RELATIVE GROWTH RATES OF VINES AND SHRUBS OF WESTERN POISON OAK, TOXICODENDRON DIVERSILOBUM (ANACARDIACEAE)[1]

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Because of the different mechanical constraints on vines and self-supporting plants, vines are thought to differ from trees and shrubs in a variety of their growth characteristics. I tested the hypotheses that vines grow faster than shrubs and that supported shoots have delayed leaf expansion relative to stem elongation, using western poison oak, *Toxicodendron diversilobum* (T. & G.) Greene, a plant that grows as a vine when externally supported but otherwise as a shrub. In the field, supported shoots (vines) had significantly higher aboveground biomass and relative growth rates than did their paired unsupported shoots (shrubs) growing nearby. This was not due to differences in leaf phenology, but may have resulted from vines growing into more favorable habitats for growth. In contrast, whereas 2-yr-old cloned plants in a common garden differed in their stem and internode lengths, they had the same aboveground dry weight, proportion of dry weight that was leaf, and relative rate of increase in primary stem length whether grown with stakes (vines) or without stakes (shrubs). These results suggest that there is no inherent requirement of vines to grow faster than shrubs. As hypothesized, leaf elongation was more delayed relative to stem elongation in staked than unstaked individuals in 19 paired plants (each pair cloned from a different source plant). Thus, physical cues resulting from the presence of support can alter the plant's spatial and temporal patterns of development, but do not necessarily dictate the quantity of biomass that will be produced.

Because of the different mechanical constraints on vines vs. self-supporting plants, vines differ from trees and shrubs in a variety of their growth characteristics. Using western poison oak, *Toxicodendron diversilobum* (T. & G.) Greene, a plant that can grow as either a vine or a shrub depending on whether it encounters physical support (Gartner, in press a), I tested two hypotheses: that vines grow faster than shrubs, and that supported shoots have delayed leaf expansion relative to stem elongation. Here, growth rate refers to biomass accumulation, and not to extension growth.

Vines are thought to have higher growth rates than shrubs because unlike shrubs, they can use external objects for their structural support,

thereby allocating fewer resources to support material and more to leaves and roots (Darwin, 1867). Such allocation patterns have been noted in individual species (Wechsler, 1977; Whigham, 1984) and in lianas as a class compared to trees as a class in estimates of community biomass (Ogawa et al., 1965; Putz, 1983). However, it is possible to envision a vine that allocates stem material to length rather than to stoutness and that therefore has the same total allocation to stem as a shrub. Certain vine species have been reported to have high relative growth rates (Wechsler, 1977), high rates of extension growth (i.e., Darwin, 1867; Wechsler, 1977; Putz, 1984), and physiological features often correlated with high growth rates (Carter and Teramura, 1988; Castellanos et al., 1989; Castellanos, in press; Teramura, Gold, and Forseth, in press), but whether vines have higher growth rates than shrubs because of their growth form per se has never been tested.

Second, vines are said to have delayed leaf expansion relative to stem extension when compared with self-supporting plants (Schenck, 1892). This is functionally interpreted as a means of reducing the bending moment on the leader that is searching for support (Raciborski, 1900). This phenomenon is more developed in twiners and tendril-climbers than root-

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climbers (French, 1977), which is consistent with the functional interpretation because twiners and tendril-climbers rely on circumnutation (Baillaud, 1962) to a greater extent than root-climbers and scramblers (for which circumnutation has never been reported, i.e., Darwin, 1867). Both mechanical and hydraulic vinelike features can be induced in *T. diversilobum* by giving the leader support (Gartner, in press a); here I tested whether support can also cause differences in the patterns of leaf and stem elongation.

MATERIALS AND METHODS

Study organism — Western poison oak (*Toxicodendron diversilobum* [T. & G.] Greene, Anacardiaceae, also called *Rhus diversiloba* T. & G.) is a widely distributed woody perennial of the western United States below 1,220 m and west of the Sierra Nevada (Gillis, 1971). It grows in a continuum of forms from woody vine to shrub. Poison oak climbs by means of scrambling (lacking specialized organs for climbing but becoming wedged within grooves and crevices) and/or root-climbing (producing specialized aerial roots that adhere to the support surface). However, some vines of poison oak have no aerial roots, and some shrubs possess aerial roots that attach to nothing. Vines can be over 30 m tall and their stems over 0.16 m in diam, but they are typically up to 10–15 m in height in the Santa Cruz Mountains where this study was performed. In this same area shrub stems can be up to 0.20 m in diam and up to about 4 m in height but more commonly reach about 2–3 m.

Common garden — *Growth* — To have replicate cloned individuals with and without support, I made a common garden of poison oak at Carnegie Institution of Washington's Department of Plant Biology, Stanford, California, USA. I propagated the plants from cuttings from source plants at Jasper Ridge, 6 km away. Source plants were generally at least 100 m apart, and so were probably genetically distinct. Ten replicate cuttings were planted for each source plant, with half of the cuttings designated to be staked. To develop uniform vines, I tied one stem of staked plants to 2.5-cm-square wooden stakes at about weekly intervals during both growing seasons.

In fall 1988 I recorded the length of the experimental (staked or unstaked) shoot, its number of nodes, and the plant's total number of leaves. Several hundred plants were measured, but I report only the values for the individuals harvested in 1989 (see below).

In July and August 1989 I harvested aboveground portions of the three largest staked and unstaked individuals from each of 11 source plants, for a total of 66 plants. Biomass was divided into five classes: stem vs. leaf from the experimental shoot (the staked or unstaked stem, including the higher order branches attached to it), stem vs. leaf from the remainder (other stems that emerged from either the ground level or the side of the cutting), and infructescences from the whole plant. The original cutting material was discarded, for its mass may have been influenced by its history before the plant's propagation. Maximum internode length was calculated as the mean length of the four longest consecutive internodes in the current year's growth of the experimental shoot.

Stem and leaf elongation rates — To learn whether staking influenced temporal patterns of shoot development, I measured relative leaf and stem elongation for one unstaked and one staked individual from 19 source plants at about 4-d intervals for 47 d in April and May 1989. I measured internode and central leaflet length (Fig. 1) for four nodes/plant, starting with leaves about 5 mm long. On 6 June, 64 d after the study began, I measured the final lengths of leaves and internodes.

French (1977) introduced five indices to describe relative rates of stem and leaf elongation in vines. He made use of the fact that although each node may develop to a different final size, a repeatable pattern in rate of attaining that size can be found by normalizing organs to final length. He found that it was clearer to compare the time required to reach 75% than 100% of the final length, because this point was easier to read off the elongation curve. Like French, I used leaf length as a nondestructive index of leaf expansion. The indices are the percent elongation of the leaf below (L_b), internode above (i_a), and leaf above (L_a) a given internode when that internode is 75% of its final length; the time difference between when the internode and the leaf below it are 75% elongated (D), and the plastochron, the time interval between when successive internodes reach 75% of their final length (see Fig. 1).

Field — *Growth* — Field work was undertaken at Stanford University's Jasper Ridge Biological Preserve, an area with abundant poison oak mixed within chaparral and within oak woodlands, in open fields, and under redwoods. Jasper Ridge, at 37°25'N, 122°15'W and elevation of 100 m, is in a mediterranean climate ecosystem. A 15-yr record indicates that the rains, which fall between October and

May, average about 580 mm annually. In 1987, 1988, and 1989, the annual rainfall was less than normal, totaling 334, 469, and 514 mm, respectively.

I used two measurements of growth in the field: aboveground dry weight of the vine or shrub shoot, which tells how much biomass accumulated over the shoot's life, and relative growth rate of the shoot from 1988 to 1989. Measurements were made after the annual growth period but before senescence.

In order to compare vine and shrub shoots with comparable light environments, I chose pairs of shoots growing on and near a 2.4-m-high chain link fence that had been installed in 1974, 14 yr before this study began. The shoots supported by the fence are analogous to vines, and those near the fence are analogous to shrubs. I chose 11 groups of four shoots each, two supported and two unsupported, matching shoots within a group for proximity, light environment (subjectively), and approximate basal diam. Some of the sets of shoots were branches of the same plant. The groups were in environments ranging from full sun to deep shade. I used specific leaf weight (leaf dry weight/leaf area) as an index of light environment (Blackman and Wilson, 1951) to categorize the 11 groups into low, medium, and high light environments (means and ranges of 26 [24–29] g/m^2, 40 [32–45] g/m^2, and 62 [56–68] g/m^2, respectively; Gartner, in press b).

The "primary stem" is the main stem I studied, "secondary stems" are those stems attached directly to the primary stem, and "higher order stems" include all stems except the primary stem. I call stems > 1 yr old "old stem" and stems < 1 yr old "current year's growth."

In 1988 I recorded length of all old stems, length of current year's growth, number of leaves, and the primary stem's basal diam (N = 22 unsupported and 22 supported shoots). I took the total number of stems of all orders to be equal to the number of growing points.

I repeated these measurements in 1989 for one of the unsupported and one of the supported shoots in each group, then harvested these shoots to determine the dry weight of old stem, current year's growth, and leaf (N = 11 unsupported and 11 supported shoots). I also noted the number of annual rings to learn whether sampled vines and shrubs were similar in age. I pressed up to 50 leaves/shoot for leaf area, and oven-dried another subsample for dry weight. Leaf area for plants in 1988 was calculated using a plant's average area/leaf in 1989 multiplied by number of leaves in 1988. Relative growth rates of shoots were calculated
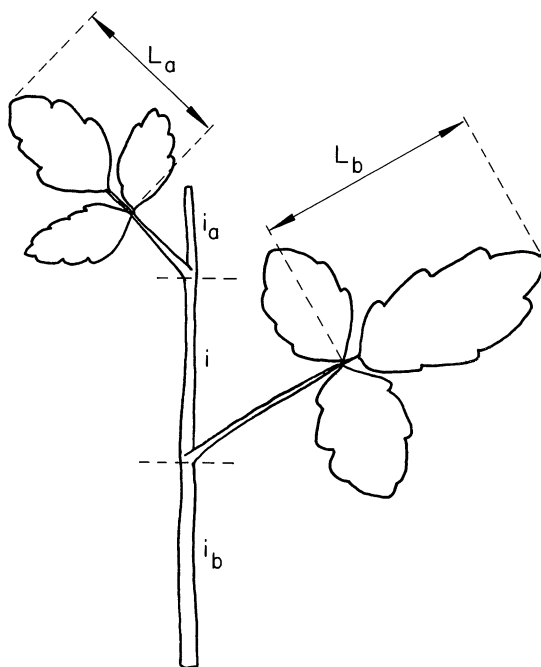

Fig. 1. Geometric measurements of stem and leaf.

as the difference between the natural log of a parameter in 1989 and the natural log of the parameter in 1988 divided by the time period, 1 yr. The values are reported as annual increases (%/yr).

Phenology—To determine whether vines and shrubs had the same phenological development, I followed 12 paired shoots, one supported by the fence, one unsupported but nearby. Each of the pairs was near a set of fence plants used for growth measurements. At about weekly intervals from 30 January to 25 April 1989 I observed five marked growing points/plant, noting the date at which buds opened; and the lengths of the current year's stem growth, the petiole of the first-produced leaf, and the central leaflet (L_a or L_b, Fig.1) of the first-produced leaf. Final lengths, determined on 5 July, were used to calculate the date when the stem, petiole, and central leaflet had expanded to ≥ 75% of their final value. From 26 July to 10 October I observed the growing points weekly to learn when the central leaflet of the first-produced leaf was shed. On some stems this occurred by abscission of the leaf; on others, individual leaflets fell separately.

RESULTS

Quantity and location of growth in the common garden—Staked stems were longer than

TABLE 1. *Architectural and allocation characteristics of the same individuals in 1988 and 1989 for unstaked and staked* Toxicodendron diversilobum *plants in the common garden (mean ± SE)*[a]

	Unstaked	Staked	P
(N)	(33)	(33)	
Experimental shoot			
Length (cm), 1988	69 ± 4	107 ± 7	**
Length (cm), 1989	113 ± 5	192 ± 10	**
Nodes (no.), 1988	23 ± 1	26 ± 1	*
Ave. internode length (cm), 1988	3.0 ± 0.2	4.1 ± 0.2	**
Max. internode length (cm), 1989	4.5 ± 0.3	6.3 ± 0.3	**
Whole plant			
Total dry weight (g)	487 ± 50	498 ± 41	ns
Leaf/total dry weight (%)	28 ± 1	27 ± 1	ns
Leaves (no.), 1988[b]	159 ± 12	143 ± 17	ns
Leaves (no.), 1989	603 ± 50	599 ± 59	ns
Experimental shoot/total dry weight (%)	43 ± 3	64 ± 4	**
Relative growth rates			
Experimental shoot length (cm/cm, %/yr)	53 ± 3	63 ± 6	ns
Leaves (no./no., %/yr)	132 ± 5	145 ± 8	ns

[a] ** $P < 0.01$, * $P < 0.05$, ns $P > 0.05$.
[b] $N = 29$ unstaked and 30 staked individuals.

unstaked stems, due to longer internodes and slightly more nodes (Table 1). However, when the whole plant was considered, staking had no significant effect on total dry weight, proportional allocation to leaf, number of leaves (Table 1), or proportional allocation to infructescence (4.6% vs. 2.5% of total dry weight, staked vs. unstaked plants, respectively, $P >$ 0.05). The experimental shoot made up a larger proportion of the total aboveground dry weight in staked than unstaked plants (Table 1). The rate of elongation of staked stems did not differ from that of unstaked stems between 1988 and

1989 (Table 1). Neither did staking increase the rate of leaf production from 1988 to 1989 (Table 1).

Quantity and location of growth in the field — Two-factor analyses of variance were conducted to learn whether the plant's light environment or presence of support affected shoot allometry, dry weight, or relative growth rate. There were no significant interactions between the support and light environments for any dependent variables tested ($P > 0.05$), so one-factor analyses were then conducted. No mea-

TABLE 2. *Allometry, age, and dry weight of the same unsupported and supported* Toxicodendron diversilobum *shoots in the fence area as a function of physical support (mean ± SE, one-factor analyses of variance)*[a]

	Unsupported	Supported	P
(N)	(11)	(11)	
Allometry, 1988			
Length of primary shoot (cm)	197 ± 17	306 ± 24	**
Total length, old stem (cm)	408 ± 65	751 ± 89	**
Secondary branches (no.)	17 ± 3	29 ± 4	*
Current year's growth (cm)	60 ± 18	128 ± 17	*
Leaf area (m²)	1.6 ± 0.3	5.2 ± 1.0	**
Leaves (no.)	80 ± 18	166 ± 28	*
Growing points (no.)	24 ± 6	53 ± 7	**
Basal stem diameter (cm)	1.1 ± 0.1	1.1 ± 0.1	ns
Age (yr), 1989	11.1 ± 0.7	12.9 ± 0.6	ns
Aboveground dry weight, 1989			
Total (g)	85 ± 21	180 ± 34	*
Old stem (g)	73 ± 18	146 ± 28	*
Leaf (g)	11 ± 3	29 ± 5	**
Current year's growth (g)	1.1 ± 0.4	4.6 ± 1.0	**

[a] ** $P < 0.01$, * $P < 0.05$, ns $P > 0.05$.

TABLE 3. *Mean relative growth rates of* Toxicodendron diversilobum *shoots in the fence area as a function of support (P from one-factor ANOVAs). Values are annual increases*[a]

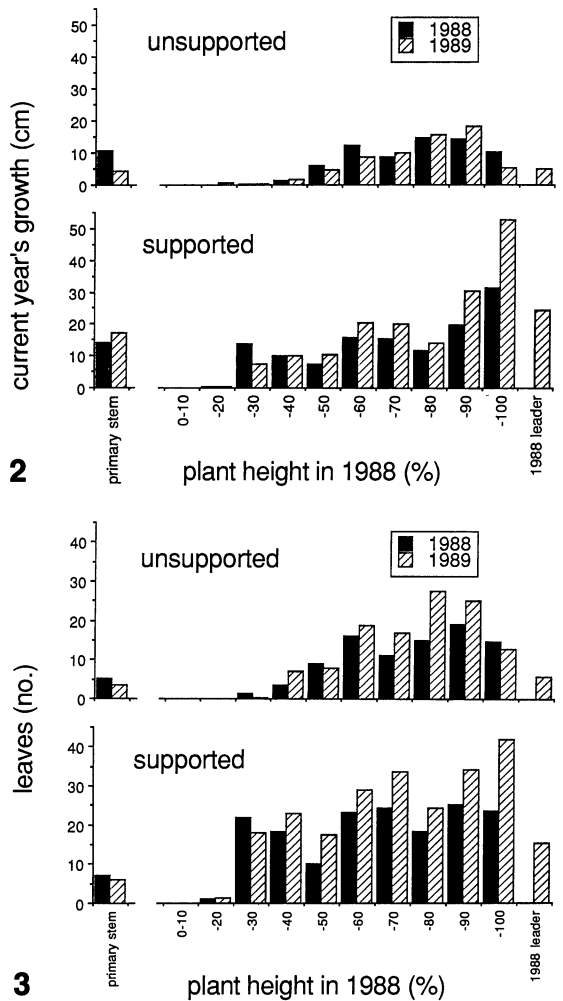|	Unsupported	Supported	P
(N)	(11)	(11)	
Current year's growth (cm/cm, %/yr)	−61	14	**
Leaves (no./no., %/yr)	33	28	ns
Secondary branches (no./no., %/yr)	−10	0.2	ns
Growing points (no./no., %/yr)	7	11	ns

[a] ** $P < 0.01$, ns $P > 0.05$.

sured parameters of allometry or dry weight differed significantly among the three light environments ($P > 0.05$, data not shown).

Supported shoots were much larger than unsupported shoots, although they did not differ significantly in age or basal diam (Table 2). Supported shoots were about 50% longer than unsupported shoots, had almost twice the length of old stem and number of secondary branches, and more than twice the length of current year's growth, area of leaves, number of leaves, and number of growing points (Table 2). Supported stems had over twice the aboveground dry weight of unsupported stems, as a result of ≥ twice the biomass of old stem, leaf, and current year's growth (Table 2).

Supported shoots did not differ significantly from unsupported shoots in the proportion of aboveground biomass that was leaf or current year's growth ($P > 0.05$). The ratio of current year's growth to leaf dry weight, a rough index of allocation to support vs. photosynthetic organs, did not differ between unsupported and supported shoots ($P > 0.05$).

Consistent with the biomass data, the data on relative growth rates indicate that supported shoots were growing more rapidly than the unsupported shoots (Table 3). Unsupported shoots had relatively less current year's growth in 1989 than in 1988, whereas supported shoots had more; this difference was statistically significant (Table 3). The relative increase in the number of secondary branches, growing points, and leaves did not differ significantly between unsupported and supported shoots (Table 3).

The current year's growth during 1989 was distributed by height similarly to that of 1988 in unsupported and supported shoots (Fig. 2). In unsupported shoots most current year's growth occurred on branches in a broad zone from 50% to 100% of the primary stem's height. In supported shoots, current year's growth was more skewed toward the plant's top, especially

Figs. 2, 3. Quantities of stem and leaf as a function of height along the primary stem where the biomass was attached, 1988 and 1989, for unsupported ($N = 22$) and supported ($N = 22$) shoots. "Primary stem" shows the quantity (length of current year's stem growth, or number of leaves) on the primary stem; "0–10," etc. shows the summed values for higher order stems that connect to the primary stem from 0–10%, etc. of the height of the stem in 1988; and "1988 leader" shows the 1989 values for material connected to the portion of the stem that was leader in 1988. 2. Length of current year's growth. 3. Number of leaves.

in 1989. Production of leaves occurred in the upper middle of the unsupported shoot's profile but throughout the majority of the shoot's profile in supported plants (Fig. 3).

Phenology of fence plants—Unsupported and supported shoots in the fence area showed the same seasonal patterns of bud-opening and leaf-shedding (Fig. 4), suggesting that the plants experienced the same length of growing season. However, the stem, petiole, and central leaflet
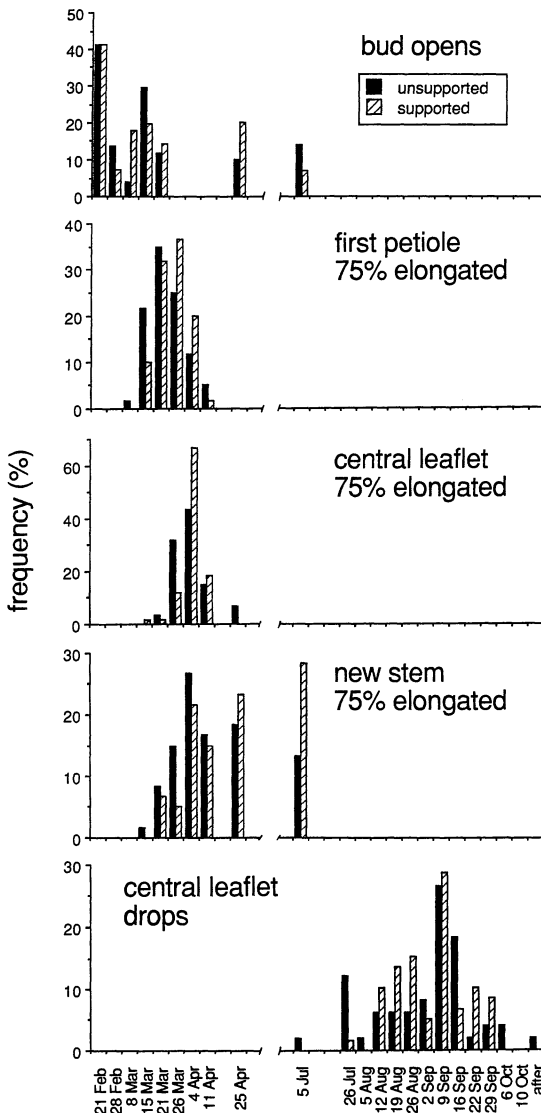
Fig. 4. Frequency distributions of phenological characteristics of unsupported and supported shoots of *Toxicodendron diversilobum* in the field ($N = 12$ unsupported and 12 supported shoots, five growing points/shoot): period when bud scales open; new stem, petioles of first-produced leaf, and central leaflet of first-produced leaf have elongated to $\geq 75\%$ their final length; and central leaflet of first-produced leaf is shed from the plant.

tended to continue elongating longer in supported than unsupported plants (Fig. 4). This may have given supported plants a net shorter growing season than unsupported plants because their leaf area would have had a shorter period to be active.

Elongation rates in the common garden—Extension growth rate of shoots was 25% higher in staked than in unstaked plants, consistent

TABLE 4. *Average values and indices of stem and leaf elongation in the common garden (mean ± SE, N) for stems of one unstaked and one staked individual propagated from each of 19 different source plants of* Toxicodendron diversilobum[a]

	Unstaked	Staked	P
Shoot growth rate (mm/d)[b]	7.6 ± 0.4 (19)	9.5 ± 0.7 (19)	*
Plastochron (d)[c]	4.7 ± 0.2 (76)	3.9 ± 0.3 (75)	*
L_b (%)[d]	75 ± 1 (76)	70 ± 1 (76)	**
i_a (%)[d]	43 ± 1 (76)	46 ± 2 (76)	ns[e]
L_a (%)[d]	56 ± 1 (76)	56 ± 2 (76)	ns
D (d)[f]	−0.3 ± 0.3 (76)	1.2 ± 0.4 (75)	*

[a] ** $P < 0.01$, * $P < 0.05$, ns $P > 0.05$.
[b] 36-d period from 3 April to 6 May 1989.
[c] The time interval between when successive internodes reach 75% elongation.
[d] L_b, i_a, and L_a are the percent elongation of the leaf below, internode above, and leaf above a given internode, respectively, when that internode is 75% elongated.
[e] $P < 0.06$.
[f] The time difference between when the leaf is 75% elongated and the internode above it is 75% elongated.

with the finding that successive internodes reached 75% of their final length more quickly in staked than unstaked plants (first two lines, Table 4).

Leaf elongation was more delayed relative to stem elongation in staked than in unstaked plants. Based on four internodes/plant, when an internode was 75% elongated, the leaf below it was less elongated in staked than in unstaked individuals (L_b, Table 3). The internode above it tended to be more elongated in staked than in unstaked individuals (i_a), whereas the leaf above it was elongated to the same extent in both treatments (L_a).

The internode reached 75% of its final length at about the same time as the leaf below it reached 75% of its final length in unstaked plants, but 1.2 d before the leaf below it reached 75% of its final length in staked plants (D). Again, this shows the delayed elongation of leaves relative to stem in staked compared to unstaked plants.

DISCUSSION

In the uniform environment of the common garden, *Toxicodendron diversilobum* plants with a staked stem did not accumulate more dry weight than did unstaked ones. They had the same biomass allocation to stem, but it was distributed differently in space: staked plants produced taller stems with longer internodes, and had relatively less biomass in stems that

emerged from near their bases. The experimental shoots (those that were staked or unstaked) had the same relative increase in length between 1988 and 1989. Neither in the common garden nor the field was there evidence that supported plants allocated a higher proportion of their biomass or of their annual aboveground productivity to leaf tissue.

In the field, however, supported shoots were much larger than unsupported shoots of the same age, implying that they had a higher relative growth rate. Supported shoots had relatively more new stem growth in the second than the first year of the study, whereas unsupported shoots had less, and this new growth was more skewed toward the tops of supported than of unsupported shoots. Leaves were not present for a longer time on vines than shrubs, so different lengths of growing season cannot explain the higher growth rate of vines than shrubs in the field. The comparison in the field differed from that in the common garden in that I compared shoots in the field rather than entire plants. However, these shoots appeared to grow independently of other shoots, and unlike the case in the common garden, I observed no production of new primary stems at the bases of the fence shoots during this study.

These data do not support the common assumption that vines allocate less biomass to support material than do self-supporting plants (i.e., Monsi and Murata, 1970; Givnish and Vermeij, 1976; Castellanos et al., 1989). Results presented here contrast with the findings in tropical forests that in community-wide harvests, lianas have a higher ratio of leaf to stem biomass than do trees (Ogawa et al., 1965; Putz, 1983). Western poison oak individuals in the vine growth form do not have an inherently higher growth rate than individuals in the shrub growth form, but in the stratified environment of the field, the vines are able to grow more rapidly. This could be due to a variety of factors, such as dissimilar light quality (Lee, 1988) and/or quantity with height (Darwin, 1867) or decreased herbivory with height by ground-based herbivores (Janzen, 1971) such as deer and rabbits. In the latter case, the *apparent* growth rate of vines would be higher than shrubs, because more of the tissue would remain attached to the less-eaten vines than the shrubs.

The often-recognized correlation between high relative growth rate and the vine habit may have more to do with the environments where vines are often found than with constraints of the growth form itself. Vines are common in early to midsuccessional habitats (Darwin, 1867; Carter and Teramura, 1988) and light gaps in forests (Peñalosa, 1983; Caballé, 1984; Putz, 1984). These are habitats that may favor vines for two reasons: most vines are twiners or tendril-climbers (Darwin, 1867; Schenck, 1892; Teramura, Gold, and Forseth, in press), which are necessarily constrained to habitats where there are suitably small plants on which they can climb (Putz, 1984); and vines have high competitive ability (sensu Yodzis, 1978; Küppers, 1985) resulting from the vine ability to capture much space per biomass invested (Wechsler, 1977). Early and midsuccessional habitats are typically rich in nutrients and light, and plants common in high-resource habitats have often evolved high relative growth rates (Grime, 1966; Grime and Hunt, 1975; Bazzaz and Pickett, 1980). The typical high relative growth rates of vines, then, may correlate with the high resource environment in which their growth form tends to live (see Carter and Teramura, 1988), rather than with the constraints imposed by allocation patterns of the growth form itself.

As has been observed for many climbers, the viney *T. diversilobum* leaders showed delayed leaf expansion relative to stem elongation, longer internodes, and higher total elongation than did the shrubby leaders. Retarded leaf elongation relative to stem elongation in climbers (Schenck, 1892; Raciborski, 1900; French, 1977; Ruiz Fernandez, 1987) is thought to be an adaptation to the biomechanical constraints on the leader. In twiners and tendril-climbers, whose leaders commonly circumnutate as a means of encountering support, a leafless (lighter weight) leader can be rotated more easily than can one with large leaves, or alternatively, a longer leafless leader can be rotated with the same amount of work as a shorter leader with leaves (Raciborski, 1900). Circumnutation has not been observed in root-climbers (Darwin, 1867) or scramblers, but nonetheless, as in the present study, French (1977) observed delayed leaf expansion relative to internode elongation in dicotyledonous root-climbers. The delay, however, was not as marked in the root-climbers as in the twiners and tendril-climbers that he studied.

Raciborski (1900) found that twining species whose leaders were deprived of support had delayed leaf expansion relative to that of supported leaders: this is the opposite of the result in *T. diversilobum*. However, Raciborski investigated the possibility that support may cue leaf expansion. In contrast, the *T. diversilobum* study investigated the effect on leaf development of a cue (support) known to induce the climbing habit.

The largest quantitative difference in the

timing of stem and leaf elongation in unstaked and staked individuals of *T. diversilobum* was in the timing of development of the leaf below a 75% expanded internode. In unstaked individuals, the leaf was 75% expanded simultaneously with the internode, whereas in staked individuals, the leaf reached that stage more than 1 d later. This time period is long, considering that the plastochron was 4–5 d in these plants.

In summary, the staking treatment in a common garden did not affect mass growth rates of western poison oak, but it did induce different temporal patterns of leaf and stem elongation. Because the *T. diversilobum* plants compared in this study were unstaked and staked clones from the same source plants, these results show that some aspect of support controls the timing of leaf and stem elongation, even in this conservative case of a root-climber and/or scrambler. In older plants in the field, vines were much larger than same-aged shrubs and also had higher growth rates during the 1-yr interval studied, indicating that some aspect of the field environment allowed the vines to achieve higher growth than the shrubs. This study suggests that the often-reported high growth rates of vines may have evolved in response to habitat constraints, and not to constraints imposed by stem vs. leaf allocation pattern of the growth form itself. Whether such results would be seen in other vine-shrub comparisons is unknown. Continued investigation aimed at understanding the constraints of different growth forms will help explain their patterns of distribution and how these growth forms function in the communities in which they live.

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