11 source plants in a common garden. Huber value (xylem transverse area/distal leaf area) was lower but specific conductivity (water volume · time^{-1} · xylem transverse area^{-1} · pressure gradient^{-1}) was higher in supported than unsupported plants both in the field and the common garden. The opposing effects of Huber value and specific conductivity resulted in the same values of leaf-specific conductivity (LSC, water volume · time^{-1} · distal leaf area^{-1} · pressure gradient^{-1}) for supported and unsupported shoots at a given site. Therefore, for the same rates of evapotranspiration, supported and unsupported shoots will have the same pressure gradients in their stems. Vessel lumen composed a higher proportion of stem cross-section in supported than unsupported plants (due to slightly wider vessels and not to greater vessel density). These results suggest that the narrow stems of supported plants are compensated hydraulically by the production of wider vessels: at a given site, poison oak plants co-ordinate their leaf and xylem development such that their stems achieve the same overall conductive efficiencies (LSCs), regardless of support conditions.

Key words: Growth form – Hydraulic architecture – Specific conductivity – Vessel diameter – Xylem

Plants with different growth forms will have different ecological interactions in a given environment because their sizes and shapes are not the same. Vines and shrubs, for example, will differ with respect to factors such as light interception, proximity to herbivores, and interactions with potential host plants. In this study I compared the hydraulic architectures of vines and shrubs to learn whether differences in growth form also dictate differences in a plant's physiological functions. Because the study plant, western poison oak, can grow as either a vine or a shrub depending upon the availability of physical support (Gartner in press a), I was able to compare hydraulic architectures of different growth forms of the same species. Hydraulic architecture is the spatial distribution of conductive capacities in the xylem. It is important to a plant's physiology because it influences the plant's distribution of water potentials (Tyree et al. 1983, Tyree 1988) which in turn can affect many features of canopy development (Farmer 1918; Huber 1928; Ewers and Zimmermann 1984a, b) and plant growth.

The pipe model (Leonardo da Vinci, translated by Richter 1970; Shinozaki et al. 1964) would predict that poison oak plants at a given site would have the same ratio of sapwood cross-sectional area to leaf area (called the Huber value) regardless of growth form. Refinements to the pipe model have already been necessary to account for systematic changes in conduit diameter throughout the plant as a function of age, height, and plant part (Fegel 1941; Carlquist 1975, 1984a; Larson and Isebrands 1978; Zimmermann 1978; Ewers and Zimmermann 1984a, b; Ewers and Fisher 1989). If vines and shrubs differ in Huber value, the pipe model will require further modification to reflect the degree to which the stems are self-supported mechanically.

In contrast, previous work with a variety of woody plants suggests that Huber value and other hydraulic parameters will differ between vines and shrubs. The xylem plays a smaller role in the mechanical support of a vine than a shrub (Roskam 1926, Gartner in press b), so one would expect lower Huber value and higher specific conductivity in a vine than a shrub. Vines and lianas

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(woody vines) have generally been shown to have lower Huber values and higher specific conductivities than self-supporting plants (summarized in Ewers 1985). Previous studies, however, compared different, often unrelated taxa growing in quite different habitats and ecosystems. The present study investigated the effects of mechanical support *per se* on hydraulic properties of xylem by comparing different growth forms that have been induced environmentally within the same species. I described Huber value, specific conductivity, and leaf-specific conductivity at the bases of stems and along their lengths. For selected points I also characterized the vessel diameters and vessel densities to determine the anatomical basis of the hydraulic properties.

Materials and methods

Plant material

Western poison oak (*Toxicodendron diversilobum* (T. & G.) Greene, Anacardiaceae, also called *Rhus diversiloba*) is a deciduous woody species that can grow as a vine or shrub (or a continuum of growth forms in between) and from full sun to deep shade in a wide variety of soil and moisture conditions (Jepson 1936). At the primary study site, Jasper Ridge, plants leaf out in February and lose their leaves in July-October (Gartner in press c), three to five months after the last rains. In this region vines can attain heights over 30 m if they encounter suitable hosts. Maximum basal stem diameters can exceed 15 cm, but more commonly range from 1-5 cm. Shrubs are tallest and stoutest in full sun where sheltered from the wind and may reach 4 m in height and 15-20 cm in diameter. Typical shrubs are 2-3 m in height and 2-10 cm in stem basal diameter.

The wood of poison oak is semi-ring-porous and the vessel elements have simple perforation plates. Carlquist and Hoekman (1985) reported mean vessel diameters and densities (vessels/mm^2) for western poison oak that are within the range of the other chaparral shrubs they surveyed. Within the genus *Toxicodendron*, the viney tendency appears to be derived from the ancestral self-supporting form (Gillis 1971).

Field plants

I undertook field work at Stanford University's Jasper Ridge Biological Reserve (37° 25′ N, 122° 15′ W, elevation about 100 m), which is an area with abundant poison oak in a variety of habitats, and at a common garden of poison oak plants 6 km away at the Carnegie Institution of Washington's Dept. of Plant Biology on the Stanford University campus. These sites experience a mediterranean climate with the majority of rain falling between November and April (mean annual total, 1974–1989, 579 mm).

In order to have viney and shrubby plants with comparable light environments I studied shoots in the field growing near a 2.4 m high chain link fence that had been installed in 1974. In each of the 11 pairs of shoots, one (the vine) was supported by the fence and one (the shrub) was unsupported nearby. I matched shoots within a pair for similarity of light environment (subjectively) and for proximity. Later the 11 pairs were classified into low, medium, or high light environments on the basis of their leaf-specific weights (Gartner 1991).

I measured Huber values, xylem area-specific conductivities, and leaf-specific conductivities of the same stem segments for each of the 22 fence shoots in mid-June to mid-July 1989. During this period plants were still fully leafed out but stem elongation and leaf expansion had ceased (Gartner in press c). Measurements were made throughout the lengths of the primary stems (those growing from the ground), for selected secondary stems (those growing from the primary stems), and for branch junctions between primary and secondary stems.

Huber value. Huber value, HV, is defined here as

$$HV = A_{xylem}/A_{leaf},$$

and is dimensionless, where A_{xylem} is xylem transverse area and A_{leaf} is the leaf area that had been growing distal to the segment. A_{xylem} was calculated as under-bark stem area minus pith area. Stem diameters were measured with vernier calipers. A_{leaf} was calculated as distal leaf number times mean area/leaf, where mean area/leaf was based on up to 50 randomly chosen leaves per shoot. Leaves did not appear to differ in size by position, and there was no difference in leaf-specific weight with position (Gartner in press b).

Specific conductivity. Xylem area-specific conductivity (specific conductivity), SC, is defined as

$$SC = K_h/A_{xylem},$$

with units of m^2 s^{-1} MPa^{-1} where K_h, hydraulic conductance (also called hydraulic conductance/length), is defined as

$$K_h = V \cdot t^{-1} \cdot (dP/dl)^{-1}.$$

V is water volume, t is time, and dP/dl is the pressure gradient across the length of the stem segment. K_h has units of m^4 s^{-1} MPa^{-1}.

Stem segments were cut from live plants under water and transferred to a liquid-filled tub where they were trimmed to 10 cm in length. The liquid in the tub was filtered (No. 2 Whatman filter paper) 10 mol/m^3 oxalic acid, which has been shown in comparison to distilled water to increase the time period during which consistent conductivity measurements can be performed (Sperry et al. 1988). The bark was removed, fresh cuts were made on both ends with a new razor blade, and cut ends were covered with connectors of latex tubing. To remove bubbles and debris, I flushed the connectors with clean fluid and then vacuum-infiltrated the biologically proximal end (which would be upstream for measurements) for at least five min.

The dilute oxalic acid was forced through the stem segment at a measured pressure varying from 11 to 60 kPa, and its rate was measured by timing the efflux on an electronic balance or the movement of the meniscus in a pipette attached to the downstream end of the sample. I determined five to seven data points/sample over a total period of 10 s to 10 min for most samples, but up to 60 min for very thin samples. Data series that were significantly non-linear were discarded. I used the same perfusing solution for up to 3 days, storing it in a refrigerator at night. Because water viscosity changes with temperature, I standardized measurements for each run to values expected for liquid with the density of water at 20° C

Leaf specific conductivity (LSC) and calculated water potential gradients. Expressing conductivity per distal leaf area rather than per xylem transverse area gives leaf-specific conductivity, LSC:

$$LSC = K_h/A_{leaf},$$

and has the same units as xylem area-specific conductivity, m^2 s^{-1} MPa^{-1}. Note also that

$$LSC = SC \cdot HV.$$

I calculated LSC for each sample on which I measured specific conductivity. Using the relationship

$$dP/dl = E/LSC + h,$$

where h is 0.01 MPa/m vertical drop, and evapotranspiration (E) is chosen as 5 mmol m^{-2} s^{-1} ($=9 \times 10^{-8}$ m^3 m^{-2} s^{-1}), I predicted the stem water potentials of representative supported and unsupported plants. This conservative value of E represents a high but feasible rate of evapotranspiration, and hence gives high water potential gradients. This value was chosen after noting values of maximum rates of E for other temperate-zone vines: for kudzu *(Pueraria lobata)* of 18 mmol m^{-2} s^{-1} (Forseth and Teramura 1987), for *Lonicera japonica* of 12.5 mmol m^{-2} s^{-1}, for *Vitis vulpina* of 10 mmol m^{-2} s^{-1}, and for *Parthenocissus quinquefolia* of 7.3 mmol m^{-2} s^{-1} (Bell et al. 1988). The assumption in these predictions of stem water potentials is that all leaves have the same evapotranspiration rate on both supported and unsupported plants. This is a reasonable starting point for a model given that some plants grow in sunny windy sites (so all leaves are exposed to the same environment), and all leaves within a plant are about the same age (they are produced in one flush and live only one growing season).

Maximum vessel length. I used the air method (Greenidge 1952) on stems of six shrubs and seven vines to determine maximum vessel lengths for plants in the field. I fitted the proximal end of the stem in a pressure chamber, raised the pressure slightly, and held the shoot tip under water to learn at what length air passed through the stem as I trimmed back from the apex.

Longevity of vessel function. Putz (1983) reported preliminary evidence that vessels of lianas remained conductive for longer periods than did those of trees. To test this hypothesis in supported and unsupported segments of poison oak, I forced filtered aqueous safranin (1 g in 99 g distilled water) through the basal segment of each shoot after having measured its specific conductivity. I recorded which growth rings were stained, but did not quantify the proportion of vessels in a growth ring that conducted dye. To increase the range of ages for this experiment, I performed dye ascents in five large shrubs (2.4–3.6 cm diameter, 18–22 years old) and six large vines (1.8–3.3 cm diameter, 15–31 years old). I sawed stems before dawn when xylem tension was presumably lowest, shaved the cut ends under water with fresh razor blades, and placed them *in situ* into beakers of aqueous safranin. Two days later I re-cut stems 40 cm up from the infusion port and counted the number of stained and unstained growth rings.

Wood anatomy. For each conductivity sample I determined specific weight on a debarked subsample as oven-dry weight/wet volume. For eight supported shoots, subsamples from segments about 20 cm above and below the end of support were saved in 50% ethanol for anatomical analysis. After sectioning and staining these segments I determined their vessel diameter distribution (inner diameter) and vessel density (vessels/mm^2) as follows.

To control for year-to-year variability, within each stem I compared the same growth rings (using all but the oldest growth ring in the upper segment). Eight-bit images (256 shades of gray) were acquired through a CCD video camera (Page-MTI, Inc., Michigan City, ID) attached to a dissecting microscope and an 8-bit Quick Captur digitizing board (Data Translation, Marlboro, MA). Images were analyzed with an Apple Macintosh II computer using the public domain program Image (v.1.26c, Wayne Rasband, NIH). I took two images (from opposite sides of the section where possible) from each sample, pooling vessels for vessel diameter distribution and averaging values for vessel density. Images usually contained 50–150 vessels.

Common garden plants

To have even-aged replicate individuals under more controlled environmental conditions, I studied plants in a common garden. The plants were grown from cuttings taken in June-September 1987 from 11 different Jasper Ridge source plants, five vines and six shrubs (see details of propagation in Gartner and Thomas 1988). Five replicates of cuttings from each source plant were planted 1 m apart outdoors, with and without a 2.5 cm square wooden stake. Staked plants were tied to their poles each week throughout the 1988 and 1989 growing seasons. In 1988 (but not 1989), I watered plants weekly between February (when they were planted) and June, then every 12 days until August, then every 16 days until late October. Every third week until June I included a light application of NPK fertilizer with irrigations. The rooted cuttings had been in the ground for 17–18 months (two entire growing seasons) before I made hydraulic measurements. I chose the largest three individuals of each staking treatment and source plant (33 unstaked and 33 staked plants) for the following determinations.

Huber value, specific conductivity, and LSC. During July-August 1989 I determined water transport properties for one segment near the base of each of the 66 plants described above. As the plants were too bushy to harvest under water, I cut stems pre-dawn, quickly immersed them in a bucket, and removed a 20-cm stem segment from the base. I put this segment in a water-filled jar for transport to the lab. In the lab I trimmed the segment further as described for field plants, such that the final segment was 10 cm long and its base was 5 cm above the top of the original cutting. I counted the number of leaves distal to the stem sample and determined the area of 50 randomly chosen leaves. Specific conductivity was measured as for the field plants and Huber value and LSC were calculated for each sample. Both annual growth rings transported safranin in all samples.

Wood anatomy. For each sample I determined wood specific weight as for the fence plants and preserved a subsample in 50% ethanol for anatomical analyses with the image analysis system described above. I took two images of the second (youngest) growth ring for each sample, with each image generally containing 75–150 vessels. I also determined vessel diameters and density in the first growth ring for a subset of these samples to show the difference between xylem produced during the establishment phase (as plants grew

Table 1. Huber value (10^{-4} xylem transverse area/distal leaf area), specific conductivity (10^{-3} m^2 s^{-1} MPa^{-1}), and leaf-specific conductivity (LSC, 10^{-7} m^2 s^{-1} MPa^{-1}) of primary stems of *Toxicodendron diversilobum* as a function of support in the fence area and the common garden (one-factor ANOVAs, mean ± SE). Samples in the fence area are from a 10-cm segment centered 5–34 cm above the shoot's base. Samples in the common garden are from a 10-cm segment centered 10 cm above the original cutting

Fence area (*n*)	Unsupported (11)	Supported (11)	*P*
Huber value	4.1 ± 0.7	1.3 ± 0.2	**
specific conductivity	4.1 ± 0.7	9.1 ± 2.1	*
LSC	15.0 ± 2.7	9.6 ± 2.2	n. s.
Common garden (*n*)	(33)	(33)	
Huber value	2.7 ± 0.1	1.8 ± 0.1	**
specific conductivity	2.8 ± 0.3	5.5 ± 0.6	**
LSC	7.5 ± 1.0	10.3 ± 1.5	n. s.

** $P<0.01$, * $P<0.05$, and n. s. $P>0.05$

Table 2. Huber value (10^{-4} xylem transverse area/distal leaf area), specific conductivity (10^{-3} m^2 s^{-1} MPa^{-1}), and leaf-specific conductivity (LSC, 10^{-7} m^2 s^{-1} MPa^{-1}) of primary stems of *Toxicodendron diversilobum* as a function of support and light environments in the fence area (two-factor ANOVA, mean ± SE). The value for an individual shoot (unsupported) or portion of shoot (supported) is the average of all its measured segments. The top of the supported shoot is above where the stem leaves the fence; the bottom is the supported part of the supported shoot

Support	Unsupported		Supported	
	entire	top	bottom	*P*
(*n*)	(11)	(8)	(11)	
Huber value	2.9 ± 0.3^a	1.5 ± 0.4^b	1.0 ± 0.1^b	**
specific conductivity	4.2 ± 0.7^a	4.5 ± 0.7^a	10.9 ± 1.7^b	**
LSC	11.7 ± 1.6	6.1 ± 1.2	10.6 ± 2.3	n. s.

Light	high	medium	low	*P*
(*n*)	(7)	(14)	(9)	
Huber value	2.2 ± 0.4	1.8 ± 0.3	1.8 ± 0.3	n. s.
specific conductivity	7.5 ± 2.0	6.4 ± 1.3	6.8 ± 1.7	n. s.
LSC	14.9 ± 0.3^a	9.1 ± 1.4^b	6.8 ± 1.0^b	*

** $P < 0.01$, * $P < 0.05$, and n. s. $P > 0.05$. The same letter following values on a line indicate they do not differ significantly at $P < 0.05$

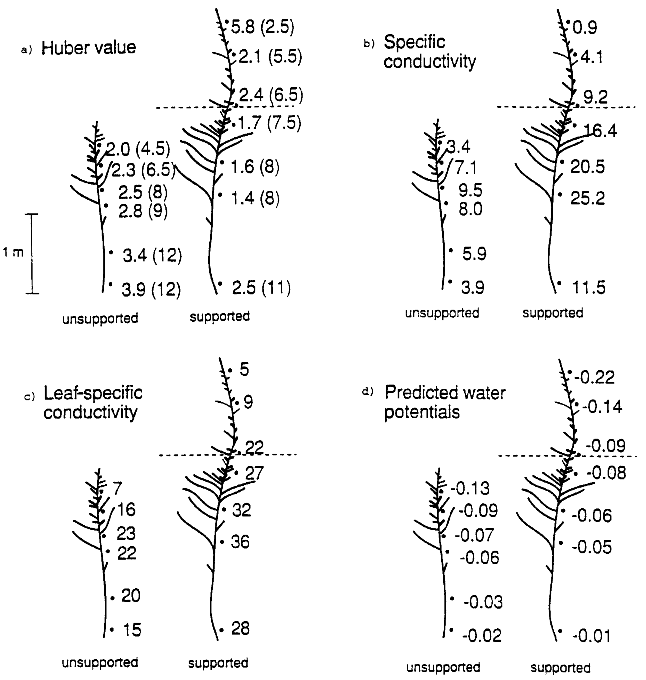

Fig. 1a–d. Example of hydraulic properties of primary stems with height for two neighboring *Toxicodendron diversilobum* shoots (one unsupported, one supported) in full sun. **a)** Huber value (10^{-4} xylem transverse area/distal leaf area) and segment age (yr) in parentheses, **b)** specific conductivity (10^{-3} m^2 s^{-1} MPa^{-1}), **c)** leaf-specific conductivity (10^{-7} m^2 s^{-1} MPa^{-1}), and **d)** predicted stem water potentials (MPa) for $E = 5$ mmol m^{-2} s^{-1}. The dashed line shows where the supported shoot leaves the chain link fence, and separates the shoot's bottom and top

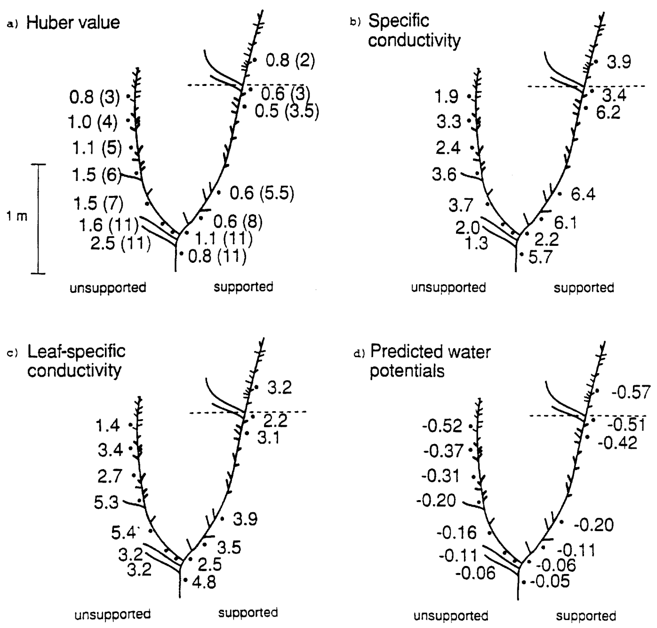

Fig. 2a–d. Example of hydraulic properties with height for a bifurcated *Toxicodendron diversilobum* plant in medium light (one stem unsupported, one supported); panels as in Fig. 1

from their initial 0.1 m to 1–3 m in height) and xylem produced during their second year.

Vessel length distribution. I measured vessel length distribution for 12 stems (one staked and one unstaked) from six source plants using the latex paint method (Zimmermann and Jeje 1981). A filtered emulsion of latex paint and water was forced into stems for eight days at about 70 kPa. Paint was introduced from the stem tip toward the base (to prevent paint exiting through branch junctions) and thus was restricted to vessels produced in the current year (1989).

Results

Hydraulic properties

At bases of plants. Unsupported shoots had higher Huber values at their bases than did supported shoots in both the fence area and in the common garden (Table 1), showing that there is more stem area/leaf area in an unsupported than a supported shoot. Specific conductivity of supported segments was twice that of unsupported ones (Table 1). Leaf specific conductivity (LSC) did not differ significantly between unsupported and supported segments at either site (Table 1).

In the common garden, supported plants had about 67% the Huber value and 200% the specific conductivity of unsupported plants (Table 1). These values are very close to those in the field, comparing average values for bottoms (below the end of support) vs. tops (above the end of support) of supported shoots: bottoms had an average of 66% the Huber value and 216% the specific conductivity of tops of the same stems (the eight supported stems having both bottom and top values, Table 2).

Table 3. Huber value (10^{-4} xylem transverse area/distal leaf area), specific conductivity (10^{-3} m^2 s^{-1} MPa^{-1}), and leaf-specific conductivity (LSC, 10^{-7} m^2 s^{-1} MPa^{-1}) of primary stems of *Toxicodendron diversilobum* as a function age in the fence area (one-factor ANOVAs, mean ± SE). Young samples are ≤ 3 years old from apices of supported and unsupported plants, primary stems only. Old samples are from the basal segment of unsupported plants and average 10.5±0.7 years old (mean ± SE)

	Young	Old	P
(n)	(21)	(11)	
Huber value	1.6±0.3	4.1±0.7	**
specific conductivity	1.9±0.4	4.2±0.8	**
LSC	2.1±0.3	15.0±2.7	**

** $P<0.01$

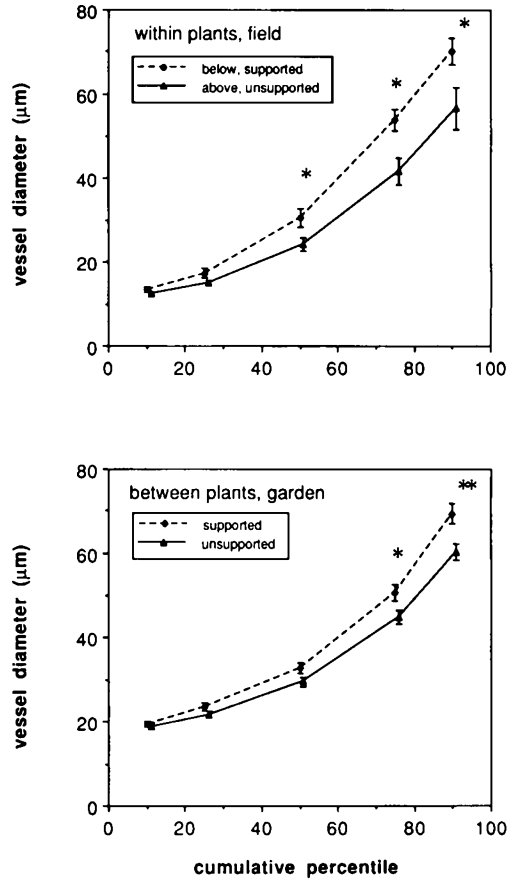

Fig. 3. Vessel diameter distributions of *Toxicodendron diversilobum* in the outer rings in the field below vs. above the end of support (one-factor ANOVAs, mean ± SE, $n=8$) and in the second (outer) growth ring in the common garden in staked vs. unstaked plants (one-factor ANOVAs, mean ± SE, $n=33$). Values show vessel diameter below which a given proportion of vessels lie.** $P<0.01$, * $P<0.05$

Table 4. Huber value (10^{-4} xylem transverse area/distal leaf area), specific conductivity (10^{-3} m^2 s^{-1} MPa^{-1}), and leaf-specific conductivity (LSC, 10^{-7} m^2 s^{-1} MPa^{-1}) of *Toxicodendron diversilobum* in the field as a function of stem order (primary or secondary stem) and support (unsupported or supported) (two-factor ANOVAs, mean ± SE)

	Support	Stem order	Primary	Secondary
Huber value	*	n. s.		
Unsupported stems ($n=7$)			2.7±0.4	2.9±1.1
Supported stems ($n=8$)			1.0±0.2	2.4±0.8
Specific conductivity	*	**		
Unsupported stems ($n=7$)			6.7±0.9	1.4±0.5
Supported stems ($n=9$)			10.5±1.9	3.6±1.4
LSC	n. s.	**		
Unsupported stems ($n=7$)			16.6±1.9	4.0±1.6
Supported stems ($n=8$)			11.5±3.3	6.2±2.4

** $P<0.01$, * $P<0.05$, n. s. $P>0.05$

Throughout lengths of plants. Unsupported stems had significantly higher Huber values and lower specific conductivities than did bottoms of supported stems (Table 2, Figs. 1, 2). Similarly, specific conductivities were more than twice as high in the bottoms (supported parts) as in the tops (unsupported parts) of supported stems ($P<0.05$) and Huber values tended to be lower in the bottoms than in the tops of supported shoots (Table 2, Figs. 1, 2). Neither specific conductivities nor Huber values differed significantly among light environments (Table 2). There were no significant interactions between light and support for Huber value, specific conductivity, or LSC ($P>0.05$) when comparing unsupported shoots, tops, and bottoms of supported shoots.

In contrast to Huber value and specific conductivity, LSC did not differ significantly as a function of mechanical support (Table 2, Figs. 1, 2) but was significantly higher in high than in medium or low light environments (Table 2). Because LSC did not differ with support, neither did the predicted profiles of water potentials within stems of supported and unsupported plants (Figs. 1, 2).

Young segments from primary stems (≤ 3 yrs old) had significantly lower Huber values, specific conductivities, and LSCs than did older, basal segments (Table 3). Nearby segments of secondary stems did not differ significantly from their primary stems in Huber value, but had significantly lower specific conductivities and LSCs (Table 4). Huber values was about twice as high in unsupported as supported primary and secondary stems, and specific conductivity were about half as high, such that there was no significant difference in LSC between supported and unsupported primary and secondary stems (Table 4). The specific conductivity of branch junctions was not significantly different than of secondary stems, but it was lower than the specific conductivity of primary stems ($P<0.05$, data not shown, $n=18$ primary stems, junctions, and secondary stems).

Wood anatomy

Vessel diameters. Supported stem segments tended to have larger diameter vessels than unsupported stem segments (Fig. 3), both in the field (comparing segments 20 cm below and above the end of support within the same individual) and in the common garden (comparing the second, outermost, growth ring of staked and unstaked clones). Mean vessel diameter and vessel lumen area in the field and in the second growth ring in the common garden were significantly higher in supported than in unsupported plants, but maximum vessel diameters and vessel density did not differ significantly between support treatments (Table 5).

There was no effect of staking on any measured anatomical quantity in the first (innermost) growth ring in

Table 5. Wood anatomy and specific weight (dry weight/wet volume) of *Toxicodendron diversilobum* plants as a function of mechanical support (one-factor ANOVAs, mean ± SE). Vessel lumen area is proportion of xylem cross-section that is vessel lumen. In the field, paired segments are taken 20 cm above (unsupported) and below (supported) the end of support on a given shoot. In the common garden, segments are taken 10 cm above top of cutting, and first (innermost) and second annual growth rings were analyzed separately

Field (*n*)	Unsupported (8)	Supported (8)	
Wood specific weight (g/cm³)	0.49 ± 0.02	0.50 ± 0.01	n. s.
Mean vessel diameter (μm)	30 ± 2	37 ± 1	**
Maximum vessel diameter (μm)	82 ± 9	93 ± 5	n. s.
Vessel lumen area (%)	4.4 ± 0.4	6.8 ± 0.7	*
Vessels/mm² (no.)	64 ± 4	63 ± 6	n. s.
Common garden	Unstaked	Staked	*P*
(*n*)	(33)	(33)	
Wood specific weight (g/cm³)	0.64 ± 0.01	0.62 ± 0.01	n. s.
Second growth ring (n)	(33)	(33)	
Mean vessel diameter (μm)	35 ± 1	39 ± 1	*
Maximum vessel diameter (μm)	100 ± 4	109 ± 3	n. s.
Vessel lumen area (%)	4.0 ± 0.2	5.6 ± 0.2	**
Vessels/mm² (no.)	44 ± 3	49 ± 2	n. s.
First growth ring (n)	(4)	(4)	
Mean vessel diameter (μm)	19 ± 2	20 ± 2	n. s.
Maximum vessel diameter (μm)	48 ± 6	44 ± 3	n. s.
Vessel lumen area (%)	3.3 ± 0.2	3.5 ± 0.2	n. s.
Vessels/mm² (no.)	122 ± 23	123 ± 27	n. s.

** $P<0.01$, * $P<0.05$, n. s. $P>0.05$

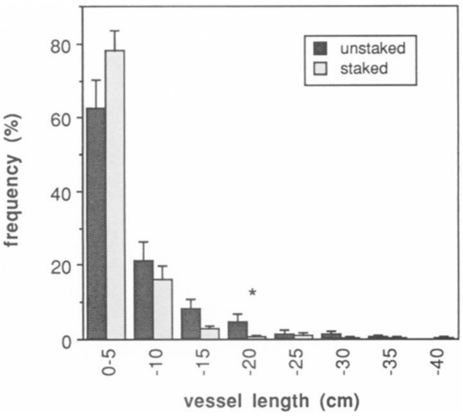

Fig. 4. Vessel length distributions of *Toxicodendron diversilobum* in second (outer) growth ring of unstaked vs. staked plants in the common garden (*t*-tests, mean ± SE, $n=6$). ** $P<0.05$

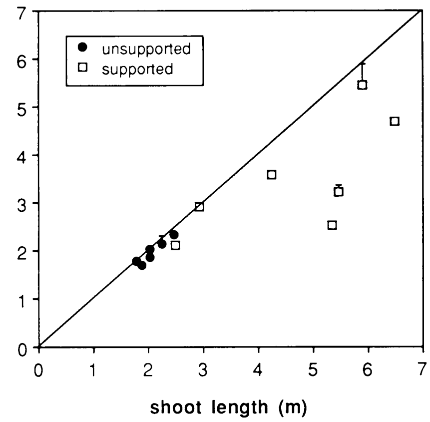

Fig. 5. Maximum vessel length in shrubs and vines of *Toxicodendron diversilobum* from the field as a function of the length of the shoot. Bars show the possible range of maximum vessel lengths, determined by the length of the segment trimmed between measurements. The diagonal shows equivalency between maximum vessel length and shoot length

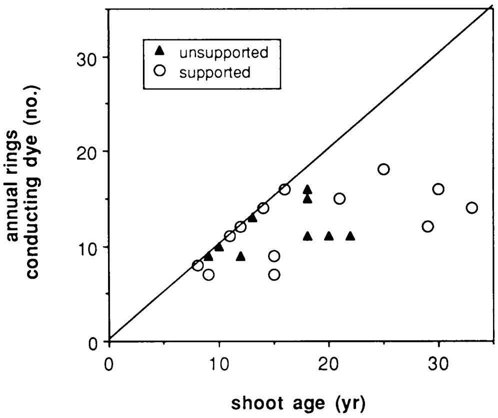

Fig. 6. Relationship between shoot age and number of annual growth rings that conducted dye in *Toxicodendron diversilobum* in the field. The diagonal shows equivalency between years of wood conducting dye and shoot age

the common garden (Table 5). Vessels produced that year were about half as wide but three times as dense as those produced in the second year. For staked plants, the vessel lumen area was significantly higher in the second than first growth ring (two-factor ANOVA, $P<0.05$); unstaked plants showed no significant difference.

Wood specific weight, which is a function of wood porosity among other factors, did not differ significantly between unsupported and supported segments in the field (Table 5). In the common garden, where growth conditions were more uniform, wood specific weight was significantly higher in unstaked than staked plants at $P<0.06$.

Vessel length. Vessel length distribution was similar for unsupported and supported plants in the common garden (Fig. 4). More than half the vessels were < 5 cm long. Although the plants in this sample ranged from 85–223 cm in height, the longest vessel encountered was < 63 cm. In contrast, in the older plants growing under field conditions at Jasper Ridge, the longest vessel was commonly as long as or almost as long as the entire shoot regardless of growth form (Fig. 5). The longest vessel I encountered in a shrub (2.47 m tall) was 2.29–2.39 m long and the longest vessel in a vine (5.90 m tall) was 5.00–5.90 m long.

Longevity of vessel function. Only the outer 7–18 annual growth rings conducted dye in the stem segments tested (Fig. 6). There was no evidence that vessels in supported segments (vines) remained conductive for more years than did those in unsupported segments (shrubs).

Discussion

Effects of mechanical support on stem hydraulics

Species that are obligate vines and lianas have previously been shown to have less stem cross-sectional area/distal leaf area (Schenck 1892, Putz 1983, Ewers 1985, but see Bullock 1990) and higher specific conductivity (Ewers 1985, Gartner et al. 1990) than shrubs and trees. Consistent with these studies but in contrast to predictions of the pipe model (Shinozaki et al. 1964), supported (viney) shoots of poison oak had lower Huber values and higher specific conductivities than did unsupported (shrubby) shoots. In poison oak these properties are induced environmentally: the effect was seen between individuals, within parts of the same individual, and between replicate individuals cloned from the same source plant (see Gartner in press a). In an earlier work, Farmer (1918) mentioned the effect of mechanical support on hydraulic properties, stating that specific conductivity is often lower at the base of a tree because the base has a higher proportion of its wood devoted to mechanical elements.

Even though both Huber value and specific conductivity differed greatly between unsupported and supported shoots, leaf-specific conductivity (LSC) did not differ as a function of support. Likewise, the reported LSCs of mature woody vines are not consistently different from those of self-supporting woody plants (Ewers 1985; Ewers et al. 1989; Ewers et al. 1991). Because LSCs are the same in unsupported and supported stems of poison oak, stems of both support environments will have the same water potential gradients if they have the same rate of evapotranspiration. This suggests that poison oak plants coordinate their production of xylem and leaf area such that similar pressure gradients are maintained in the stem of plants of all growth forms. Much of this growth adjustment appears to occur at the level of the stem, for unsupported plants devote a higher proportion of their cross-section to mechanical function than do supported plants (see below) and consequently become stouter for a given distal leaf area or height above the ground (Gartner in press b). The signal through which this growth adjustment occurs is unclear, but since LSCs are higher in high than medium or low light, the signal may be a factor positively correlated with light. However, because most xylem differentiation occurs earlier in the growing season than does most production of leaf area, the signal may be related indirectly to light environment through a quantity such as growth rate, that may be determined during the previous year.

Huber value, specific conductivity, and LSC were higher for old stems than for the young stems of poison oak, and specific conductivity and LSC were also higher in primary than secondary stems. This pattern is very common in plants (for an exception, see Ewers et al. 1989). Drops in specific conductivity of branches vs. the main stem have been inferred from water potential gradients (Hellkvist et al. 1974), and the pattern of lower LSC in branches than the main stem has been measured in a variety of trees (Zimmermann 1978; Thompson et al. 1983; Tyree et al. 1983; Ewers and Zimmermann 1984a, b; Tyree and Sperry 1988). Lower LSCs at branch tips than along the main stem indicate that water potential will drop more steeply at a shoot's tip than elsewhere along its length. Under severe water stress this will protect the old body of the plant (into which many resources have been invested) at the expense of newer structures (Zimmermann 1983) and will allow upper leaves on the leader (needed for growth and for competition with neighbors) to compete with lower leaves on lateral branches for water (Zimmermann 1978).

Effects of mechanical support on wood anatomy

Vessels were of slightly larger diameter in supported than unsupported shoots but occurred in the same density. As with the hydraulic values, this was environmentally determined (see Gartner in press a). Vine species typically have some wider vessels than self-supporting plants (i.e. Schenck 1893, Carlquist 1975, Ewers 1985), whether closely related plants are compared (Roskam 1926; Bailey and Howard 1941; Ayensu and Stern 1964; Carlquist 1984a, b; Bamber 1984; Ewers et al. 1990) or unrelated plants are compared from the same habitat (Gartner et al. 1990). In poison oak, these wider vessels accounted for the higher conductivity of vines than shrubs. A slight shift in vessel diameter distribution with constant density will have a large effect upon specific conductivity because of conductivity's dependence on conduit radius to the fourth power. For example, a vessel 39 μm in diameter will have 54% higher conductivity than one 35 μm in diameter (means for second growth ring, staked and unstaked plants, respectively).

Vessel length distributions did not appear related to whether a stem was grown with external support, except that in the field both growth forms had at least one vessel that was very long, often almost as long as the entire stem. Greenidge (1952) noted maximum vessel lengths close to the lengths of stems in ring-porous (but not in diffuse-porous) trees. However, these very long vessels comprise a small fraction of the total number of vessels in poison oak and in other species studied (Zimmermann and Jeje 1981; Ewers and Fisher 1989; Ewers et al. 1990) so their lengths are probably hydraulically insignificant: most vessels of poison oak were very short, regardless of support.

Both vessel diameter distributions and mean vessel diameters were similar in the common garden and the field even though plants at the two sites differed greatly in size, growth rate (Gartner in press), and local environment. In older lianas growing in very shady sites (such as within the canopies of the large evergreen tree *Umbellularia californica*), the anatomy of poison oak more closely approximated that of "typical" vines: growth rings difficult or impossible to detect, and larger maximum vessel diameters (largest was 166 μm, personal observation). In a comparison of four well-developed lianas from the shade and four well-developed shrubs from the sun, 25% of the vessels were wider than 48 μm in shrubs and 56 μm in lianas. Less than 1% of the vessels in shrubs exceeded 100 μm in width, compared to 9% of the vessels in lianas (personal observation).

In contrast to results in a tropical forest (Putz 1983), vines of poison oak did not differ from unsupported plants in longevity of their vessel function. Because minimizing the weight of a vine stem is important to the vine's success (lest it topple off its host, Peñalosa 1984), there may be selection in vines on production of wood with high specific conductivity. It has been speculated that this may be achieved in part by possession in vines of a mechanism to restore conduction to air-blocked vessels (Putz 1983) but there is no evidence for such a mechanism in poison oak.

In climbing species it is not unusual for wood produced when the plant is young to differ dramatically from that produced later, with wider and longer vessels produced as the stem becomes older (Ewers and Fisher 1989, Carlquist and Hanson 1990). This may be related to the fact that many vine species are self-supporting when juvenile (Richards 1952; Breteler 1973; Cremers 1973, 1974; Putz 1984; Hegarty 1989). In the common garden, wood produced in the first year was anatomically indistinguishable between unsupported and supported plants, suggesting that unlike older plants, juvenile poison oaks grow according to an ontogenetically-set pattern.

Conclusions

Compared to shrubs, vines of western poison oak have wider vessels in the xylem and have narrower stems for the same distal area of leaves. Consequently, if vines and shrubs have the same evapotranspiration rate, their stems will exhibit similar pressure gradients. These compensating morphological characteristics (xylem anatomy and leaf/stem area) allow poison oak plants to sense similar conditions of water potential while functioning ecologically in more than one growth form. Poison oak's morphological flexibility results in a restricted range of physiological conditions that individuals of the species will encounter, and no doubt adds to the success of the species over a broad geographic range and in numerous types of habitats (Jepson 1936). Further studies relating an organism's shape to its performance will shed light on why certain growth forms or plant structures are found in given environments, and the manner in which plants of diverse growth forms contribute to the functioning of ecosystems.

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