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OBSERVATIONS ON FUNCTIONAL WOOD HISTOLOGY OF VINES AND
LIANAS: VESSEL DIMORPHISM, TRACHEIDS, VASICENTRIC
TRACHEIDS, NARROW VESSELS, AND PARENCHYMA

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ABSTRACT

Types of xylem histology in vines, rather than types of cambial activity and xylem conformation, form the focus of this survey. Scandent plants are high in conductive capability, but therefore have highly vulnerable hydrosystems; this survey attempts to see what kinds of adaptations exist for safety and in which taxa. A review of scandent dicotyledons reveals that a high proportion possesses vasicentric tracheids (22 families) or true tracheids (24 families); the majority of scandent families falls in these categories. Other features for which listings are given include vascular tracheids, fibriform vessel elements, helical sculpture in vessels, starch-rich parenchyma adjacent to vessels, and other parenchyma distributions. The high vulnerability of wide vessels is held to be countered by various mechanisms. True tracheids and vasicentric tracheids potentially safeguard the hydrosystem by serving when large vessels are embolized. Many vines and lianas have many narrow vessel elements (often fibriform vessel elements) in addition to wide vessel elements. The narrow vessel elements are held to increase safety. In comparing scandent with nonscandent genera within a family, one finds in some cases that tracheids occur in the scandent species, whereas fiber-tracheids or libriform fibers occur in the nonscandent ones. The same is true of vasicentric tracheids in vining species as compared to nonvining relatives; vasicentric tracheids are so abundant in some families (Passifloraceae) that libriform fibers have been lost partially or wholly. New familial records for presence of vasicentric tracheids include Cucurbitaceae and Polygonaceae, and new generic records include *Antigonon*, *Lycopersicon*, and *Mandevilla*. Various xylem features suggest presence of auxiliary conductive capabilities when main vessels fail. Parenchyma distributions in vines, especially those in which parenchyma surrounds fiber-sheathed vessels, may offer mechanical flexibility in vines, just as presence of wide rays does. However, starch-rich axial parenchyma adjacent to vessels may provide not merely a means of storing to facilitate growth events but, additionally, a way in which hydrolysis of starch could result in movement of sugar into vessels, permitting osmotic entry of water into given areas. Adaptations which seem to lend safety to the hydrosystem are much less in vines and lianas of perpetually moist tropical regions than they are in taxa subject to periods of drought or frost.

Key words: conduction, lianas, tracheids, vasicentric tracheids, vines, xylem, wood anatomy.

INTRODUCTION

Attention has been focused on various types of cambial activity in lianas and vines. This preoccupation led to several large monographs (Schenck 1893; Pfeiffer 1926; Obaton 1960). Relatively little attention has been paid to the cellular composition of the xylem in scandent plants. Various authors have mentioned that vines tend to have unusually wide vessels. While true, this is but one feature of xylem histology of such plants.

In a review of the occurrence of vasicentric tracheids in wood of dicotyledons at large (Carlquist 1985), the prominence both of true tracheids and vasicentric tracheids became evident. Groups of plants with these cell types seem to have entered the scandent habit out of proportion to their numbers in the world flora

at large. In addition, the phenomenon of vessel dimorphism (Carlquist 1981) and presence of fibriform vessel elements are common in scandent species. All of these xylem conditions suggest that scandent dicotyledons may have subsidiary conductive mechanisms which could conduct when the large vessels are disabled (but also, of course, when the large vessels are functional). Scandent dicotyledons are distinctive in the high probable vulnerability of their hydrosystems to failure from air embolisms because of the small number of relatively wide vessels; mechanisms to insure integrity of the hydrosystems must exist, and therefore listing of various histological features relevant to such insurance has been attempted. In this regard, parenchyma presence must be considered. Scandent dicotyledons mostly have wide rays and other forms of parenchymatization which can serve for enhancement of mechanical flexibility. However, starch content and distribution of parenchyma are examined to see if functions other than mechanical flexibility are indicated. Starch storage as a means of providing for flushes of growth is to be expected, but in view of the attention paid in recent years to osmotic enhancement of conduction, one should see if parenchyma distributions suggest this function. Thus far, workers have focused on deciduous trees, in which conversion of starch into sugar can cause rise of sap, as in the sugar maple, when the sugar moves into vessels. However, if this phenomenon exists in deciduous trees, there is reason to believe it could exist and is available for occasional function in other kinds of plants as well.

MATERIALS AND METHODS

Some dried wood samples were used, but because of the interest inherent in function of parenchyma in vines, however, an effort was made to preserve as many samples as possible in liquid. For the purpose of these studies, 50% ethyl alcohol proved a convenient fixative; preservation of fine cytological details was not a requisite. Sections were prepared on a sliding microtome for species with relatively hard wood. However, the larger vessels and highly parenchymatous nature of wood in climbing plants renders standard wood sectioning techniques unsatisfactory. To avoid excessive fracturing of cells, an alternative method (Carlquist 1982a) proved successful. Sections were stained with a safranin-fast green combination in order to contrast parenchyma with tracheary elements and to demonstrate the nature of pits clearly. Macerations were prepared by means of Jeffrey's fluid. Macerations were necessary for determining dimensions of vessel elements and imperforate tracheary elements. In addition, macerations are essential for revealing presence of vasicentric tracheids, since a section of a given narrow vessel element may not reveal perforation plates.

Specimens cited are represented in the herbarium of the Rancho Santa Ana Botanic Garden unless otherwise indicated. A number of specimens (all liquid-preserved) were collected from the living collections of the Los Angeles State and County Arboretum (cited as LASCA). Wood of some commonly cultivated species was collected in Claremont without preparation of accompanying voucher specimens.

Criteria for designation of cells as tracheids are much like those of Bailey (1936); this definition has been discussed earlier (Carlquist 1985), along with definitions of vasicentric and vascular tracheids. Tracheids of any kind are held to have pit size, border diameter, and density approaching those of lateral wall pits of vessels.

Fiber-tracheids have pits which are bordered, but which fall short of tracheid pits in one or more of these three respects. Vascular tracheids are held to be at the ends of growth rings only, and can be regarded as latewood vessels which lack perforation plates; vascular tracheids do not occur intermixed with vessels of various diameters as do vasicentric tracheids. In highly xeromorphic woods with vascular tracheids, the tracheids may occur in earlier portions (e.g., *Salvia*) of a growth ring or throughout the wood (*Loricaria*; some cacti), in which case vasicentric tracheids are said to occur.

ANATOMICAL DATA

Vessel Dimorphism and Vessel Element Morphology

Vessel elements in wood of scandent dicotyledons tend to be notably wide or notably narrow, with relatively few intermediate widths, unlike the normal distribution curve one might expect in a cell population. This phenomenon was designated "vessel dimorphism" in Nepenthaceae (Carlquist 1981); it probably occurs in numerous groups of dicotyledonous vines and lianas and can be seen in the illustrations for wood of various genera, such as *Illigera* (Shutts 1960) or *Calycopteris* (Vliet 1979). Vessel dimorphism is illustrated in the present paper by *Adenocalymma paulistarum* Bur. (Fig. 19).

In vessel dimorphism, the narrow vessel elements may have terminal perforation plates, but similarly narrow fibriform vessel elements with tapered tips and lateral perforation plates may be common. The latter have been reported under other terms, such as "tracheids with perforations" (Mennega 1969). Fibriform vessel elements have been reported in the scandent representatives of the families Combretaceae (Vliet 1979), Convolvulaceae (Mennega 1969), and Passifloraceae (Woodworth 1935; Ayensu and Stern 1964). However, fibriform vessel elements may be found in entirely nonscandent groups with no apparent vessel dimorphism; such groups include *Eriodictyon* (Carlquist et al. 1983) and other Hydrophyllaceae (Carlquist and Eckhart 1984), *Ixanthus* of the Gentianaceae (Carlquist 1984a), certain Loasaceae (Carlquist 1984b), three genera of Polemoniaceae (Carlquist et al. 1984), *Corokia* of the Cornaceae (Patel 1973), and, in Rubiaceae, the genus *Ceratopyxis* (Vales and Babos 1977) and the tribe Anthospermeae (Koek-Noorman and Puff 1983). Fibriform vessel elements are probably somewhat longer, in general, than the wider vessels they accompany. This is not surprising, since in a growth ring of ring-porous dicotyledons, narrow latewood vessel elements are a little longer than the wide earlywood vessel elements in a given specimen (Butterfield 1973).

Vessel Dimensions

Vessel diameter is greater in scandent species than in their nonscandent relatives (Ayensu and Stern 1964; Bailey and Howard 1941a; Carlquist 1975, 1981, 1984b, c, d; Klotz 1977; Vliet 1981; Bamber 1984). Carlquist (1975) reported that vessel elements in a sample of vining or lianoid dicotyledons had relatively moderate lengths. Subsequent studies have demonstrated that scandent species have vessel elements much the same in length as those of related genera and species (Ayensu and Stern 1964; Carlquist 1984b, c, d; Vliet 1981).

Only a few studies have computed number of vessels per mm² in wood of

Fig. 1-4. Wood sections of vines which bear tracheids.—1-2. *Jasminum officinale* (cult. Claremont).—1. Transection; vessels are solitary; all imperforate tracheary elements are tracheids.—2. Tangential section; helical sculpturing is present on vessel; bordered pits present on tracheids.—3-4. *Araujia sericofera*—3. Transection, showing large vessels as well as narrower ones; a few representative

scandent species. When computed, it tends to fall slightly short of the value for other growth forms (Carlquist 1975, 1984c, d; Vliet 1981). However, the conductive area of vessels computed as a fraction of the xylem transection in which they occur reveals that notably wide vessel diameter coupled with moderate vessel density produces a higher conductive area (total vessel area per mm²) in vines than that typical of trees or shrubs (Carlquist 1975, 1984d; Sieber and Kučera 1980; Bamber 1984). These figures do not, probably, include many narrower vessels (which may be mistakenly identified as imperforate tracheary elements in transections). The figures definitely omit true tracheids, vasicentric tracheids, and vascular tracheids. Thus even when one includes only obvious vessels, vines and lianas show conductive area markedly higher than that of their relatives. If between a third and a half of the wood of vines and lianas is composed of vessels, why should the area not be even higher? What are the constraints on formation of conductive tissue in scandent plants?

Tracheids

Scandent taxa belonging to the following families prove to have true tracheids as the imperforate tracheary element type which forms the groundmass of secondary xylem:

Actinidiaceae: *Actinidia* (Metcalf and Chalk 1950).

Apocynaceae: *Alyxia olivaeformis* Gaud. (USw-27099).

Aristolochiaceae: *Aristolochia* (Metcalf and Chalk 1950).

Asclepiadaceae: see discussion of *Araujia* and *Hoya* in the listing of taxa with vasicentric tracheids.

Austrobaileyaceae: *Austrobaileya* (Bailey and Swamy 1949).

Caprifoliaceae: *Lonicera* (Metcalf and Chalk 1950).

Celastraceae: *Celastrus scandens* L. (USw-5811); *Tripterygium* (Metcalf and Chalk 1950); see also *Hippocratea* in listing of taxa with vasicentric tracheids.

Convolvulaceae: *Dicranostyles* (Mennega 1969); *Mina lobata* Cerv. (cult. Claremont).

Dilleniaceae: *Hibbertia* (Dickson et al. 1978); *Tetracera* (Metcalf and Chalk 1950).

Dioncophyllaceae: *Tiphyophyllum peltatum* Airy Shaw (*Baldwin 14178*, US); tracheids in this species were reported as fiber-tracheids by Gottwald and Parameswaran (1968).

Goodeniaceae: *Scaevola oppositifolia* Roxb. (*Carlquist 1386*, RSA).

Hamamelidaceae: *Bucklandia* (Metcalf and Chalk 1950).

Hernandiaceae: *Illigera* (Shutts 1960).

Icacinaceae: scandent genera have tracheids (Bailey and Howard 1941b).

Lardizabalaceae: vining genera (Carlquist 1984d).

Loasaceae: *Fuertesia* (Carlquist 1984b).

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tracheids are indicated by arrows.—4. Tangential section; a few uniseriate rays are present. (Fig. 1, 3, 4, magnification scale above Fig. 1 [divisions = 10 μm]. Fig. 2, scale above Fig. 2 [divisions = 10 μm].)

Fig. 5-8. Wood sections of vines.—5-6. *Trachelospermum jasminoides* Lam. (cult. Claremont), transections.—5. Portion including growth ring terminus ($\frac{1}{4}$ distance from bottom); wide thick-walled vessels evident.—6. Portion near vessel to show vasicentric tracheids; bordered pits evident as darker ellipses among the thick-walled cells which have wall thickness like that of fibers. The row of cells lying to the left of the two pointers and between them are all vasicentric tracheids.—7. *Tacazzea*

Loganiaceae: *Gelsemium* (Mennega 1969).
 Menispermaceae: scandent genera (Metcalfe and Chalk 1950).
 Myrtaceae: see listing below under vasicentric tracheids.
 Nepenthaceae: *Nepenthes* (Carlquist 1981).
 Oleaceae: *Jasminum* (Fig. 1, 2; see also Metcalfe and Chalk 1950).
 Passifloraceae: see listing below under vasicentric tracheids.
 Polemoniaceae: *Cobaea* (Carlquist et al. 1983).
 Rosaceae: *Rosa* (Metcalfe and Chalk 1950).
 Rubiaceae: *Chiococca alba* (L.) C. L. Hitchcock (*Hitchcock 4978*, POM).
 Sabiaceae: *Sabia japonica* Maxim. (*Carlquist 15795*, RSA).
 Saxifragaceae: scandent species of *Hydrangea* (Stern 1978).
 Schisandraceae: *Schisandra* (Bailey and Nast 1948).

To this list one might possibly add Trimeniaceae (Carlquist 1984c), in which the scandent genus *Piptocalyx* has fiber-tracheids with moderate pit borders, whereas the arboreal *Trimenia* has virtually no pit borders on imperforate tracheary elements. Also, some scandent paleotropical Melastomataceae have fiber-tracheids (Vliet 1981). More significantly, one should cite *Gnetum* and *Ephedra*, since they have tracheids in addition to vessels. The scandent habit of some *Gnetum* species is well known, but the fact that there is a truly scandent species of *Ephedra*, *E. pedunculata* Engelm. (Cutler 1939), is not generally appreciated.

Vasicentric Tracheids

A review of vasicentric tracheid occurrence has been offered recently (Carlquist 1985). The genera below are reported to have vasicentric tracheids in that paper, and documentation is supplied there unless otherwise stated:

Ancistrocladaceae: *Ancistrocladus*.

Apocynaceae: *Beaumontia*, and *Trachelospermum* (Fig. 5–6) have vasicentric tracheids, and *Mandevilla splendens* (*Carlquist 15900*, RSA) can be added as a new report for the family.

Araliaceae: *Hedera*.

Asclepiadaceae: *Araujia sericofera* Brot. (cult. Santa Barbara) is shown in Figures 3–4. The wood contains tracheids but no libriform fibers; it may possibly be tracheid-bearing secondarily rather than relictually, as discussed below. Other Asclepiadaceae with vasicentric tracheids cited earlier (Carlquist 1985) include *Asclepias*, *Periploca*, and *Tacazzea* (Fig. 7). Periplocaceae is included here under Asclepiadaceae. *Hoya multiflora* Blume (cult. Claremont) has tracheids as its imperforate tracheary element type and lacks libriform fibers. Although the tracheids in *Hoya* are like those in tracheid-bearing Apocynaceae, the anomaly of its lack of libriform fibers is like that of *Araujia*. *Stephanotis* has vasicentric tracheids (Carlquist 1985), but was misplaced under Apocynaceae in that paper.

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apiculata (LASCA 80-S-801); tangential section; about a third of the axial cells shown are vasicentric tracheids is at center.—8. *Thunbergia laurifolia* Lindl. (LASCA 67-0-674), transection; fibers sheathe vessels but large parenchyma zones (gray) are present. (Fig. 5–7, magnification scale above Fig. 1. Fig. 8, scale above Fig. 8 [finest divisions = 10 μ m].)

Fig. 9-12. Wood sections of Vitaceae.—9-11. *Vitis vinifera* (cult. Claremont).—9. Transection; end of growth ring about $\frac{1}{3}$ distance from top; both wide and narrow vessels are evident; vascular tracheids indicated by arrows.—10. Tangential section; ray at left; at right, vascular tracheids (indicated by arrows) plus axial parenchyma.—11. Portion of transection at end of growth ring; narrowest

Bignoniaceae: *Doxantha*, *Phaedranthus*.

Combretaceae: *Calycopteris*, *Combretum*.

Connaraceae: much of the family (Metcalf and Chalk 1950).

Cucurbitaceae: *Zanonia indica* L. (Hartley 10037, RSA). This represents a new report of vasicentric tracheids for the family. *Zanonia* has secondary growth, and the wood contains both vessel elements and tracheids; the latter are interpreted here as vasicentric tracheids rather than true tracheids for the same reasons as in Passifloraceae, to which Cucurbitaceae is probably closely related.

Fabaceae: *Wisteria* (Fig. 13, 14).

Hippocrateaceae: usually now included in Celastraceae. Mennega (1972) reports vasicentric tracheids in *Hippocratea*, but these cells are not easily separable from the other imperforate tracheary elements in material I have examined (*Hippocratea volubilis* L., MADw-21964). Therefore, *Hippocratea* may be regarded as having either vasicentric tracheids or true tracheids.

Loganiaceae: *Strychnos*, *Usteria*. These genera, although not cited by Mennega (1980) as examples of vasicentric tracheid occurrence, should be included because her descriptions mention both fibers and tracheids together in wood of these genera.

Malpighiaceae: *Stigmaphyllon*.

Menispermaceae: Metcalf and Chalk (1950) mention that enlarged tracheids in *Abuta* and *Tiliacora* may possibly be regarded as vasicentric tracheids.

Myrtaceae: *Metrosideros* in New Zealand has several scandent species. *Metrosideros* has been reported to have vasicentric tracheids by Ingle and Dadswell (1953). In *Metrosideros*, however, vasicentric tracheids are so similar to the cells in the remainder of the wood that one could interpret the genus as having true tracheids rather than vasicentric tracheids plus fiber-tracheids.

Passifloraceae: some Passifloraceae have both libriform fibers and tracheids in secondary xylem, and therefore can be cited as having vasicentric tracheids (Carlquist 1985). Some species of *Passiflora* fall in this category, but others have only tracheids, and therefore can be regarded as having tracheids secondarily (following loss of libriform fibers) rather than relictually. I would use the term vasicentric tracheid for the cells Ayensu and Stern (1964) term fiber-tracheids. The alternative hypothesis, that Passifloraceae have true tracheids, is regarded as less likely here because related families (e.g., Flacourtiaceae, Turneraceae) have libriform fibers rather than true tracheids as their imperforate tracheary element type.

Pittosporaceae: *Billardiera*, *Marianthus*, and *Sollya*.

Polygalaceae: *Securidaca* (without species) was listed by Metcalf and Chalk (1950) as having vasicentric tracheids. I can confirm this on the basis of *S. diversifolia* (L.) S. F. Blake (cult. U.C.L.A. Botanic Garden).

Polygonaceae: in my earlier paper (Carlquist 1985), *Polygonum baldschuanicum*

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tracheary elements are vascular tracheids (indicated by arrows).—12. *Parthenocissus quinquefolia* (cult. Claremont), transection showing terminus of a growth ring; latewood fibers contain starch (below), as do earlywood fibers (above). (Fig. 9–10, magnification scale above Fig. 1. Fig. 11, 12, scale above Fig. 2.)

Fig. 13–16. Wood sections of vines with vasicentric or vascular tracheids.—13–14. *Wisteria sinensis* (LASCA 68-P-29).—13. Transection; earlywood in upper half of photograph; the libriform fibers vary in thickness, forming distinctive bands.—14. Tangential section through latewood; most of the elongate cells are vasicentric tracheids (representative ones indicated by arrows).—15–16. *Bou-*

Regel was noted as having too few tracheids to constitute an example of vasicentric tracheid presence. However, in *Antigonon leptopus* H. & A. (cult. Lawai-kai, Hawaii), vasicentric tracheids are more abundant and this species should be cited, therefore. This represents the first valid report of vasicentric tracheids for the family Polygonaceae.

Ranunculaceae: *Clematis*.

Sapindaceae: *Serjania*.

Solanaceae: *Lycopersicon esculentum* Mill. (cult. Claremont).

Verbenaceae: *Lantana*.

Violaceae: *Agation*.

Vascular Tracheids

Vascular tracheids have been observed in wood of the following scandent species:

Anacardiaceae: *Toxicodendron diversilobum* (T. & G.) Greene (scandent specimen, Claremont).

Nyctaginaceae: *Bougainvillea glabra* Choisy. (Fig. 15, 16).

Vitaceae: *Parthenocissus quinquefolia* Planch. (Fig. 12); *Vitis vinifera* L. (Fig. 9–11).

Starch-bearing Parenchyma Adjacent to Vessels

Starch-rich parenchyma adjacent to vessels was observed in the following taxa (collection data above or in Carlquist 1985 unless otherwise noted):

Basellaceae: *Boussingaultia gracilis* Miers (LASCA).

Bignoniaceae: *Adenocalymma* (Fig. 19) and *Phaedranthus* (Fig. 20). Very likely many other species in the family could be added when studied on the basis of liquid-preserved material. A phenomenon allied to parenchymatization is the presence commonly of septate fibers in vining Bignoniaceae; septate fibers occur in only a few nonvining Bignoniaceae (Metcalf and Chalk 1950).

Fabaceae: *Hardenbergia* (Fig. 17), *Mucuna* (Fig. 18), *Wisteria* (Fig. 13, 14) can be cited; doubtless others can be added when suitable material is studied.

Malpighiaceae: *Stigmaphyllon* (Metcalf and Chalk 1950).

Moraceae: *Ficus pumila* L. (cult. Claremont); doubtless other species could be added.

Polygonaceae: *Polygonum baldschuanicum* Regel (LASCA).

Solanaceae: *Solanum jasminoides* Paxt. (Carlquist 15867, RSA).

Urticaceae: *Poikilospermum* (Bonsen and ter Welle 1983).

Vitaceae: *Parthenocissus* (Fig. 12); *Vitis* (Fig. 9–11).

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gainvillea glabra (cult. Claremont).—15. Transection; ray at left; phloem and vessel-bearing xylem, right.—16. Tangential section through last-formed tracheary elements, which are vascular tracheids (representative ones indicated by arrows). (Fig. 13–16, scale above Fig. 1.)

Fig. 17–20. Wood sections of Fabaceae and Bignoniaceae.—17. *Hardenbergia monophylla* Benth. (LASCA), wood transection; parenchyma bands evident between patches of thick-walled fibers.—18. *Mucuna gigantea* (Stern & Carlquist 1324, RSAw), wood transection; portion of vessel at upper right; at left, axial parenchyma enclosing strands of fibers (representative ones indicated by arrows).—19.

Other Features

In addition to notably wide vessels, scandent taxa of the two families listed below have distinctive patterns of parenchymatization not related to anomalous secondary thickening:

Acanthaceae: *Thunbergia* has abundant parenchyma, but not adjacent to the vessels, which are sheathed by libriform fibers (Fig. 8).

Cactaceae: concentric bands of apotracheal parenchyma occur in stems of *Pereskia aculeata* Mill. (Bailey 1962).

Fabaceae: in *Mucuna* (Fig. 18), vessels are exceptionally wide and thick walled; the axial xylem other than vessels consists of parenchyma in which strands of libriform fibers are embedded.

No special adaptations were observed in taxa of the following families studied: Annonaceae (*Uvaria*); Marcgraviaceae (*Marcgravia*); Melastomataceae (old world scandent species: Vliet 1981); Verbenaceae (*Petreaea*). In the taxa listed for these four families, material studied was not liquid-preserved, and therefore we do not know if starch-rich parenchyma was present or not. Also, note should be taken of the fact that the four families listed grow in frost-free areas where moisture is abundant. The tropical lianas with anomalous secondary thickening likewise occur in habitats free from drought or frost.

FUNCTIONAL SYNTHESIS OF FEATURES OF WOODY DICOTYLEDONOUS VINES AND LIANAS

Wide vessels may be said to compensate for the limited transectional area of stems in scandent dicotyledons. Woody stems which achieve great length while remaining proportionately narrow in diameter, i.e., vines and lianas, appear to do so by expending greater amounts of energy on elongation than on growth in diameter. In so doing, the cylinder of tissue is modified in that more effective water-conducting cells (vessel elements) are produced at the expense of mechanical cells (fibers) in contrast to the situation in self-supporting woody dicotyledons. For example, wide vessels offer low friction and conduct large volumes of water per unit time. However, wide vessels are vulnerable to air embolisms and each such vessel represents a substantial loss to the hydrosystem, if embolism occurs. Vessels in vines may be additionally vulnerable if they are long, as appears to be the case in *Vitis* (Zimmerman and Jeje 1981: note that vessels, not vessel elements are discussed in this connection). Therefore, to the extent that air embolisms are likely to occur, mechanisms which can confer a degree of safety to the hydrosystem can be expected. To be sure, many tropical lianas grow in very moist areas, such as along riverbanks, where water stress and frost never occur, and lack of safety mechanisms in such lianas would not be surprising. Many vines do occur in areas

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Adenocalymma paulistarum Bur. (LASCA 65-S-116) wood transection; narrow vessels present (some indicated by arrows) in addition to libriform fibers. — 20. *Phaedranthus buccinatorius* (cult. Claremont) wood transection; narrow vessels at left; starch-bearing libriform fibers at right (some indicated by arrows). (Fig. 17–19, scale above Fig. 1. Fig. 20, scale above Fig. 2.)

where drought or frost can be moderate, but vines are absent in areas of extreme drought and cold.

Vasicentric Tracheids and True Tracheids

Vasicentric tracheids and true tracheids offer ideal subsidiary conductive systems in case of embolism of the vessels of a woody dicotyledon (Carlquist 1985). In scandent dicotyledons, the loss caused by embolism of all of the major vessels would be severe, and might be tolerated only if the vessels should be cleared of embolisms in a brief time. If only a portion of the vessels is embolized, a subsidiary conducting system formed by vasicentric tracheids or true tracheids could still be valuable because three-dimensional rerouting of the water conduction pattern would not be necessary, inasmuch as the tracheids adjacent to a vessel, not ones farther away, can serve.

Although remedy of vessel failure is dramatic, and does occur to a certain extent in certain plants (Zimmermann 1983), the prime function of structural adaptation in wood can be held to be prevention of failure—a relatively imperceptible process—rather than mechanisms for repair of the failure. Repair of vessel failure in vines is as yet virtually unstudied. We know that positive pressures occur in xylem in late winter in *Vitis* (Scholander et al. 1955), and this mechanism could theoretically expel air from vessels, but we do not know whether this is a general mechanism in vines or not.

During the earlier survey of occurrence of vasicentric tracheids and true tracheids (Carlquist 1985), the probable role of these structures in vines as well as in dryland shrubs became apparent. Because no three-dimensional rerouting of the conductive pathways would be required in the case of vessel failure, water supply to leaves would not be jeopardized and evergreen plants could retain foliage despite temporary drought. Vascular tracheids do not have the same capability as do vasicentric tracheids. Because vascular tracheids are formed at the end of a growth ring, they can safeguard water supply to a stem and to cambium adjacent to the vascular tracheids, but probably not to each leaf; thus, occurrence of vascular tracheids in *Toxicodendron*, *Parthenocissus*, and *Vitis*, all deciduous, is understandable. *Bougainvillea* forms vascular tracheids as each cambium ceases activity. However, several cambia are formed annually in *Bougainvillea*, so functionally the vascular tracheids are scattered adjacent to vessels at numerous points in the stem and thereby have a distribution much like that of vasicentric tracheids in a plant with normal cambial activity.

Selective Value of Tracheids

In my 1985 survey, the systematic and geographic distributions of species with true tracheids and those of species with vasicentric tracheids were stressed. One can interpret presence of true tracheids as relictual, but presence of vasicentric tracheids probably represents a relatively recent series of innovations. In most families in which vasicentric tracheids occur, only a small proportion of the genera have these cells, and these few genera are most commonly in temperate, often dryland areas. Thus, we can infer a relatively strong selective value for vasicentric tracheids. The taxonomic groups listed above for various kinds of adaptations to be found in scandent dicotyledons represent by far the majority of families in

which a climbing habit may be found, and relatively few families in which this occurs have been omitted, I believe. The fact that such a high proportion of the families in which a climbing habit occurs have either true tracheids or vasicentric tracheids suggests that occurrence of either of these cell types preadapts a phylad for entry into a scandent niche. In fact, if one compares scandent with nonscandent taxa within particular families, one finds that in some families, the scandent genera have tracheids, whereas the nonscandent genera have fiber-tracheids or libriform fibers, suggesting preferential retention of the tracheid. This is true in *Hernandiaceae* (Shutts 1960), *Icacinaceae* (Bailey and Howard 1941b), and *Lardizabalaceae* (Carlquist 1984d). This also holds true if we compare the scandent family *Schisandraceae* (Bailey and Nast 1948) with a sister-family which is nonscandent: *Illiciaceae* (Carlquist 1982b).

Vasicentric tracheids appear increased in abundance in vines when one compares them to nonvining relatives. Arboreal *Passifloraceae* and some scandent ones still have libriform fibers, but libriform fibers can be hypothesized to have vanished in some species of *Passiflora* (Ayensu and Stern 1964). Thus, tracheids are secondarily present in the fiber-free species of *Passiflora*, which therefore must be said to have vasicentric tracheids rather than true tracheids. The illustration of *Clematis* offered earlier (Carlquist 1985) shows a state of near extinction of libriform fibers when one keeps in mind the relative abundance of libriform fibers in nonscandent relatives (*Berberidaceae*). *Araujia* (Fig. 3–4) of the *Asclepiadaceae* is a possible example of secondary tracheid presence, and *Gelsemium* (*Loganiaceae*), and even *Lardizabalaceae* are worthy of reexamination on this basis. The enhanced prominence of tracheid or vasicentric tracheid presence in scandent groups is clear in any case.

Narrow Vessels

The role of narrow vessel elements, some of which qualify as fibriform vessel elements, cannot be discounted because these are so abundant in most scandent woody dicotyledons, even though not mentioned specifically above. In many vining species, narrow vessels outnumber wide vessels by far. For example, in *Cardiospermum hirsutum* Willd. (LASCA) of the *Sapindaceae*, *Polygonum baldschuanicum* (LASCA) of the *Polygonaceae*, and *Solanum jasminoides* (Carlquist 15867) of the *Solanaceae*, narrow vessels outnumber wide vessels by far, and even a few vasicentric tracheids may be found. (Because the number of vasicentric tracheids in these species is so limited, they were not included in the listings above). In *Turbina stenosphon* (LASCA 80-S-56) of the *Convolvulaceae*, wide vessels are few, tracheids are relatively few, and by far the majority of the tracheary elements are fibriform vessel elements. Narrow vessels certainly confer considerable potential safety, and we should do well to emphasize not merely the wide vessels of vines, but the abundance of narrow ones. As the species just named illustrate, narrow vessels can grade into vasicentric tracheids, and this suggests a possible mechanism for origin of vasicentric tracheids in scandent dicotyledons: evolutionary shift from production of wide vessels plus narrow vessels together with a very few vasicentric tracheids, to production of wide vessels plus few narrow vessels and more numerous vasicentric tracheids. Certainly transitional groups with respect to vasicentric tracheid presence are to be expected. The abundance of narrow vessels in scandent dicotyledons is reminiscent of abundance of late-

wood vessels in nonscandent taxa, a phenomenon which is recognized in designation of the Type VIII growth ring (Carlquist 1980).

Helical Sculpture in Vessels

Helical sculpture (helical thickenings) is common in woody temperate plants, evidently chiefly those of dry habitats (Webber 1936) and cold areas (Carlquist 1982b). Vines and lianas tend not to occur in areas of extreme cold or drought, but they do occur where these risks are occasional and moderate. Helical thickenings occur in vessels of *Clematis vitalba* L. (Sieber and Kučera 1980); several genera of Lardizabalaceae (Carlquist 1984d); *Jasminum officinale* L. (Fig. 2); and *Solanum jasminoides* (Carlquist 15867). These examples are few enough so as to constitute exceptions. *Clematis vitalba* and the Lardizabalaceae with helical thickenings grow in areas which experience frost, and the other two species are drought-tolerant.

Parenchyma

If presence of mechanical tissue is minimized in scandent dicotyledons in favor of conductive tissue, why should not parenchyma be present only minimally? Evidently there are reasons for appreciable parenchyma presence.

A function in enhancing stem flexibility has been ascribed to parenchyma presence, especially in those stems in which anomalous cambial activity results in sheathing of vessel groups with parenchyma. However, vines with normal cambial activity typically have wide rays which are extensions of primary rays and which segment the fascicular xylem into portions. Several workers have inferred that such parenchyma distributions permit vessel-bearing segments to twist without fracture, much like strands in a cable; damage to phloem may also be minimized in such a view (Schenck 1893; Haberlandt 1914; Carlquist 1975; Sieber and Kučera 1980). Parenchymatous tissue could conceivably function in regeneration, compensating for conductive tissue lost by injury. While this last-named function is not ruled out, it seems less significant because evolution tends to favor prevention of damage over recovery from damage, and the embolism-vulnerable nature of vine xylem means that if seriously damaged, the hydrosystem would fail and regeneration of tissues would be of little avail.

The pattern of parenchyma seen in *Thunbergia* (Fig. 8) is not often cited, since it results from a normal cambium, not from anomalous secondary thickening. The tendency in *Thunbergia* for segmentation of the xylem into numerous groups containing several vessels each sheathed by fibers, is evident. This pattern may help minimize damage to the hydrosystem. The thick walls of vessels of *Mucuna gigantea* DC. (Fig. 18) are noteworthy and may represent a means of minimizing vessel fracture; thick-walled vessels can be seen commonly in other scandent taxa as well (Fig. 5, 6, 17, 19, 20). Stems of *Mucuna gigantea* have optimal potential flexibility, for libriform fibers occur as strands, each strand surrounded by parenchyma (Fig. 18). Concentric parenchyma rings (e.g., *Pereskia aculeata*, Bailey 1962) may enhance flexibility, but since *Pereskia* is to some extent a succulent, a water-storage function is certainly conceivable.

Some vining dicotyledons in which starch-storing parenchyma is prominent grow in flushes, so that storage of photosynthates preparatory to rapid growth can

be envisioned, as in *Wisteria sinensis* Sweet (Fig. 12), which is deciduous, and *Phaedranthus buccinatorius* (DC). Miers, which is evergreen. However, some of the vining species studied in which starch presence is notable grow and flower continuously: *Solanum jasminoides*, for example. Perhaps a further function of parenchyma is operative, as noted in the following examples.

Scholander et al. (1955) showed positive xylem pressures in the grapevine in late winter, although they did not identify the cause of this pressure. Plumb and Bridgman (1972) conceived the idea that carbohydrates form a mechanism for the ascent of sap; hydrolysis of starch into sugar, movement of the sugar into the water of a vessel, and osmotic pulling of water into that vessel portion, are what they envision. This idea has been taken up by others (Sauter 1972, 1980; Czaninski 1977). Those authors based their ideas on the well-known rise of sap in the sugar maple. However, this idea may be operative not merely in temperate trees but in tropical ones (Braun 1983) and in herbaceous perennials (Carlquist and Eckhart 1984). If this idea is applicable to scandent dicotyledons, it could explain how water in xylem could be under pressure, as in the observations of Scholander et al. (1955). The idea may be applicable to situations other than pressure in late winter in the grapevine. If wide vessels in a vine were damaged by air embolisms, movement of sugars into narrow vessels left intact could restore the conductive system, providing even a mechanism for clearing of the wide vessels of air. Because the cambia of vines yield derivatives slowly, replacement of faulty vessels by new ones is not a feasible mechanism. In fact, probably much of the hydrosystem of a vine is intact at any one time: Sieber and Kučera (1980) have shown two to three years of xylem function in *Clematis vitalba*, despite the fact that this species experiences frost annually. One can hypothesize that maintenance of the hydrosystem failure-free or else rapid removal of air embolisms must be basic to the functioning of the hydrosystem of a vine or liana. Axial parenchyma may be worthy of study as the source of a mechanism for prevention of hydrosystem failure in these kinds of plants.

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