Functional Ecology 1991, **5**, 696–704

Is the climbing habit of poison oak ecotypic?

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Abstract. Morphological, physiological, and growth characteristics of western poison oak (*Toxicodendron diversilobum* (T. & G.)) Greene in a Californian site suggest that the shrub *vs* vine growth forms are determined by an environmental factor (the presence or absence of physical support), and not by ecotype. In a common garden, clones of shrubs and vines differed as a function of support in 11 variables (stem length, stem taper, internode length, mean and median vessel diameter, vessel lumen area/stem area, Huber value, specific hydraulic conductivity, and three indices of leaf *vs* stem elongation) but differed as a function of plant origin (shrub or vine) in only one variable (vessel density). In the field, supported (viney) and unsupported (shrubby) parts of the same plants differed significantly for seven variables: stem taper, stem modulus of elasticity in bending, Huber value, specific hydraulic conductivity, vessel lumen area/stem area, and mean and median vessel diameters; differences by plant origin could not be tested. Although much of the variation was due to plasticity, common garden experiments showed that source plants also differed from one another in many of the measured characteristics. Individuals of *T. diversilobum* will function ecologically as vines if grown with support but as shrubs in the absence of support.

Key-words: Ecotype, growth form, phenotype, plasticity, shrub, vine

Introduction

Since the classic studies on plasticity of plant form and function more than half a century ago (Clausen, Keck & Hiesey, 1940, and the work of Kerner, Bonnier & Turesson, summarized therein), botanists have been investigating the relative constancy of plant characters (reviewed in Bradshaw, 1965; Schlichting, 1986). Many species show great morphological plasticity with respect to their canopy shape and size, but nonetheless, they do not change from one growth form (*sensu* Du Rietz, 1931) to another. Examples include trees that grow preferentially away from one another (Jones, 1985; Franco, 1986), forbs that are branchier in sparse stands than dense ones (Maillette, 1985; Weiner, Berntson & Thomas, 1990), and trees with higher branching ratios in more open habitats than in forest understorey (Pickett & Kempf, 1980). Here, I investigated the plastic *vs* ecotypic basis of growth form variability in western poison oak, *Toxicodendron diversilobum* (T. & G.) Greene (also known as *Rhus diversiloba* T. & G.). If the vines and shrubs of poison oak result from the same genotype, then this species exemplifies an extreme in plasticity of shoot architecture.

The poison oaks and ivies have long been recognized as plants that vary in appearance from site to site, and as plants capable of living in a wide range of habitats (Horsfield, 1798; Jepson, 1936; Gillis, 1971). Western poison oak may be the most variable species in the genus, for mature plants are common in a variety of forms ranging from erect shrub to ropey vine. Jepson (1936) says of this species that it grows in a wider geographic range and in a wider range of environmental conditions with respect to rainfall, soil, temperature and light, than any other California shrub.

The characteristics evaluated here were derived from a larger study on the functional morphology of vines *vs* shrubs (Gartner, 1990, 1991). The larger study addressed the following hypotheses for poison oak. Because vines have a lower requirement than shrubs to provide their own support, (1) vines will have stems that are less structurally stable than those of shrubs, (2) vines will have less of their stem cross-section devoted to support and so will have higher area-specific hydraulic conductivity than shrubs, and (3) vines will allocate less material to stem and consequently will have higher growth rates than shrubs. Cloned plants were grown in a common garden with and without a stake to separate effects of physical support from plant origin. In naturally occurring plants in the field, values were compared between unsupported and supported segments of the same individual to assess the effects of physical support within one plant.

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Materials and methods

Western poison oak is a deciduous, dioecious plant that is locally abundant from sea-level to an elevation of about 1220 m along the west coast of the USA and Baja California (Gillis, 1971). In the extremes, vines of this species (plants that gain support from other objects) can be over 30 m tall and up to 15 cm diameter at the base whereas shrubs (self-supporting plants) can grow as very erect plants up to 4 m tall with basal diameters of up to 15–20 cm. More commonly vines reach 3–10 m and shrubs about 2 m in height. In sunny sites, both forms produce drupes (hereafter called seeds).

Fence area

Field work was conducted at Stanford University's Jasper Ridge Biological Preserve in the Santa Cruz Mountains of western central California (37° 25 'N, 122° 15 'W, elevation about 100 m). The site has a mediterranean climate with over 80% of the rainfall between November and March (total annual average, 1974–1989, 579 mm). At this site, poison oak grows in meadows, oak woodland, a redwood grove, chaparral, and both sunny and shaded seasonally wet creek beds. It grows on both sandstone- and serpentine-derived soils.

Because supported (viney) poison oak plants usually grow on trees, they experience very different light, wind and moisture conditions than do unsupported (shrubby) plants. Therefore, to compare supported and unsupported shoots under the same conditions pairs of naturally occurring shoots were studied, one supported by a 2·4-m high chain-link fence (installed in the autumn of 1974) and one unsupported, but growing nearby. Within a pair, shoots were chosen for proximity and similarity of light envirionment. Occasionally, both shoots were ramets of the same plant. Among the study plants, unsupported and supported plants averaged about 2·3 and 3·1 m in height, respectively.

For within-plant comparisons I divided the primary stems into 'bottom' and 'top' (Gartner, 1990). 'Bottom' for supported plants was that portion of the stem that was within or leaning on the fence and 'top' was the part above or not touching the fence. For unsupported plants, bottom was separated from top using the mean proportion calculated from supported plants.

Mechanical properties of stems. Taper was determined (decrease in overbark radius/height) for primary stems of plants in the fence area in 1988 (Gartner, 1990). Bottom and top were analysed separately.

Material stiffness, E_b, (also called apparent modulus of elasticity in bending) was determined with cantilever bending tests on 124 unsupported stems, 105 bottoms of supported stems and 58 tops of supported stems. Measurements were made with bark intact (Gartner, 1990).

Hydraulic properties of stems. During June–July 1989 I determined Huber value (xylem transverse area/distal leaf area) and xylem area-specific hydraulic conductivity (water volume $\times$ time^{-1} $\times$ xylem transverse area^{-1} $\times$ pressure gradient^{-1}) for the primary stem of 22 shoots in the fence area (Gartner, 1991), distinguishing between bottom and top for the supported shoots. Liquid was forced through excised stem segments (10 cm long) at low positive pressures (11–60 kPa). Its rate of efflux was determined by timing its accumulation in a beaker on an electronic balance. Care was taken in sample collection and preparation to avoid embolizing stems. Values of unsupported shoots, bottoms of supported shoots, or tops of supported shoots are means for all such measured segments (up to seven) on the stem.

Anatomy. Pairs of wood samples were taken from about 20 cm below and 20 cm above the end of support for eight primary stems. For each stem, growth rings produced in the same years in both samples were compared (Gartner, 1991) to determine vessel density (no. mm^{-2}), proportion of transverse area that is vessel lumen, and mean, median and maximum vessel diameters (taken inside vessel walls). This was done with images captured through a video camera that was attached to a microscope, digitizing board, and computer (Gartner, 1991).

Common garden

In 1987 cuttings were taken from 22 source plants (15 shrubs and seven vines) at Jasper Ridge. In February 1988, the rooted cuttings (about 10 cm tall) were planted at 1-m intervals into a disced field. Up to five replicates of each source plant were planted with or without a stake using a randomized block design: each source plant was assigned two spots in each of the five blocks, one unstaked and one staked spot. Unstaked and staked spots were alternated in a checkerboard pattern. As plants grew, those in the staked treatment were tied to their stakes as necessary (about

Table 1. Description of the variables studied in the common garden and reported in Tables 5 and 6.

Variable name	Description
Top diameter	Overbark stem diameter below terminal bud
Stem taper	Decrease in overbark stem diameter/stem height*
Stem length	Length of primary stem
Vessel density	No. vessels mm^{-2}, second (oldest) growth ring†
Median vessel diameter	Median vessel diameter, second growth ring†
Mean vessel diameter	Mean vessel diameter, second growth ring†
Maximum vessel diameter	Maximum vessel diameter, second growth ring†
Lumen area (%)	Transverse area that is vessel lumen, second growth ring (%)†
Huber value	Xylem transverse area/distal leaf area†
Conductivity	Specific conductivity (water volume × $time^{-1}$ × xylem transverse $area^{-1}$ × pressure $gradient^{-1}$)†
Wood density	Dry weight of debarked stem/wet volume†
Internode length	Average length of four longest consecutive internodes produced in 1989*
Biomass	Above-ground dry weight*
Leaf biomass (%)	Leaf dry weight/dry weight of whole plant above ground*
L_a	Elongation (%) of leaf above a given internode when that internode is 75% elongated*
L_b	Elongation (%) of leaf below a given internode when that internode is 75% elongated*
i_a	Elongation (%) of internode above a given internode when that internode is 75% elongated*
D	Time interval between when internode and leaf below it are 75% elongated*
Plastochron	Time interval between when successive internodes are 75% elongated*

References are given if the variable has been described elsewhere: * Gartner, 1990; † Gartner, 1991.

weekly). Horticultural methods are described in more detail in Gartner (1991).

Growth, hydraulic, and allometric characteristics. During April–May 1989 relative elongation of stem *vs* leaf was measured for one unstaked and one staked individual from 19 source plants (13 shrubs and six vines; Gartner, 1990). This was to test the hypothesis that the stems of vines elongate quickly relative to the leaves when compared with trees (Schenck, 1982). This phenomenon is interpreted as a means of having a reduced lever arm on the vine leader as it searches for support (Raciborski, 1900; French, 1977).

During July–August 1989, near the end of the growing season, the three largest unstaked and staked plants of each of 11 source plants were harvested (six shrubs and five vines). Their taper was measured, along with their wood hydraulic and anatomical properties, and their patterns of biomass allocation using methods detailed elsewhere (Gartner, 1990, 1991). The measured or calculated variables are described in Table 1.

Aerial roots. Aerial roots are used by vines to adhere to the host, but their development in shrubs serves no known purpose. Therefore, production of aerial roots by staked clones from shrubs constitutes support for the hypothesis that growth form is environmentally determined. At the end of the first growing season, staked plants from each shrub source plant were evaluated for the presence of aerial roots.

Results

Field plants

Stem taper significantly differed with respect to position on plant (Table 2). The bottoms of unsupported stems were significantly more tapered than the bottoms of supported stems but the tops of unsupported and supported stems (both of which actually were not supported) did not differ significantly from one another.

Material stiffness, E_b, varied with stem diameter (Fig. 1) and was significantly higher for unsupported segments than for segments from bottoms of supported stems for most diameter classes. Tops of supported stems were significantly stiffer than bottoms of supported stems, but did not differ significantly from unsupported stems in the two diameter classes in which sample sizes were the largest.

Table 2. Stem taper (mm) of *Toxicodendron diversilobum* plants growing naturally along a fence at Jasper Ridge (one-factor ANOVA, mean ± SE).

	Top		Bottom	
	Unsupported	Supported	Unsupported	Supported
Taper	2·2 ± 0·2^{ab}	2·4 ± 0·3^{a}	1·6 ± 0·1^{b}	0·7 ± 0·2^{c}
n	28	25	28	27

The same letters following values indicate they do not differ significantly (Fisher's Protected Least Significance Difference *post hoc* test, $P > 0{\cdot}05$).

Table 3. Huber value (10^{-4} xylem transverse area/distal leaf area) and specific conductivity (10^{-3} m^2 s^{-1} MPa^{-1}) of primary stems of *Toxicodendron diversilobum* as a function of support in the fence area (one-factor ANOVAS, mean ± SE).

	Unsupported entire	Supported top	Supported bottom	*P*
n	11	8	11	
Huber value	2·9 ± 0·3^{a}	1·5 ± 0·4^{b}	1·0 ± 0·1^{b}	**
Conductivity	4·2 ± 0·7^{a}	4·5 ± 0·7^{a}	10·9 ± 1·7^{b}	**

** $P < 0{\cdot}01$. The same letter following values on a line indicate they do not differ significantly (Fisher's Protected Least Significant Difference *post hoc* test, $P > 0{\cdot}05$).

Table 4. Wood anatomical properties above *vs* below the end of support on the same stem (ANOVAS, mean ± SE, $n = 8$). Lumen (%) is the proportion of the xylem transverse area that is vessel lumen.

	Above end of support	Below end of support	*P*
Lumen (%)	4·4 ± 0·4	6·8 ± 0·7	*
Vessel diameter (μm)			
Mean	30 ± 2	37 ± 1	**
Median	24 ± 2	31 ± 2	*
Maximum	82 ± 9	93 ± 5	–
Vessels mm^{-2} (no.)	64 ± 5	63 ± 6	–

* $P < 0{\cdot}05$; ** $P < 0{\cdot}01$; – $P > 0{\cdot}05$.

Huber values did not differ significantly between tops and bottoms of supported shoots, but Huber values of supported shoots were significantly lower than those of unsupported shoots (Table 3). The tops of supported shoots had significantly lower conductivities than did the bottoms of supported shoots, and did not differ significantly from unsupported shoots.

Anatomy. The proportion of xylem transverse area that is vessel lumen was significantly higher in sections taken below than above the end of support from within the same stems (Table 4). Mean and median vessel diameters were also higher below than above the end of support, but maximum vessel diameter and vessel density did not differ significantly by support.

Common garden

Effects of support and origin on plants from shrub and vine sources pooled. Eleven variables were significantly different as a function of support (unstaked or staked) in the common garden in two-factor ANOVAS for support and plant origin (Table 5): stem length, internode length, stem taper, specific conductivity, Huber value, lumen area (%), median and mean vessel diameter, and the stem and leaf elongation variables D, L_b, and the plastochron.

Nine variables were significantly different as a function of origin (whether source plant was a shrub or vine; Table 5). Although the hypothesis of no difference between shrubs and vines is rejected, the results are in contrast to what would be expected based on reported biological observa-

Table 5. Characteristics of *Toxicodendron diversilobum* plants in the common garden as a function of support (unstaked *vs* staked) and origin (source plant was a shrub or vine; two-factor ANOVAS, mean ± SE).

	Support			Origin		
	Unstaked	Staked	P	Shrub	Vine	P
Stem length (cm)	113 ± 5 (33)	192 ± 10 (33)	***	170 ± 11 (36)	132 ± 9 (30)	***
Conductivity (10^3 m^2 MPa^{-1} s^{-1})	2·8 ± 0·3 (33)	5·5 ± 0·6 (33)	***	5·5 ± 0·6 (36)	2·6 ± 0·3 (30)	***
Mean vessel diameter (μm)	35 ± 1 (33)	39 ± 1 (33)	*	39 ± 1 (36)	35 ± 1 (30)	**
D (days)	−0·3 ± 0·3 (76)	1·2 ± 0·4 (75)	*	1·0 ± 0·3 (104)	−0·6 ± 0·4 (47)	**
L_b (%)	75 ± 1 (76)	70 ± 1 (76)	*	71 ± 1 (104)	76 ± 1 (48)	**
Internode length (cm)	4·5 ± 0·3 (33)	6·3 ± 0·3 (33)	***	5·7 ± 0·3 (36)	5·1 ± 0·4 (30)	–
Stem taper (mm)	6·2 ± 0·2 (33)	3·2 ± 0·1 (33)	***	4·9 ± 0·3 (36)	4·5 ± 0·3 (30)	–
Huber value (10^{-4} m^2/m^2)	2·7 ± 0·1 (33)	1·8 ± 0·1 (33)	***	2·2 ± 0·1 (36)	2·3 ± 0·2 (30)	–
Lumen area (%)	4·0 ± 0·2 (33)	5·6 ± 0·2 (33)	***	5·0 ± 0·3 (36)	4·7 ± 0·2 (30)	–
Median vessel diameter (μm)	29 ± 1 (33)	33 ± 1 (33)	*	33 ± 1 (36)	29 ± 1 (30)	–
Plastochron (days)	4·7 ± 0·2 (76)	3·9 ± 0·3 (75)	*	4·4 ± 0·2 (104)	4·2 ± 0·4 (47)	–
Vessel density (no./mm^2)	44 ± 3 (33)	49 ± 2 (33)	–	43 ± 2 (36)	51 ± 3 (30)	*
Maximum vessel diameter (μm)	100 ± 4 (33)	109 ± 3 (33)	–	112 ± 4 (36)	96 ± 3 (30)	**
Biomass (g)	487 ± 50 (33)	486 ± 41 (33)	–	559 ± 45 (36)	400 ± 41 (30)	**
L_a (%)	56 ± 1 (76)	56 ± 1 (76)	–	54 ± 1 (104)	61 ± 2 (48)	***
Wood density (10^{-2} g/cm^3)	64 ± 1 (32)	63 ± 1 (32)	–	62 ± 1 (35)	65 ± 2 (29)	–
Top diameter (mm)	3·3 ± 0·1 (33)	3·3 ± 0·1 (33)	–	3·3 ± 0·1 (36)	3·2 ± 0·1 (30)	–
Leaf biomass (%)	28 ± 1 (33)	28 ± 1 (33)	–	27 ± 1 (36)	29 ± 1 (30)	–
i_a (%)	42 ± 1 (76)	46 ± 2 (76)	–	44 ± 1 (104)	46 ± 2 (48)	–

There were significant interactions between support and origin ($P < 0·05$) for stem length, stem taper, and L_a. * $P < 0·05$; ** $P < 0·01$; *** $P < 0·001$; – $P >$ 0·05.

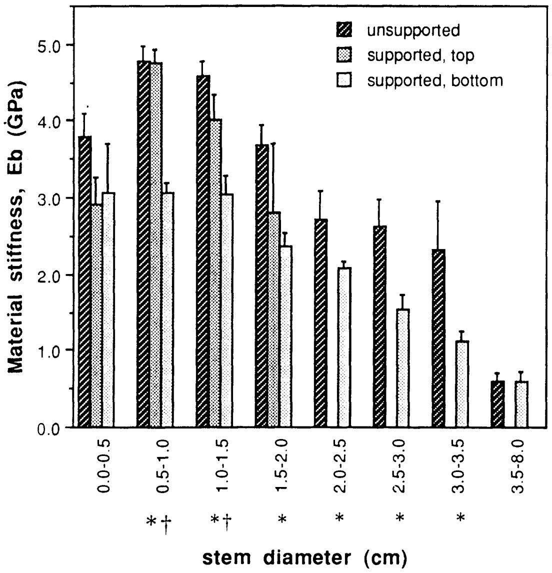

Fig. 1. Material stiffness, E_b, of stem segments of *Toxicodendron diversilobum* (mean ± SE for a total of 124 unsupported stems, 58 tops of supported stems, and 105 bottoms of supported stems). * Shows where means for unsupported and supported stems differ significantly (ANOVA, $P < 0{\cdot}05$). †Shows where unsupported portions of supported stems differ significantly from supported but not unsupported stems (ANOVA, $P < 0{\cdot}05$). Note that the last diameter class is larger than the other diameter classes.

tions and hypotheses for all but one variable (vessel density, for which there is no hypothesis). The hypothesis that origin is a determinant of the measured values must be rejected for eight of these nine variables for the following reasons.

If origin is important, vines are expected to have longer primary stems (as seen in the field), higher specific conductivity (Table 3), wider mean and maximum vessel diameters (to facilitate higher specific conductivity, which is a function of vessel radius to the fourth power, e.g. Roskam, 1926; Carlquist, 1975; 1984; Ewers, 1985), higher D and lower L_a and L_b (stems of vines are thought to expand quickly relative to their leaves compared to shrubs and trees as seen in French [1977] and under 'support' in Table 5), all opposite to that observed. Biomass was expected to be higher in vines than shrubs because vines are thought to have higher relative growth rates. In no case do these data support the hypotheses that were being tested because the relative values for the shrub and vine source plants are reversed from those expected.

Four variables showed no significant difference among support environments or origins: wood density, diameter at top of a stem, proportion of dry weight that is leaf, and the stem and leaf elongation variable i_a.

Several of the variables in Table 5 were auto-correlated. The variables that had $r^2 > 0{\cdot}40$ (>40% of the variance in one variable was explained by the other variable) are as follows: taper and internode length; stem length and internode length; stem length and specific conductivity; and mean vessel diameter and specific conductivity, vessel density, median vessel diameter, and maximum vessel diameter. However, because these variables had different responses to support and origin, they have all been included in the table.

Effects of support and origin on plants from shrub and vine sources separately. Plants grown from shrub source plants were also analysed separately from those grown from vine source plants. The most striking result was that there was genetic variability for most of the measured variables in shrubs and for many of the measured variables in vines (second and fourth columns, Table 6): within a given plant origin (vine or shrub), cuttings from some source plants had significantly different characteristics than those from other source plants. The lower variability of vines than shrubs may have resulted from the smaller number of vine than shrub source plants compared. The variables for which support had a significant effect in vines and shrubs pooled (first 11 variables, Table 5) generally had a significant effect in either shrubs or vines alone (first and third columns, Table 6).

Aerial roots. The staking treatment induced production of aerial roots. Whereas only four of the 15 shrub source plants had aerial roots in their natural habitat, aerial roots were present in some staked clones of 13 of the 14 source plants in which > three individuals survived. With rare exceptions, aerial roots were only observed in unstaked plants where branches contacted the ground.

Discussion

The difference between growth forms in western poison oak at Jasper Ridge appears to be determined by the presence or absence of physical support, although there was also genetic variability for many of the reported morphological, mechanical, and anatomical characteristics. In the field, many variables were influenced by environment (Table 7). In the common garden, a dozen of the measured variables were influenced by environment but only one varied significantly and as hypothesized by plant origin (Table 7). These results are consistent with my observations from

Table 6. Effects of support (unstaked *vs* staked) and source plant (individual from which cutting was taken) on shrubs or vines (separately) for *Toxicodendron diversilobum* in the common garden (two-factor ANOVAs). There were significant interactions ($P < 0{\cdot}05$) for L_a and L_b in shrubs, and lumen (%) in vines.

	Shrubs		Vines	
	Support	Source plant	Support	Source plant
Stem length	***	***	***	***
Conductivity	***	***	***	***
Mean vessel diameter	–	***	**	–
D	***	***	–	–
L_b	***	***	–	–
Internode length	***	***	*	**
Stem taper	***	**	***	*
Huber value	**	*	***	**
Lumen (%)	***	***	***	–
Median vessel diameter	–	***	*	–
Plastochron	**	–	–	–
Vessel density	–	***	–	–
Maximum vessel diameter	–	***	–	–
Biomass	–	*	–	–
L_a	–	***	–	–
Wood density	**	***	–	*
Top diameter	–	***	–	***
Leaf biomass (%)	–	**	–	**
i_a	–	–	–	–

* $P < 0{\cdot}05$; ** $P < 0{\cdot}01$; *** $P < 0{\cdot}001$; – $P > 0{\cdot}05$.

the field, where plants grow in a continuum of forms, not just as vines and shrubs. Seeds are bird dispersed (Martin, Zim & Nelson, 1951; Gillis, 1971). Along a fence, plants grow as shrubs in all places except where there is a tree or telephone pole, in which case they usually grow as vines. This pattern is unlikely to result from differential deposition of vine or shrub seeds in different habitats: McDonnell (1983) showed that seed of the congener *T. radicans* (L.) Kuntze and two other vines were deposited in all habitats tested, not preferentially under trees. I observed shoots of both forms growing from the same plant. Lateral branches of tall vines are often erect and shrubby, giving the appearance of shrubs attached to a vine stem. After vines fall from their host, new shoots often grow as shrubs. It appears that if a shoot encounters support, it will grow as a vine; otherwise, it will grow as a shrub.

Changes in the environment over short distances may lead to the evolution of plasticity because it is unlikely that different ecotypes will evolve in very close proximity (Bradshaw, 1965). In poison oak's range of habitats at Jasper Ridge (woodland, chaparral, meadow edge and meadow), such short-distance changes in environment are due to trees and shrubs that provide support for some individuals of poison oak, but not for others.

Phenotypic plasticity may have adaptive value by allowing a plant to exploit favourable habitats or avoid unfavourable ones (Bradshaw, 1965; Schlichting, 1986). In the field, vines had higher growth rates than did shrubs, perhaps by growing

Table 7. Summary of measured variables for *Toxicodendron diversilobum* for which environment (unsupported or supported) or origin (shrub or vine) had a significant effect in the field or the common garden.

	Differed by environment	Differed by origin
Field	Stem taper E_b Huber value Specific conductivity Lumen (%) Median vessel diameter Mean vessel diameter	
Common garden	Stem length Stem taper Internode length D L_b Plastochron Huber value Conductivity Lumen (%) Mean vessel diameter Median vessel diameter Leaf specific weight	Vessel density

into more favourable light environments or growing away from ground-based herbivores. In low-light environments, shrub stems are thinner and less tapered, and consequently less structurally stable than in high-light environments (Gartner, 1990), which would make them more prone to toppling. By toppling, a stem will explore a new space for support, and thus enhance its chance of becoming a vine. If the higher growth rate is positively and strongly correlated with fitness, then plasticity of growth form may have adaptive value in poison oak by allowing it to persist in several environments (with and without support), while excelling in one of the environments (with support).

The parallel changes in suites of characteristics in response to support lead to distinct vine and shrub growth forms. These changes may be an integrated phenomenon (Schlichting, 1989) or a cascade of phenotypic alterations resulting from one change. For example, supported stems have slightly wider vessels, lower material stiffness, a higher proportion of stem transverse section that is vessel lumen, and higher specific conductivity than unsupported stems. These characteristics all appear adaptive for the vine strategy. However, all of these characteristics could result from a support-related signal to the vascular cambium causing vessels to be wider.

In conclusion, the variation in growth form of *T. diversilobum* appears to result almost solely from environmental responses, not from different genetic races of origin. Even if they are rooted near one another, plants with different growth forms will encounter different environments and behave differently (Weiner *et al.*, 1990). This example demonstrates that one species can have a broader range of environments, morphologies and, consequently, ecological interactions, by possessing the ability to respond plastically to its environment through production of more than one growth form.

Acknowledgments

I thank M. W. Denny, M. W. Feldman, P. B. Green, H. A. Mooney, and two anonymous reviewers for comments on drafts of this manuscript. The Jasper Ridge Biological Station provided rainfall data. The Carnegie Institution of Washington, Department of Plant Biology, kindly permitted me to grow poison oak on their grounds.

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Received 9 July 1990; revised 6 February 1991; accepted 28 February 1991