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STRUCTURAL STABILITY AND ARCHITECTURE OF VINES VS. SHRUBS OF POISON OAK, *TOXICODENDRON DIVERSILOBUM*[1]

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Abstract. To learn whether vine stems are less structurally stable than shrub stems, I studied the architecture, anatomy, and mechanics of western poison oak (*Toxicodendron diversilobum*), a plant that grows as a vine when provided with external support but otherwise as a shrub. I assessed the relative structural stabilities of vines and shrubs, and the relative importance of stem morphological vs. material properties for this structural stability using the following types of information: aboveground architecture and biomass distribution, and geometric, anatomical, and material properties of the stems. Shoots that were supported by a fence (vines) had a lower proportion of their dry mass in primary stem and had more aboveground dry mass, more leaves, and a greater total length of stem than did unsupported shoots (shrubs). Both growth forms had about the same proportion of their biomass at a given relative height above the ground. Supported shoots were taller and had lower stem taper (change in radius per unit length of stem) than did unsupported shoots, and, in a common garden, had longer internodes. Xylem of supported shoots had a higher proportion of vessel lumen and lower maximum thicknesses of fiber cell walls than did xylem of unsupported shoots. Supported stems were less stiff (had lower apparent material stiffness in bending) than unsupported stems at diameter ≤ 3.5 cm. A simple model showed that the lower taper and lower material stiffness of vines yielded much lower flexural stiffness in vine than in shrub stems. A second model showed that simplified shrub stems could reach almost 11 m before becoming structurally unstable. Actual shrubs from the modelled environment, however, never exceeded 3.2 m in height. A simplified vine modelled for the same environment would become unstable at 1.2 m, whereas vines in the field can be over 30 m tall. These findings suggest that for poison oak (1) shrubs are overbuilt and vines are underbuilt for self-support, and (2) the higher structural stability of shrubs than vines is due mainly to differences in stem geometry, not to differences in stem material properties.

Key words: biomechanics; California; growth form; material stiffness; mechanical architecture; mechanics of vines vs. shrubs; poison oak; shrub; structural stability; taper; Toxicodendron; *vine.*

INTRODUCTION

Because vines do not need to provide as much of their own support as do shrubs, I hypothesized that vine stems are less structurally stable than are stems of shrubs. This difference in structural stability could derive from differences in geometry of the stems and/or differences in stem material properties. The mechanical aspect of plant biology is important, not only to understand the relationship between structure and function of different growth forms, but also from a cost–benefit perspective. If the cost of mechanical support is lower in vines than in shrubs, then vines may be able to grow faster than shrubs, with consequent increases in their competitive and reproductive capacities.

The functional comparison of different growth forms has been hindered by the fact that most pairs of plants with different growth form also differ in important characteristics such as habitat or phylogeny. Moreover, the immediate environment of a vine often differs from that of a shrub because the vine's external support (such as a tree) alters the light, moisture, and wind environments. I avoided these problems by studying western poison oak, *Toxicodendron diversilobum* (T. & G.) Greene, (Anacardiaceae; also called *Rhus diversiloba* T. & G.), a species that grows as a vine when externally supported and otherwise as a shrub (Gartner 1991*a*). I was able to compare adjacent shoots of vines and shrubs where a chain-link fence supported the vines without altering their microenvironment.

I define a vine as a plant that gains its vertical support from an external object, and a shrub as a plant that provides its own support. In this paper I compare the architecture and biomass distribution, stem material properties, and wood anatomy of vines and shrubs of *Toxicodendron diversilobum* to assess their relative structural stabilities and to learn whether structural stability in these plants derives more from their morphological or their material properties.

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MATERIALS AND METHODS

Plant system and study site

Western poison oak (*Toxicodendron diversilobum*) is a widespread woody perennial of the western United States at elevations below 1220 m and west of the Sierra Nevada (Gillis 1971). At the site of the present study, vines can be >30 m tall and have basal stem diameters >16 cm, and shrubs can be up to 3.8 m tall with basal stem diameters to 20 cm. Plants can also be found growing in a continuum of forms from woody vine to shrub. Poison oak is common in such a wide variety of soil and moisture conditions and in so many vegetation communities that one source (Jepson 1936) opined that poison oak may be the most abundant shrub in California.

I undertook the field work at Stanford University's Jasper Ridge Biological Preserve in the Santa Cruz Mountains, California (37°25′ N, 122°15′ W, elevation: ≈100 m). Jasper Ridge has a mediterranean climate with >80% of the rains falling from November through March (mean annual rainfall 1974–1989: 579 mm). It is an area with abundant poison oak growing in chaparral, oak woodlands, and fields, and under redwoods. I minimized my incidence of dermatitis through a variety of means that included using protective clothing, rinsing contaminated objects with water, and applying a prescription steroid ointment to parts of my skin when bad rashes began to develop (Gartner 1990).

Architecture in the field

If a vine is growing on a tree, its light, wind, and moisture environments may differ greatly from those of a nearby shrub. To avoid these microenvironmental differences, I studied supported shoots growing within the mesh of a 2.4 m high chain-link fence (installed 14 yr previously) and unsupported shoots growing nearby. The supported shoots (those touching the fence) had grown as vines and the unsupported shoots had grown as shrubs. I chose 12 groups of four shoots each, two supported and two unsupported. Within a group, the four shoots were chosen for proximity to one another and (subjectively) for similar light environment. Some of the sets of shoots may have been ramets of the same plant.

The 12 groups were in sites that ranged from full sun to deep shade. To estimate light environments based on leaf specific mass (dry mass per unit leaf area; Blackman and Wilson 1951), I took four punches from each of 10 leaves per shoot in July 1988. Mean leaf specific mass for all shoots in a group was then used to classify the group's light environment as low, medium, or high. Most measurements are reported only for shoots in medium light because shoots in low light did not always grow vertically and so their mechanical loads may have been more complicated, and shoots in high light at the study area were relatively scarce.

For each shoot I measured the length of the primary stem ("shoot height"), the length of all stems ≥1 yr old ("old stem"), the length of each segment of current year's stem growth ("current year's extension growth"), and the number of leaves on each growing point. I then measured stem diameter (average of two orthogonal measurements, over the bark) at the base of all stems and at points every 0.2 m along their length. I defined primary stems as those coming from the ground, and higher order stems (secondary, etc.) as those branching off a stem one order lower. I took the total number of stems (of all orders) to be equal to the number of growing points. For several individuals in each light environment I measured top stem diameter just below each terminal bud. For supported shoots I noted the stem height where physical support by the fence ended. I defined the segment of the stem below this height as "bottom" and that above as "top." "Bottom" averaged 62% of the total stem length in the supported shoots that I sampled, so to control for relative height along the stem, I divided unsupported shoots into "bottom" and "top" using the same proportions (62:38).

To define a stem's taper ($\Delta r/\Delta h$), I used the slope of the best-fit regression line between radius (r, measured every 0.2 m) and stem length (h). The model of a linear change in radius with height fit the data well; for 23 of the 25 "tops" of supported shoots and 21 of the 28 unsupported shoots, the coefficient of determination was ≥0.90. Because all shoots tapered to about the same top diameter (0.3 cm), this definition provides a way to describe the stoutness the bottoms would have in shoots of the same height. Note that taper is defined differently in some studies of plant biomechanics (e.g., King and Loucks 1978, Cannell et al. 1988). I determined taper separately for the "bottom" and "top" of supported and unsupported stems. To control for butt swell, the localized bulge at the base of a shoot due to local stress concentration, I discarded the basal data point if the taper between it and the subsequent point was ≥3 times the taper of the rest of the bottom of the stem.

To compare the geometries of unsupported and supported shoots, I calculated the proportions of canopies as a function of relative position along the primary stem. The compared values were the total length of old stem, the length of current year's extension growth, the number of leaves for the shoots in medium light (1988), and total aboveground dry mass (1989). Biomass was divided into old stem, current year's extension growth, and leaf, and the average area per leaf was estimated with a sample of up to 50 pressed leaves per shoot.

Architecture in the common garden

I grew cloned plants from cuttings in a common garden in order to have replicate, even-aged individuals in the same environment. I took stem cuttings in the summer of 1987 from 21 source plants, all from Jasper Ridge. In late February 1988 I planted the rooted cuttings 1 m apart in an open field at the Carnegie Institution of Washington's Department of Plant Biology on the Stanford University campus, 6 km from Jasper Ridge. The ground surface was covered with woven polypropylene cloth to discourage the growth of weeds and to conserve water.

The common garden consisted of two experiments. In the support experiment, I planted cuttings in a randomized block design having five blocks. Each block contained two individuals of each source plant, one of which was staked. I tied staked plants to 2.5-cm square wooden stakes with plastic tape on about a weekly basis through two consecutive growing seasons. In the light experiment, cuttings from eight source plants were grown unstaked (three replicates per source plant) under two levels of shade cloth (45% and 15% full sun). These were compared to controls from the same clones growing in full sun.

To learn how the light environment affected leaf specific mass, in June 1989 I harvested leaf disks from the light experiment clones. I sampled eight source plants at each light level, with three (45% sun, 15% sun) or five (full sun) individuals per source plant, and 16 leaf punches (four punches from each of four leaves) per individual. To calculate the taper of new stem growth, in the fall of 1988 I measured the length of primary stem (excluding the old material in the cutting) and the basal and top diameters of plants in the light experiment.

One year later (1989) I determined architectural characteristics of individuals from 11 source plants in the support experiment. For the three largest staked and three largest unstaked plants from each of these source plants, I measured the length of primary stem (excluding the old material in the cutting), basal and top diameters of plants, and maximum internode length (length of the longest four consecutive internodes in the 1989 stem).

Wood anatomy

In 1989 I collected stem samples to determine if anatomical properties of wood were affected by support. From the fence area I collected two samples from each of eight supported stems; I took one sample from ≈0.2 m below and one from ≈0.2 m above the end of support. From the common garden I collected samples near the bases of 33 unstaked and 33 staked individuals (propagated from 11 source plants, 3 replicates of each). To control for interannual variations, anatomical analyses were performed for second-year wood of the garden plants and for wood produced in the same years above and below the end of support of shoots from the field.

From stained transverse sections of all wood samples I calculated the proportion of the section that was vessel lumen (using a computer-based system for analysis of digitized images, Gartner 1991*b*) and I measured directly the density of each debarked sample (dry mass per fresh volume, USDA 1987). Lastly, I examined one unstaked and one staked sample from each of the 11 source plants to estimate the maximum thickness of fiber cell walls.

Stem mechanics

To describe the ability of a stem to resist deformation I needed to know its material stiffness and its geometry. Material stiffness (E, with units of gigapascals) is the proportionality factor between a sample's stress (σ, force per unit area over which the force is acting) and its strain (ϵ, unitless, change in length divided by initial length):

$$E = \sigma/\epsilon. \tag{1}$$

Material stiffness is independent of a homogeneous material's geometry—a copper wire and a copper rod have the same E. However, biological tissues are not necessarily homogeneous. A stem is nonhomogeneous throughout its cross section due to bark, growth rings, pith, and irregularities such as variable water content or wounds. Also, a stem may deviate slightly from the assumed (columnar) geometry. Because the material stiffness of a tissue integrates the effects of the tissue's nonhomogeneities, it describes a property of an imaginary material with the σ/ϵ relationship of the tissue. Also, I measured material stiffness in bending rather than in pure tension or compression. To distinguish between a true material property and the one measured here, I refer to a material's stiffness as E and a tissue's stiffness measured in bending as E_b, the apparent material stiffness in bending.

The parameter describing a structure's stiffness is EI, flexural stiffness (units of $\mathrm{GPa \cdot m^4}$), where I is the structure's second moment of area. The second moment of area for a solid beam of circular cross section is

$$I = \pi r^4/4, \tag{2}$$

where r is the beam's radius. With the simplifying assumption that the load on a stem is due to the stem's mass alone, the maximum force the stem can bear before becoming unstable to small perturbations (its "critical load") is directly proportional to its flexural stiffness. Therefore, relative values of flexural stiffnesses of vines and shrubs will describe their relative abilities to withstand mechanical loads.

Measurements of material stiffness, $\mathrm{E_b}$.—Material stiffness (in the axial direction) was determined using cantilever bending tests (Timoshenko 1955) and the equation

$$E_b = FL^3/3\delta I, \tag{3}$$

where F is force (in newtons), L is sample length (in metres), δ is the deflection of the sample (in metres) caused by the force, and I is the second moment of area. I used a force for each sample that caused a deflection of $<10\%$ of the sample's length, assuming that in this range deflection was reversible and linearly related to the load.

I determined material stiffness of several sections per plant for plants from the fence area (12 supported and 12 unsupported) and for larger plants growing nearby (14 supported by trees, 12 unsupported). I used samples 18–93 cm long, all of which had ratios of length to diameter >14 (the ratio used for standardized tests of wood material, USDA 1987). Bark was not removed. The radius of the anatomically distal end averaged 90% that of the proximal end. For an initial subset I found that a sample's light environment had no effect on material stiffness; therefore, I did not track light environment further.

Model 1: Flexural stiffness as a function of height.—I modelled the flexural stiffness of hypothetical stems of vines and shrubs to learn if shrubs produce stems that are more structurally stiff than vines, and to assess the relative importance of material stiffness (E_b) and second moment of area (I) to flexural stiffness. This model was for perfect uniform columns with no lateral loads (e.g., wind, forces due to masses of branches and leaves, forces due to leaning of the stem, unbalanced moments from asymmetrical canopies). Material stiffness and second moment of area were modelled as a function of stem height for hypothetical stems 3 m tall with top diameters of 0.3 cm. Second moment of area was calculated from taper, where taper values are from the "bottom" of unsupported and supported shoots in medium light in the fence area. Material stiffness was taken as a function of radius for unsupported and supported samples.

Model 2: Critical heights of tapered columns.—I calculated the maximum height (critical height, h_{cr}) a tapered column could attain and still be structurally stable, as a function of taper and material stiffness. A stem will exhibit elastic (Euler) buckling if the potential energy lost exceeds the elastic energy gained when it is deflected by a load. Greenhill (1881) showed that the critical height of a right circular cone is

$$h_{cr} = 7.63\ E\ (r/h)^2 \cdot w^{-1} \cdot g^{-1} \qquad (4)$$

where E is material stiffness (in gigapascals), r is basal radius (in metres), h is height (in metres), w is density of the cone (in kilograms per cubic metre), and g is acceleration due to gravity (9.81 m/s^2). Values for E are taken as E_b and values for r/h are taken from taper values. The value for w was determined to be 847 ± 4 kg/m^3 (=0.847 ± 0.004 g/cm^3; mean ± 1 SE) based on fresh mass of four debarked stem segments. Because poison oak stems taper to diameters of $\approx$0.3 cm rather than to a point, the values of h_{cr} given here are the h_{cr} given by the equation minus the length of stem between 0 and 0.3 cm in diameter for the given taper.

To determine the actual maximum heights of unsupported plants, I measured the vertical height of the tallest poison oak shrubs in the vicinity of the fence, in low, medium, and high light environments.

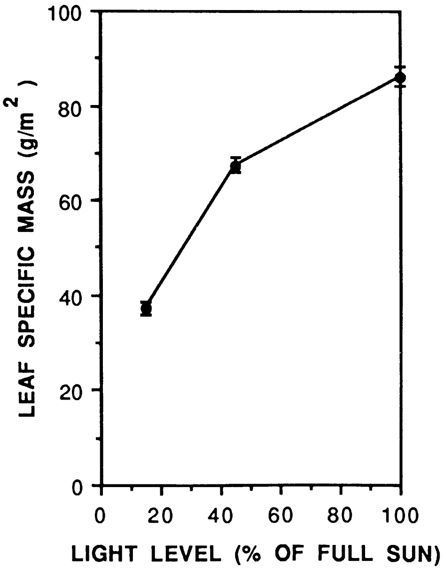

FIG. 1. Leaf specific mass (leaf dry mass per unit of leaf area) of *Toxicodendron diversilobum* in the common garden, comparing cuttings from the same source plants in each of three light treatments (mean ± 1 SE, n = 8).

RESULTS

Light environment

Common garden experiments showed that leaf specific mass was strongly and positively correlated with the light level in which cloned plants had been grown (Fig. 1). This result allowed me to use leaf specific mass as an index of the light environment of groups of shoots in the field. Shoots in low, medium, and high light had means and ranges of leaf specific mass of 26 g/m^2 (24–29 g/m^2), 40 g/m^2 (32–45 g/m^2), and 62 g/m^2 (56–68 g/m^2), respectively. These group classifications also coincided with my subjective assessment of the light environments. When I sampled leaves systematically from the top to the bottom of the field shoots, I found no significant effects on leaf specific mass due to either position in the canopy or the presence/absence of external support (ANOVA, $P < .05$).

Architecture

Unsupported shoots were significantly shorter than supported shoots of the same age and had significantly shorter internodes (Table 1). In the field, unsupported shoots were shorter and smaller than the supported shoots examined for this study (Table 1). They had about half the number of leaves, half the length of old stem and current year's extension growth, half the number of growing points, and two thirds the number of secondary stems of supported shoots (Table 1), but 130% of their basal cross-sectional area (1.24 vs. 0.96 cm^2, not significantly different, $P > .05$). The dry mass of unsupported and supported shoots did not differ significantly with the sample sizes used (112 vs. 193 g,

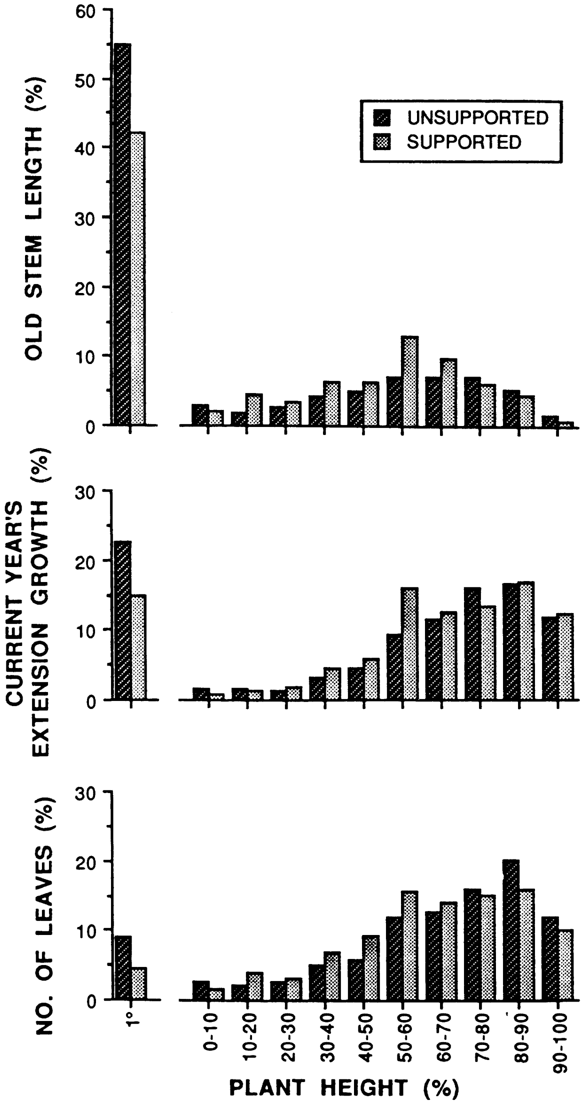

FIG. 2. Proportion of old stem length, length of current year's extension growth, and number of leaves on the primary stem (first pair of bars) or on higher-order stems off the primary stem along deciles of the shoot's 1988 height in *Toxicodendron diversilobum,* medium light, fence area (n = 12 supported and 13 unsupported shoots).

TABLE 1. Age and architecture of unsupported and supported *Toxicodendron diversilobum* shoots in the field in a medium light environment (1988) or in the common garden (1989). (Data are means ± 1 SE.)

Fence	Unsupported (n = 12)	Supported (n = 12)	P
Age (yr)	11.0 ± 0.6†	10.4 ± 1.0	NS
Basal diameter (cm)	1.3 ± 0.1	1.1 ± 0.1	NS
Height (cm)	230 ± 13	306 ± 22	**
Leaves (no.)	92 ± 16	187 ± 29	**
Current year's extension growth (cm)	73 ± 15	165 ± 33	*
Old stem (cm)	452 ± 46	798 ± 104	**
Growing points (no.)	33 ± 5	66 ± 11	*
Secondary stems (no.)	21 ± 3	32 ± 3	**
Common garden	Unstaked (n = 33)	Staked (n = 33)	P
Age (yr)	2	2	
Basal diameter (cm)	2.6 ± 0.2	2.1 ± 0.2	NS
Height (cm)	113 ± 5	192 ± 10	**
Maximum internode length (cm)	4.5 ± 0.3	6.4 ± 0.3	**

** $P < .01$, * $P < .05$, NS $P > .05$ (ANOVAs).
† $n = 11$.

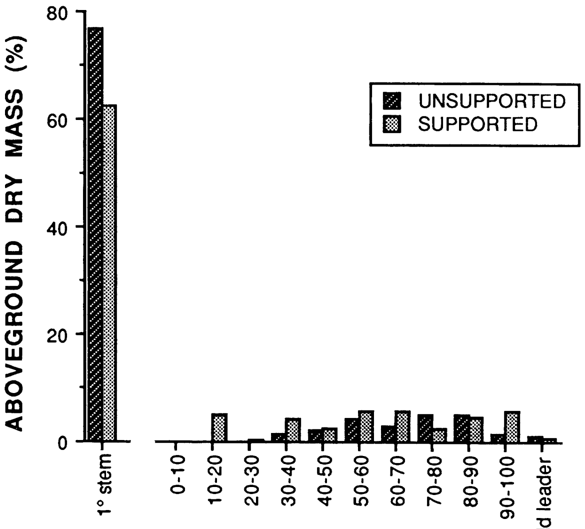

FIG. 3. Proportion of aboveground dry mass of the primary stem (first pair of bars) or of higher-order stems off the primary stem along deciles of the shoot's 1988 height and along the 1988 leader (old leader) in *Toxicodendron diversilobum* in 1989, medium light, fence area (n = 5 supported and 5 unsupported shoots).

respectively, $P > .05$), although they did differ significantly when plants from all light environments were compared (Gartner 1991*c*).

Architecture of unsupported and supported shoots of the medium-light habitat were similar to one another when normalized by total quantities and height (Fig. 2). For example, both growth forms had ≈15% of their leaves on stems attached from 70–80% of the shoot's height. Old stem made up a higher proportion of total dry mass in unsupported than in supported shoots (88% and 82%, respectively, $P < .05$), but the proportion of dry mass that was current year's extension growth (<3%) or leaves (11–16%) did not differ significantly between supported and unsupported shoots ($P > .05$).

The majority of the dry mass was actually located on the primary stem; this includes the old and new stem of the primary stem, and that stem's leaves (Fig. 3). The rest of the dry mass was distributed rather uniformly throughout the height of the shoots (Fig. 3). These mass distributions were similar in unsupported and supported shoots.

TABLE 2. Stem taper of *Toxicodendron diversilobum* shoots (mm/m) in the field or in a common garden in a variety of light and physical support environments.†

	High light		Medium light		Low light	
Field	$\bar{X}$ ± 1 SE	*n*	$\bar{X}$ ± 1 SE	*n*	$\bar{X}$ ± 1 SE	*n*
Shoot "bottom"						
Unsupported [a]	2.0 ± 0.3	7	1.6 ± 0.2	12	1.3 ± 0.2	9
Supported ‡,[b]	1.1 ± 0.4	7	0.8 ± 0.3	12	0.4 ± 0.2	9
Shoot "top"						
Unsupported [c]	2.5 ± 0.2	7	2.6 ± 0.3	12	1.4 ± 0.3	9
Supported ‡,[c]	3.9 ± 0.7	5	2.2 ± 0.2	12	1.7 ± 0.3	9
	100% sun		45% sun		15% sun	
Common garden	$\bar{X}$ ± 1 SE	*n*	$\bar{X}$ ± 1 SE	*n*	$\bar{X}$ ± 1 SE	*n*
1988, Light experiment	3.6 ± 0.3	17 [d]	1.6 ± 0.2	14 [e]	1.5 ± 0.2	16 [e]
1989, Support experiment						
Unstaked [f]	6.2 ± 0.2	33				
Staked [g]	3.2 ± 0.1	33				

† The same letter following two values means values were not statistically different at $P = .05$ (separate ANOVAs for a-b, c, d-e, and f-g). Significance values for the light experiment, common garden, are from Fisher's (1949) protected least significant difference a posteriori test.

‡ Supported plants were growing within the mesh of a chain link fence.

Taper

Unsupported segments of stem and those in high light had higher taper than did supported segments and those in low light, both in the fence shoots and in the common garden (Table 2). In the field the "tops" of unsupported and supported stems (neither of which was supported; for definition see *Materials and Methods: Architecture in the field*) did not differ in taper.

Wood anatomy

The proportion of xylem cross-sectional area that is vessel lumen was lower in unsupported than supported stem segments (Table 3). This was true both within a single stem (having both treatments) and between stems (with different treatments), suggesting that some wood anatomical properties are environmentally controlled. Wood density was higher in unsupported than supported segments from the common garden ($P < .054$), but did not differ significantly in the field samples. The maximum thickness of fiber cell walls was higher in unsupported than supported stems.

Material stiffness, E_b

Material stiffness was highest at intermediate stem diameters and lowest at very small stem diameters (where stem was mostly pith) and at the largest diameters tested (Figs. 4 and 5). In diameter classes from 0.5 to 3.5 cm, supported stems had significantly lower material stiffness than unsupported stems (Fig. 5). At other diameter classes they did not differ significantly.

TABLE 3. Anatomical properties of *Toxicodendron diversilobum* wood above (unsupported) and below (supported) the end of support on the same shoot in the field, and for unstaked and staked stems from the same source plants. (Data are means ± 1 SE.)

Within a shoot, field	Unsupported	Supported	*P*
	(*n* = 8)	(*n* = 8)	
Lumen (%)	4.4 ± 0.4	6.8 ± 0.7	**
Wood density (g/cm³)	0.49 ± 0.02	0.50 ± 0.01	NS
Between plants, common garden	**Unstaked**	**Staked**	***P***
	(*n* = 33)	(*n* = 33)	
Lumen (%)†	4.0 ± 0.2	5.6 ± 0.2	**
Wood density (g/cm³)‡	0.64 ± 0.01	0.62 ± 0.01	NS§
	(*n* = 11)	(*n* = 11)	
Maximum fiber cell wall thickness (μm)	2.2 ± 0.1	1.8 ± 0.1	**

** $P < .01$, NS $P > .05$ (ANOVAs).

† Lumen (%) is the proportion of transverse xylem area that is vessel lumen in certain growth rings (see *Materials and methods: Wood anatomy*).

‡ Wood density is dry mass divided by wet volume.

§ $P = .054$.

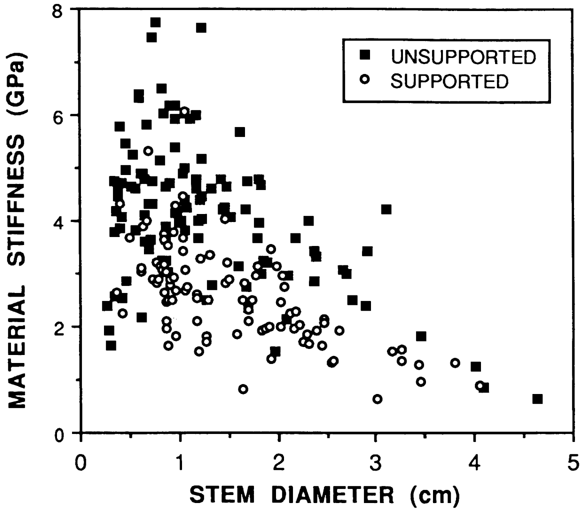

FIG. 4. Material stiffness, E_b, by stem diameter for 112 unsupported and 95 supported stem segments of *Toxicodendron diversilobum.*

For segments ≤2 cm in diameter I compared material stiffness of unsupported stems (n = 95) and of "tops" (n = 58) and "bottoms" (n = 69) of supported stems. Supported stem tops did not differ significantly from unsupported stems ($P > .05$) in material stiffness, but both supported stem tops and unsupported stems were significantly stiffer than supported stem bottoms ($P < .05$) at diameters of 0.5–1 and 1–1.5 cm (paired t tests, data not shown). In the other two diameter classes there were no significant differences. This result supports the hypothesis that material stiffness is environmentally determined in this species (also see Gartner 1991*a*).

Mechanical models

Model 1: Flexural stiffness as a function of height.— I modelled flexural stiffness of tapered columns as a function of height (Fig. 6) using average taper values of unsupported and supported shoots (with 1.6 or 0.8 mm/m for their tapers, respectively, from Table 2, medium light, "bottom" of fence shoots) and using values of material stiffness for unsupported and supported shoots from Fig. 5. About three quarters of the aboveground dry mass of the shoots from the fence area was in the primary stem (Fig. 5), so this model seems appropriate for an approximate comparison of structural stability of unsupported and supported shoots.

The unsupported shoot would require 2.1 times the stem volume (=biomass) of the supported shoot to reach the same height (calculated from Fig. 6a). The unsupported shoot has a higher second moment of area than does the supported shoot (Fig. 6b) and has somewhat higher material stiffness (Fig. 6c) at most points in the height profile, so their product, flexural stiffness, is much higher in the unsupported than the supported stem throughout most of its profile (Fig. 6d).

The base of the unsupported stem is 10 times as flexurally stiff as is the base of the supported stem (Fig. 6d and Fig. 6e). Even two thirds of the way up the stem, the unsupported stem is five times as structurally stiff as is the supported stem. Therefore, with 2.1 times the biomass of the supported stem, an unsupported stem gains over five times the flexural stiffness, and consequently can withstand over five times the load of the supported stem along the lower two thirds of its length (Fig. 6e). The higher flexural stiffness of unsupported than supported stems is due primarily to contributions of the second moment of area, not the material stiffness (Fig. 6e).

Model 2: Critical heights of tapered columns.—The tallest shrubs in the field were 3.0 m in low light, 3.2 m in medium light, and 3.8 m in high light. I used Model 2 to learn to what degree vines and shrubs are under- or overbuilt, assuming the load on the stem came solely from gravity acting on the stem's mass.

The higher the material stiffness, the taller is a tapered column before it becomes unstable to small perturbations (see Eq. 4 and Fig. 7a). If a column has the taper of an unsupported stem in the sun (2.0 mm/m, Table 2), its critical height is 17.6 m or 10.3 m for a material stiffness of 5 GPa or 3 GPa, respectively. These critical heights are 2.7–4.3 times as high as the measured maximum height in that light environment, suggesting that in full sun, shrub stems are built with a large margin of safety for self-support. Using the same approach, Fig. 7a also shows that at the taper of me-

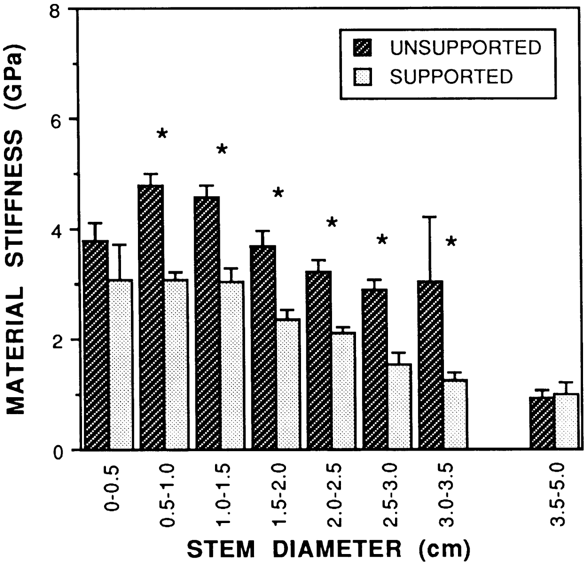

FIG. 5. Material stiffness, E_b, of stem segments of *Toxicodendron diversilobum* as a function of stem diameter class (mean and 1 SE, for 112 unsupported and 95 supported stems). Asterisks show where means for unsupported and supported stems differ significantly (t tests, $P < .05$).

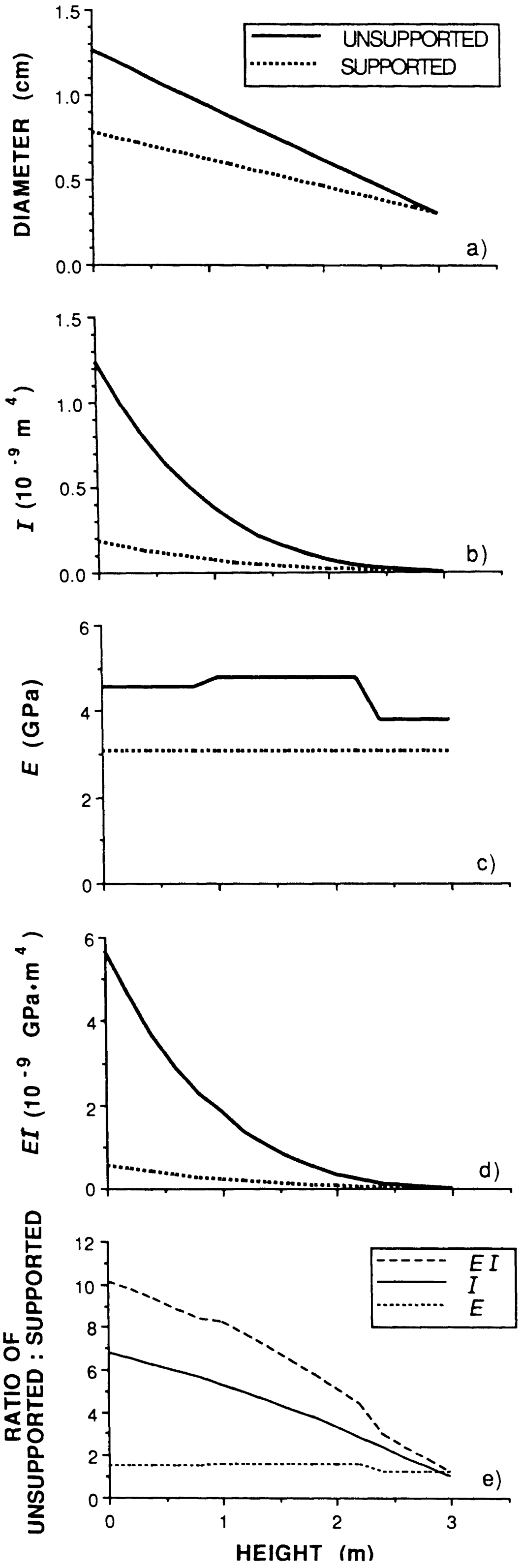

FIG. 6. Calculations to estimate the flexural stiffness of two hypothetical *Toxicodendron diversilobum* stems having taper characteristics of medium-light fence shoots (Table 2) and material stiffness as a function of diameter (Fig. 5). The stems are 3 m tall and have a top diameter of 0.3 cm. (a) stem diameter; (b) second moment of area, I; (c) stiffness of material, E; (d) flexural stiffness, EI, as a function of height; and (e) factor by which the unsupported stem has higher flexural stiffness, second moment of area, and material stiffness than the supported stem, as a function of height.

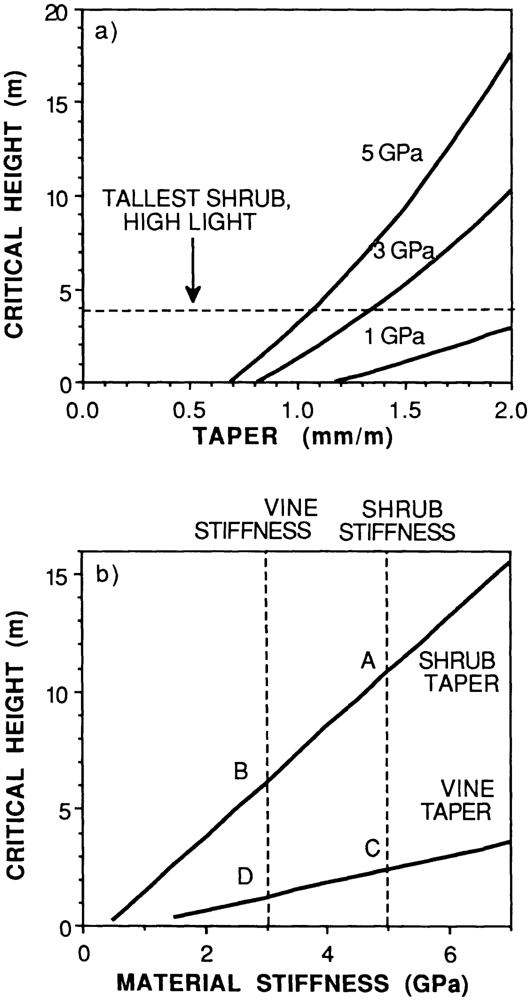

FIG. 7. (a) The calculated critical height of right-cylindrical tapered columns as a function of taper for three values of material stiffness. (b) The calculated critical height of right-cylindrical tapered columns as a function of material stiffness for two values of taper, that of an unsupported and a supported shoot in medium light (1.6 mm/m and 0.8 mm/m, respectively, from Table 2). In both cases, critical heights for hypothetical *Toxicodendron diversilobum* stems are where the diameter of the tapered columns is 0.3 cm.

dium-light shoots, critical heights are 1.6–3.8 times higher than the measured maximum in that light environment. Likewise, at the taper found in low light, critical heights are 1.5–2.0 times the measured maximum heights. These calculations suggest that stems in high light are overbuilt for self-support to a greater extent than are those in lower light environments.

Fig. 7b compares critical heights for columns having the taper of the "bottom" of an average unsupported or supported stem in medium light (from Table 2, referred to as vine and shrub) as a function of material stiffness. Assume a typical shrub had material stiffness of 5 GPa and a typical vine had material stiffness of 3 GPa throughout its height profile. A column with the taper and material stiffness of a shrub would reach 10.8 m (Fig. 7b: point A) before becoming unstable to small perturbations (much higher than the maximum observed height of 3.2 m). A column with the taper and material stiffness of a vine would reach 1.2 m (Fig. 7b: point D); clearly, vines reach heights much greater than 1.2 m, doing so by using the support of external objects.

Material stiffness has less of an effect on critical height than does taper (see Eq. 4 and Fig. 7b): a column with the taper of a shrub and stiffness of a vine would still reach 6.1 m in height (Fig. 7b: point B). In the reverse situation, a column with the taper of a vine and material stiffness of a shrub would reach 2.4 m (Fig. 7b: point C).

This simple model indicates that unsupported stems (shrubs) are overbuilt for self-support when the main force is gravity on the primary stem. In contrast, supported stems (vines) are vastly underbuilt if they would be required to hold themselves up. Had butt swell been included in taper calculations, the critical buckling height of the stems might have been even greater.

DISCUSSION

The hypothesis that shrub stems are built for self-support and vine stems are not appears true in *Toxicodendron diversilobum*. Although this hypothesis has not been tested directly before, the results concur with anatomical comparisons of vines and shrubs or trees that have been reported in the literature. In the present study, viney segments of wood had a significantly lower proportion of their cross section in structural material than did shrubby sections (although their wood densities were significantly different only at $P < .054$). Studies of related vines and self-supporting plants (Roskam 1926, Carlquist 1975, Bamber 1984) generally show that vines have a lower proportion of their cross section in structural material. In the present study, maximum thicknesses of fiber cell walls were lower in supported than unsupported plants. Roskam (1926) showed in a comparison of 20 vines and 14 shrubs of five genera that vines tended to have thinner maximum wall thicknesses of fibers, pith, and "parenchyme ligneux."

The simplified models presented here suggest that shrubs, like other woody plants and palms (i.e., McMahon 1975, King and Loucks 1978, King 1986, 1987, Rich et al. 1986), are overbuilt for their self-support. Consistent with the observation that tropical lianas commonly slip from their hosts (Putz 1990), the vines in the present study appear underbuilt for self-support. External support is also necessary to hold up trees that were grown with lateral shade and/or stakes (Leiser et al. 1972, Holbrook and Putz 1989), and to hold up sea palms (marine macro-algae) that grew in clumps (Holbrook et al. 1991). Surprisingly, even though shrubs of poison oak appear more overbuilt than do vines, the two forms had the same growth rates in the common garden (Gartner 1991*c*). The differences in mechanical abilities of different growth forms of poison oak stems appear to confer it flexibility in how to exploit a given habitat and not to confer an inherent growth advantage to the vine over the shrub form.

The greater structural stability of shrubs than vines of poison oak results primarily from second moment of area (a function of stem geometry) and not from stiffness of the material involved. Taper is positively correlated with second moment of area if plants are the same height and have the same top diameter. In many plants, taper is induced by a plant's sway. Decreases in taper have been observed in staked or guyed trees (Jacobs 1954, Burton and Smith 1972, Leiser et al. 1972, Holbrook and Putz 1989) and wind-sheltered and/or shaded trees (Larson 1965, King 1986, Holbrook and Putz 1989). These studies indicate that the second moment of area commonly changes in plants in response to mechanical loads.

Reports are less common on changes in the material property of a plant as a function of its mechanical load. Where such changes have been sought in woody plants, they have been found to be minor. The xylem of shrubby poison oak is the shrub's basal state, and not "reaction wood," a morphologically distinct tissue induced by local stress concentrations (Scurfield 1973). Holbrook and Putz (1989) found that staking or staking plus shading of tree saplings had no significant influence on the material stiffness of their stems. In contrast, Cannell and Morgan (1987) report lower material stiffness in tree branches than in trunks for three species, which may relate to their support environment, or perhaps to their age. In arborescent palms that are developmentally unable to increase their stem diameter as they increase in height (Rich et al. 1986), the stiffness of their stem material increases with time (Rich 1987). This is probably accomplished through continued lignification of cells that had already been produced (Rich 1987).

The higher material stiffness in small- than in large-diameter stems is opposite to the pattern observed in timber species (Bendtsen and Senft 1986). The usual pattern is to produce wood of low density and low stiffness in the first several years, with both values increasing to an asymptotic value in later growth rings. It may be that only at very small diameters does the high stiffness of wood become important to the self-support of small shoots; at larger diameters the contribution of second moment of area takes over. For example, it may be less costly for a plant to achieve a 10-fold increase in flexural stiffness through a 10-fold increase in second moment of area (an increase in transverse area by a factor of 3.2) than through a 10-fold increase in material stiffness.

Lower stiffness may confer greater flexibility on vines, which could be mechanically advantageous for a growth form that may hang, swing, or be coiled at different times in its life. However, the lower material stiffness of supported than unsupported stems may result from aspects of plant biology unrelated to biomechanics. First, the vessel lumen made up a larger proportion of the xylem of vines than shrubs. This will have a large effect on hydraulic conductivity (a function of the sum of vessel radii to the fourth power), but a small effect on material stiffness (roughly a function of wood density to the 0.8 power, USDA 1987). Therefore, the lower material stiffness of vine wood than of shrub wood could result from selection for hydraulic properties rather than mechanical ones. Second, vines and shrubs of poison oak differ in their temporal and spatial patterns of stem elongation (Gartner 1991*c*). It would be interesting to learn whether they also differ in microfibril angle in the S_2 layer of their cell walls, because this angle may be related to the rate of cell wall maturation, and it is negatively correlated with stiffness in hardwood trees (Bendtsen and Senft 1986, Schniewind and Gammon 1986). More work is needed to see if the lower material stiffness of vines is correlated with greater flexibility and to see if there are ultrastructural differences in xylem cell walls of vines vs. shrubs.

Differences in taper of primary stems in high vs. medium light could have resulted from different distributions of the mass or leaf area of higher order stems. If there were more dry mass in lateral branches per unit length of primary stem in high than medium light, then high-light stems would require wider bases, for both mechanical and hydraulic support. This would cause high-light shoots to have higher taper. Likewise, a greater leaf area per unit length of primary stem would result in higher loads from wind drag. I calculated the dry mass, length of old stem, and area of leaves of higher order stems, and divided each by the length of the primary stem to give a value per metre. None of these values per metre differed between shoots from high and medium light ($P > .05$). Therefore, the higher taper in high light must result from light or some factor correlated with light and not from differences in the distribution of biomass or leaf area along the primary stem.

Poison oak shoots growing in shadier sites had lower critical heights than did those in full sun. Decreases in the ratio of stem mass to length have also been reported for some tropical vines growing in the shade (Lee 1988). As a consequence of its lower critical height, a shaded shoot may have an increased probability of encountering support because if the leader falls, a lateral will grow upward, with the renewed possibility of encountering support. In shaded habitats, climbers would present their leaves to sunnier habitats than would shrubs. This leaf positioning, in turn, may improve the shoot's competitive ability (Givnish 1982, Weiner et al. 1990). Vines at Jasper Ridge accumulated more dry mass per year than shrubs (although in the common garden, rates of biomass accumulation were the same, Gartner 1991*c*). If fitness is positively correlated with these growth parameters under field conditions, then this capacity to "forage for support" may have evolved through natural selection. This plasticity of form appears to allow poison oak plants to exploit a variety of habitats, and thus may contribute to the species' wide range and great abundance.

In conclusion, shrubs are more structurally stable than are vines of poison oak. Their increased stability is achieved primarily through differences in morphological properties rather than in material properties of the stem. Shrub stems had a lower proportion of vessel lumen (and consequently a higher stem proportion of structural material) than did vines. Shrub wood also had slightly higher material stiffness for stems of mid-diameter range. Shrubs in the field seldom attained the modelled critical height beyond which stems would fail elastically, whereas vines in the field almost always exceeded the critical height predicted by these simple models.

More studies of this type may help us understand mechanistically why certain growth forms tend to live in certain environments (Grisebach 1872, DuReitz 1931, Adamson 1939, Takhtajan 1959) and why the same growth forms have evolved convergently in similar habitats (Turesson 1925, Mooney and Dunn 1970, Walter 1979). Such studies will also help us evaluate how form constrains function in different types of plants. We can thus gain a better understanding of the consequences for a plant of life in one growth form or another.

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