

# Diversity of Mechanical Architectures in Climbing Plants: An Evolutionary Perspective

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## ABSTRACT

Mechanical architectures of a wide range of climbing plants are reviewed from a wide phylogenetic range and evolutionary contingencies. They include an herbaceous lycopod (Lycopodiaceae), a woody tropical liana (Apocynaceae), temperate climbers, herbs and shrubs (Ranunculaceae), and two representative climbing palms (Arecoideae, Calamoidae). Trends in mechanical properties during development are reviewed and interpreted via changes in anatomical development of the stem and type of connection to host supports. The results indicate that there are some biomechanical features common to diverse climbing plants including (1) phases of relatively rigid stem growth where the climbing stem has to span between supports and (2) a mechanism to achieve greater compliancy towards the base or at points where the slender climbing stem is at risk from excessive mechanical stress. Evolutionary contingencies such as basal plesiomorphic constraint, complexification, simplification and developmental loss can drastically influence ways in which different plants have evolved different biomechanical climbing architectures. Two key

developmental features controlling the biomechanics of the climbing stem are (1) the presence/absence of secondary growth and (2) the number, complexity and coordination of development of primary or secondary tissues with varying mechanical properties. Recent research has suggested that evolution of specialized climbing architectures can canalize subsequent evolution of alternative growth forms. The results suggest that the origin and *type* of climbing architecture can be heavily influenced by ancestral growth forms and architectures. Despite the extremely complex patterns of plant growth form evolution involving “escapes” to and from more specialized or simpler bauplans, selective pressure towards non-self-supporting growth forms is a remarkably persistent and iterative feature of growth form evolution in land plants.

**Key words:** Bauplan; Biomechanics; Climbers; Diversity; Evolution; Growth form; Secondary growth

## BIOMECHANICS OF GROWTH FORMS

Biomechanical properties of the plant stem can change markedly during growth from young development at the apex to the load-bearing parts of

more basal, older parts of the plant. Different growth forms such as trees, shrubs, herbs, semi-self-supporters and climbers can show radically different trends in mechanical properties from young to old stages of development (for example, Niklas 1992; Speck and Rowe 1999). Such trends are often finely tuned to the mechanical demands required of different growth forms and at different stages in the development towards the adult plant (Gartner 1991; Putz and Holbrook 1991; Rowe 1996; Rowe and Speck 1997; Gallenmüller and others 2001; Isnard and others 2003a). In self-supporting plants, young apical parts of the plant body are relatively compliant and older stages are relatively stiff. One aspect of this developmental variation is linked to the fact that young compliant stages can deform under high wind pressures and reduce bending and torsional moments on supporting parts of the plant body that comprise stiffer tissues (for example, Speck 2003). An opposite situation is seen in many climbing plants where young axes are relatively stiff and adapted to traversing spaces between potential supports and older stages that can be highly compliant and protect the relatively slender mature stem from excessive stresses caused by movement and even breakage of host supports.

Underlying these basic mechanical features of different plant growth forms is the fact that a plant's anatomical organization and development are nearly always by necessity a "design compromise" combining several often conflicting functions (Niklas 1992). Mechanical support and hydraulic supply are two essential and potentially conflicting functional requirements, particularly among self-supporting growth forms. Tissue components comprising older stems of self-supporting plants must supply mechanical support as well as hydraulic efficiency. Mechanical support is best provided by thick-walled stiffening tissues with narrow cell lumens, whereas hydraulic supply is most efficient with conductive tissues that have wide lumens. The plant stem must somehow combine both. This conflict in function between hydraulics and mechanics has probably operated at many levels during the evolution of different plant growth forms (Rowe and Speck 2003). Climbing plants, to some extent, evade this issue by foregoing the need for supporting the entire plant from the base.

## EVOLUTIONARY CONSTRAINTS AND GROWTH FORM EVOLUTION

In addition to requiring different mechanical properties during the life span and accommodating

conflicting functions, a given plant group or species can only act within the developmental potential it has evolved with. Overall body size, stem diameter and height are strongly dictated by different evolutionary constraints between major groups (Niklas 1993a, b, 1994). Bryophytes have never produced large bodied forms; extant sphenopsids are restricted to herbaceous growth forms and lycopsids are confined to herbaceous or epiphytic growth forms, as are most filicopsids, although arborescent representatives were common in all three groups in the fossil record. The ability to produce large-bodied stems and variable growth habits might depend on the range and repertoire of different tissues and whether growth and development are confined to primary or secondary growth (Niklas 1997; Rowe 2000; Rowe and Speck 2003). The early evolution and radiation of plant architectures has been shown to involve a series of hydraulic and mechanical innovations including the appearance of hydrostatic structures depending on turgescence living cells (Speck and Vogellehner 1994; Bateman, and others 1998; Rowe 2000; Rowe and Speck 2003), the appearance of a hypodermal sterome in which an outer ring of thicker walled fiber-shaped cells was placed towards the outside of the stem and contributed significantly to the stiffness of the stem (Niklas 1992; Speck and Vogellehner 1994) and the appearance of lateral meristems producing secondary mechanical and/or hydraulic tissues (Rowe and Speck 2003; Speck and Rowe 2003; Speck and others 2003).

The evolutionary appearance, conservatism, modification, complexification and simplification of these innovations underpin the potential mechanical architectures of different plant groups. Changing selective regimes might favor increased body size (trees) or large-bodied climbers (lianas) or reduction and simplification from larger-bodied growth forms to shrubs, herbs or vines. Some plant groups such as bryophytes and herbaceous lycopsids might show significant levels of canalization in terms of mechanical and hydraulic architecture, which originate from constraints appearing early in the evolution of the groups.

Both extant gymnosperms and angiosperms show considerably derived mechanical architectures over basal clades, but nevertheless show complex patterns of structural innovation, complexification and simplification. Such changes might radically influence the subsequent structural evolution and potential range of size, shape and growth form. Highly variable patterns of growth form evolution have been relatively little investigated using quantitative biomechanical ap-

proaches. Effects of canalization and developmental constraints resulting from profound changes in growth form have been investigated recently for a number of extant groups including the evolutionary pattern of herbs, lianas and trees in the Aristolochiaceae among basal angiosperms (Speck and others 1997; Speck and Rowe 2003), the likely influence of herbaceous and rhizome-forming ancestral bauplans on the radiation of growth forms in the Ranunculaceae (Isnard and others 2003a), and the evolution of shrub-like growth forms in lianoid Asclepiadaceae (Civeyrel and Rowe 2001; Rowe and Speck 2003; Speck and others 2003). Many plant clades show profound change or simplification of a more complex bauplan and mechanical architecture (Bateman 1996). In angiosperms one of the most ecologically and evolutionary significant examples is represented by the appearance of monocotyledons with predominantly herbaceous growth forms and its subsequent radiation to include tree-sized and climbing forms without the mechanical and hydraulic potential conferred by a secondary vascular cambium.

In the following account we discuss four examples of how mechanical properties change during growth in plants showing widely differing evolutionary constraints. We will explore how trends in primary and secondary growth contribute to the overall mechanical properties of the growth form. The four examples have been chosen among recent and ongoing research projects and sample (i) An archetypal bauplan representing a herbaceous scrambling to climbing lycopod *Lycopodiella cernua*; (ii) a derived angiosperm climber showing a large complement of primary and secondary developmental features (*Condylocarpon guianense*, Apocynaceae); (iii) an angiosperm climber and related herb and shrub derived from herbaceous and rhizome-forming basal groups (*Clematis*, *Xanthorhiza*, Ranunculaceae); (iv) climbing "lianoid" monocotyledons representing large-bodied, climbing growth forms without a secondary vascular cambium (*Calamus tetradactylus*, *Desmoncus orthacanthos*, Palmae).

All four examples show some degree of climbing behavior and mechanical specialization. We will explore how such forms produce a variety of climbing mechanical architectures resulting from a wide range of evolutionary constraints, from a primordial hypodermal organization differing little from some of the earliest land plants, to some of the most vegetatively derived lianoid angiosperms and to plants that have radiated from simplified angiosperm bauplans.

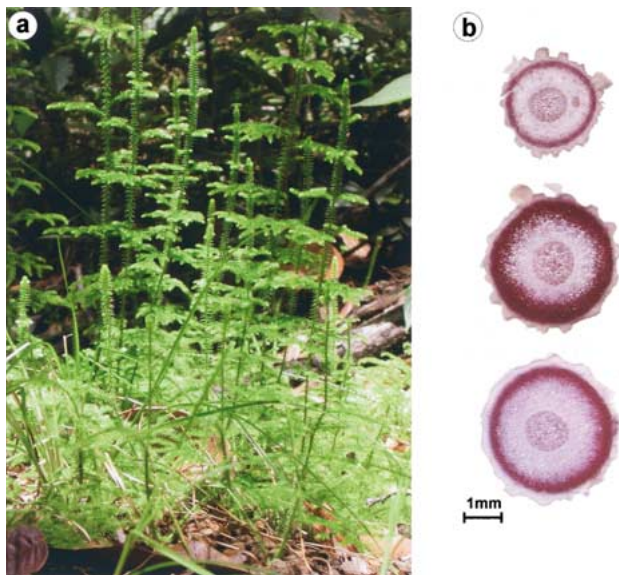
## MATERIALS AND METHODS

New mechanical data presented here for *Xanthorhiza*, *Desmoncus* and *Calamus* are based on 3- and 4-point bending experiments. The structural Young's modulus  $E_{str}$  is calculated after applying a series of weights to stem and rhizome segments (Rowe 1996; Gallenmüller and others 2001; Isnard and others 2003a). For the climbing Palms *Calamus* and *Desmoncus*, an experimental approach was used to find out the relative mechanical contribution of the inner stem and outer leaf sheath to bending mechanical properties. In this case, segments of the axis were measured before and after removing the leaf sheath from the axes tested.

This paper also focuses on correlations of the geometric properties of principal tissues in terms of axial second moment of area with the structural Young's modulus of the stem. New data are presented for *Lycopodiella cernua* and *Condylocarpon guianense* based on the contribution of principal tissue types to the axial second moment of area of the stem. Stem cross-sections were stained in 6% phloroglucinol in 90% ethanol after soaking in 25% HCl, to stain lignified tissues red (thin sections) or polished with fine grade abrasive discs (large woody stem segments) to enhance outlines of major tissue types. Entire cross-sections were then digitized and main tissues were outlined using appropriate color thresholds with the Image analysis software "Optimas" (Media Cybernetics, Inc., Silver Spring, MD USA). The axial second moment of area of each entire cross-section as well as that of each individual tissue were calculated by a program kindly supplied by J. Schmidt (University of Freiburg).

## ARCHETYPAL BAUPLAN WITH PRIMARY GROWTH AND MECHANICAL HYPODERM

*Lycopodiella cernua* belongs to a basal clade of predominantly terrestrial herbaceous Lycopodiaceae and is distributed worldwide within the tropics. It comprises a relatively simple growth form combining upright axes bearing lateral branches and horizontal rhizome-like axes (Figure 1a). Upright climbing branches have been observed to reach over 2 meters in length in dense surrounding vegetation. The plant most often forms clonal mats of horizontal and upright axes up to over a meter in height. Vertical axes often become unstable and recline on the mat of horizontal axes and other fallen stems. The biomechanics of the stem is reviewed with data quantifying the mechanical importance of each tissue in these relatively simple mechanical architec-



**Figure 1.** (a) *Lycopodiella cernua* growing in forest margin in French Guyana, S. America. Upright axes are branched and reach lengths of 0.7-1.2 m as self-supporting stems and up to 2.5 m as climbers and scramblers. Axes interact and become supported by the surrounding vegetation and are partially interlinked with the supporting host plants via the lateral branches. (b) Transverse sections of proximal (lower), median (middle) and apical (upper) stem segments of *L. cernua*. Sections are stained with phloroglucinol / HCl in 95% alcohol which stains lignified mechanical tissues red. The ring of sclerenchyma tissue (mechanical hypodermal sterome) increases in thickness from the basal to median part of the stem and diminishes towards the apex. This has a strong influence on the mechanical properties along upright stems in terms of the contribution of the sclerenchyma to the axial second moment of area and the influence of this on the stiffness along the stem.

tures. In terms of anatomy, the hypodermal organization resembles archetypal organizations observed in Devonian Euphyllophytes such as *Psilophyton* and *Zosterophylls* such as *Zosterophyllum* (Speck and Vogellehner 1994) as well as later carboniferous lycopsids such as *Selaginellites* (Rowe 1988) and *Oxroadia* (Bateman 1992).

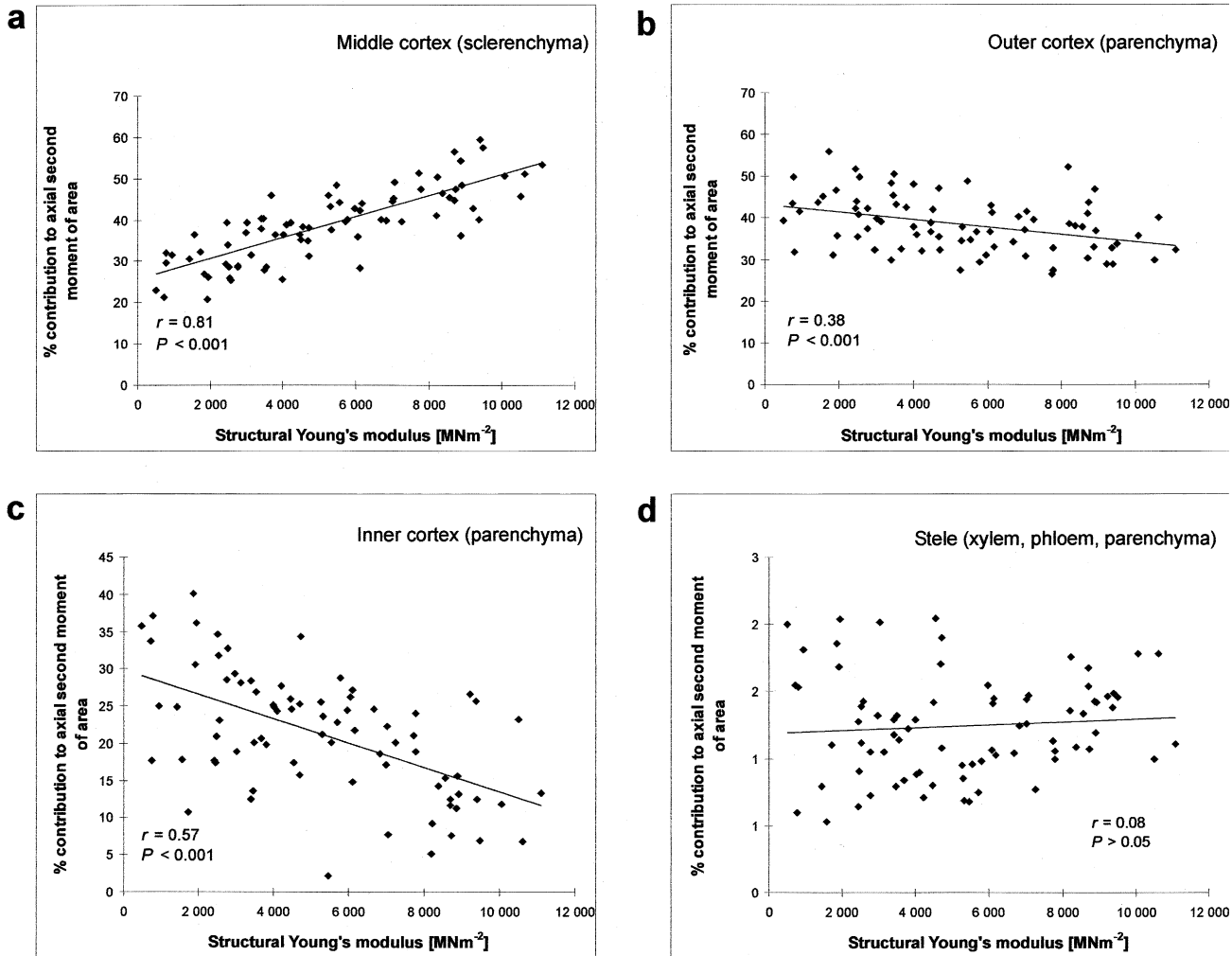
## Mechanical Architecture

The overall mechanical architecture of *Lycopodiella* shows a characteristic pattern. Firstly, mechanical properties of the upright stems are significantly stiffer than horizontal axes both in terms of flexural stiffness and structural Young's modulus (Rowe and Speck 1997, 1998). Upright axes consist of a central actinostele, a band of inner parenchymatous cortex, a middle cortical layer of sclerenchyma and an outer

zone of parenchymatous photosynthetic tissue including slightly swollen microphyll bases (Figure 1b). Relative contributions of each tissue to the axial second moment of area ( $I$ ) of the entire stem indicate that the contribution of the sclerenchyma to axial second moment of area correlates well with the changes in structural Young's modulus ( $E_{str}$ ) of the stem. The tissue varies from 20-60% with values of structural Young's modulus of 500-11,000 [ $\text{MNm}^{-2}$ ] (Figure 2a). Both outer (Figure 2b) and inner (Figure 2c) cortical parenchyma show slight negative correlations with  $E_{str}$  and relatively high contributions of these tissues to second moment of area of the entire stem. The relatively dense tissues of the stele, including thick-walled primary xylem elements, contribute little to  $I$  (below 2%) and is not correlated with changes in  $E_{str}$  (Figure 2d).

Contributions of each tissue along two representative individual stems indicate that the contribution of the ring of sclerenchyma to  $I$  follows concurrently the increase and then decrease of  $E_{str}$  from the base to the apex (Figures 3a,b). The contributions of both the inner and outer parenchymatous cortex mirror those of the sclerenchyma ring and the trend in  $E_{str}$ . The development of the sclerenchyma ring also changes in terms of the density of the fiber cells as well as the thickness of the band of tissue itself (Figure 3c). Changes in density correspond well to changes in  $E_{str}$  of the entire stem. Very similar trends are seen for an unstable upright axes (Figure 3a) and a longer partially scrambling or climbing axis (Figure 3b), which has established itself in the surrounding vegetation. Interestingly the scrambling axis shows a longer phase of high contribution of sclerenchyma tissue and high  $E_{str}$  corresponding to the segment of stem scrambling through supporting neighboring plants.

*Lycopodiella cernua* can produce self-supporting stems up to approximately 0.7-1.2 m in length, above which they become unstable and non-self-supporting. The mechanical architecture is relatively simple and stiffness is conferred to the stem via a ring of sclerenchyma tissue positioned in the mid region of the cortex. The thickness of the sclerenchyma ring is modified along the stem. Basal parts of the plant show lower values of  $E_{str}$  as a result of a limited development of sclerenchyma. These properties confer a lower stiffness at the base of the plant which is not typical of self-supporting plant growth forms. The higher compliance at the base of upright stems is similar to that of the flexible horizontal rhizome and possibly related to the fact that early growth of upright stems often occurs under sheltered conditions within a basal mat of



**Figure 2.** *Lycopodiella cernua*, bivariate plots of contributions of principal tissues to the axial second moment of area I and structural Young's modulus  $E_{\text{STR}}$ : (a) middle cortex (sclerenchyma), (b) outer cortex (parenchyma), (c) inner cortex (parenchyma), (d) stele (primary xylem, phloem, parenchyma). A strong positive correlation is observed for the % contribution of the middle sclerenchymatous cortex, while other cortical tissues show slightly negative correlations despite relatively large contributions to axial second moment of area. The stele shows a very low contribution to axial second moment of area and does not influence stem stiffness. Data is based on 3- and 4- point bending tests presented elsewhere (Rowe and Speck 1997, 1998) on segments from 10 upright to scrambling and rhizome-like stems; measurements of second moments of area are based on digitized images of entire stained sections in TS as seen in Figure 1b.

vegetation (Rowe and Speck 1997, 1998). Such conditions may have invoked a thigmomorphogenetic response during development resulting in the production of less sclerenchyma tissue than more distal segments of stem emerging from the basal vegetation. Whatever the underlying cause of the basal reduction in  $EI$  at the base of upright stems, this is critical for the height and posture of upright stems. This basal compliance probably allows vertical stems to recline to a procumbent orientation if a support has not been located avoiding fracture of the stem and hydraulic supply and thus continue growth as a procumbent axis.

## HIGHLY DERIVED BAUPLAN WITH SECONDARY GROWTH

*Condylocarpon guianense* (Apocynaceae) is a common liana in the lowland rainforest of French Guyana in South America and has served as a developmental model for studies on the biomechanics of lianas over recent years (Rowe and Speck 1996; Rowe and Speck 1998; Speck and Rowe 1999; Hoffman and others 2002). It is a woody liana reaching diameters of up to 30 cm and that commonly reaches the canopy with lengths of 30-40 m by twining on the trunks and

branches of host plants. The biomechanical and overall developmental details of this plant have been presented elsewhere (Rowe and Speck 1996; Hoffman and others 2002). Like many tested lianas, young individual plants and the leaders or searchers of mature plants show relatively high values of structural Young's modulus and older wider stems show a significant drop in  $E_{\text{str}}$  by up to 95%. In the following section we outline the detailed developmental transitions in anatomy that underline the profound changes in mechanical properties of the stem and branches.

## Mechanical Architecture

There are significant changes in all three principal tissue contributions to axial second moment of area during development when plotted against structural Young's modulus (Figure 4). Both the cortex and contribution of a compliant, lianoid wood type show significant negative correlations with structural Young's modulus. Contribution of the cortex to  $I$  changes from just over 50% in young stages to between 70 and 80% (Figure 4a) corresponding to a change in  $E_{\text{str}}$  from a maximum of 5000 down to 260 [ $\text{MNm}^{-2}$ ]. The early part of the development of the plant, corresponding to a high value of  $E_{\text{str}}$ , is marked by the development of a cylinder of dense wood, which reaches a maximum contribution to  $I$  of 40-46% (Figure 4b). After a certain point of development is reached, which is probably linked to the attachment to a host support, the vascular cambium ceases to produce dense wood. A second type of wood develops (lianoid wood), which has densely arranged, wide diameter vessels and less dense interstitial fibers. This is clearly seen in the drop in contribution of dense wood in stem segments with values of  $E_{\text{str}}$  less than 2000 [ $\text{MNm}^{-2}$ ] and where the contribution of dense wood to  $I$  drops below 12%. The production of lianoid wood increases at this point and this is correlated with a further drop in  $E_{\text{str}}$  of the stem (Figure 4c). Correlation of lianoid wood is relatively scattered because the onset and volume of lianoid wood can be variable, presumably related to differing mechanical and hydraulic constraints of different parts of the plant body.

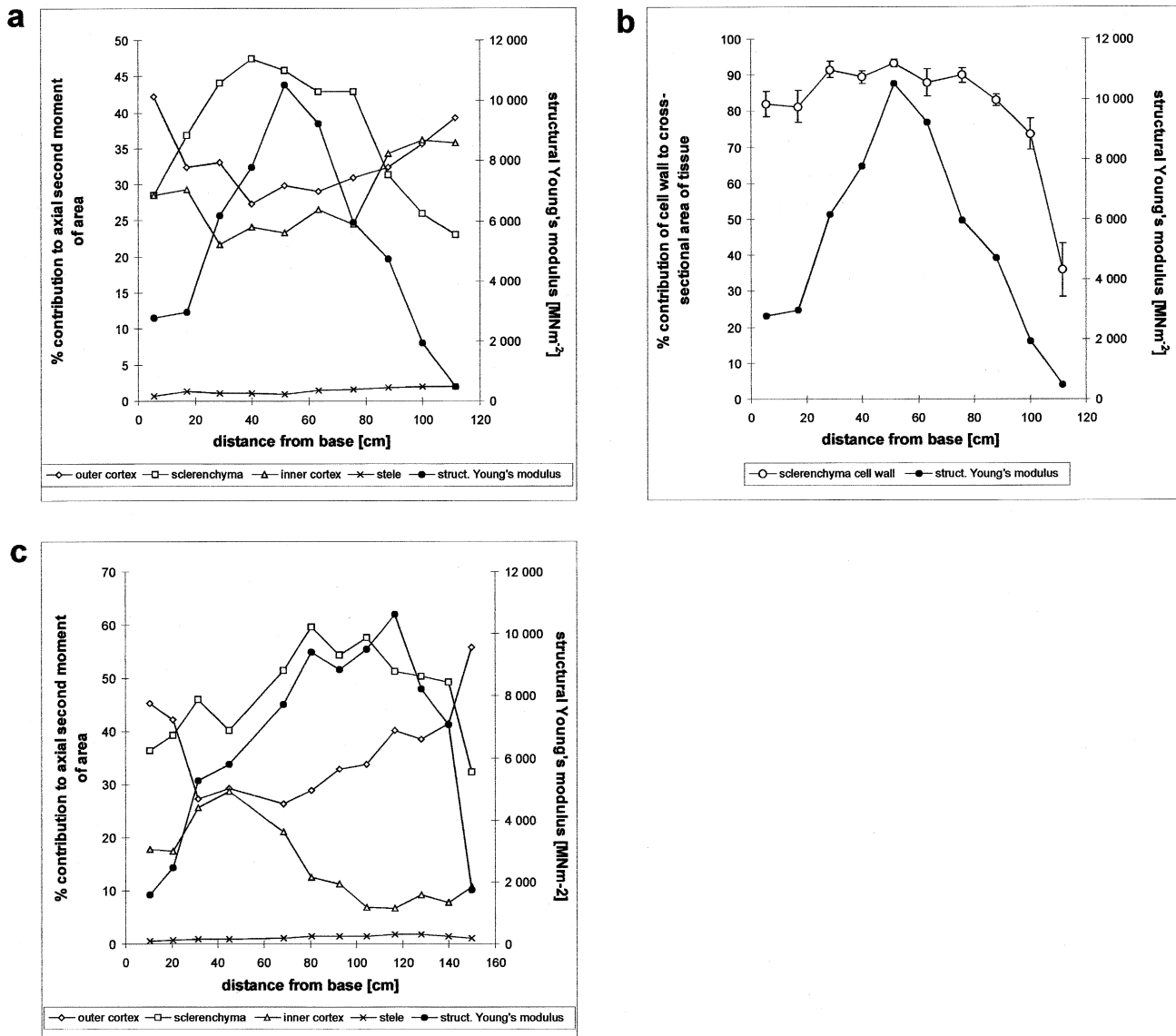
These data correspond well with the inferred mechanical constraints along the plant body. The apical part of the crown comprises searchers with relatively low contributions of outer compliant cortex to  $I$  (55%), relatively high levels of dense wood with a few scattered narrow diameter ves-

sels, small wood rays and little or no compliant lianoid wood (Figures 5a, 6a,b). Such stems have relatively high values of  $E_{\text{str}}$  and are positioned in the canopy near to the apex of the plant some 35-40 m from the base (Figure 5b). Their relatively stiff mechanical properties are consistent with their function as searchers spanning spaces between host supports.

After approximately 5 meters below the canopy the value of structural Young's modulus drops to levels below 500 [ $\text{MNm}^{-2}$ ], concomitant with contributions of outer cortex and lianoid wood (Figs. 6c,d) which stabilize at levels approximating 70 and 30%, respectively (Fig. 5). Approximately 5 meters below the crown the contribution of the remaining dense wood diminishes to insignificant levels compared with newly formed tissues.

The development of lianoid wood shows further cambial variation in older basal parts of the stem and becomes lobed (Figures 6e-g). This organization probably engenders even greater compliance in bending and torsion and lower structural Young's moduli in oldest stages, which can drop below 300 [ $\text{MNm}^{-2}$ ].

From a developmental perspective, *Condylocarpon* represents an example of a derived angiosperm in which secondary growth produces a complex pattern of mechanical properties and a specialized climbing growth form. Secondary development is an essential element of the change in mechanical properties where high stiffness is conferred by a cylinder of dense wood for young searchers and after attachment, increasingly larger amounts of compliant lianoid wood are produced by the same cambium (Rowe and Speck 1996; Hoffman and others 2002). Further changes and compliance are brought about by geometric dissection or lobing of the already compliant wood cylinder, a feature well known among woody lianas as a type of cambial variant (Carlquist 1988, 1991). Different wood densities in terms of fiber content and vessel diameter and distribution are apparently fine-tuned, at least in terms of bending biomechanics, for the different functional demands of different parts and positions of the plant (Putz and Holbrook 1991; Rowe and Speck 1998). Although we discuss the biomechanical trend only in terms of bending, the lobed organization of the wood cylinder and the compliant living tissue between the lobes probably play important additional roles. These may include resisting and repairing fracture and damage to the hydraulic supply after catastrophic movement and stresses (Fisher and Ewers 1989, 1991).

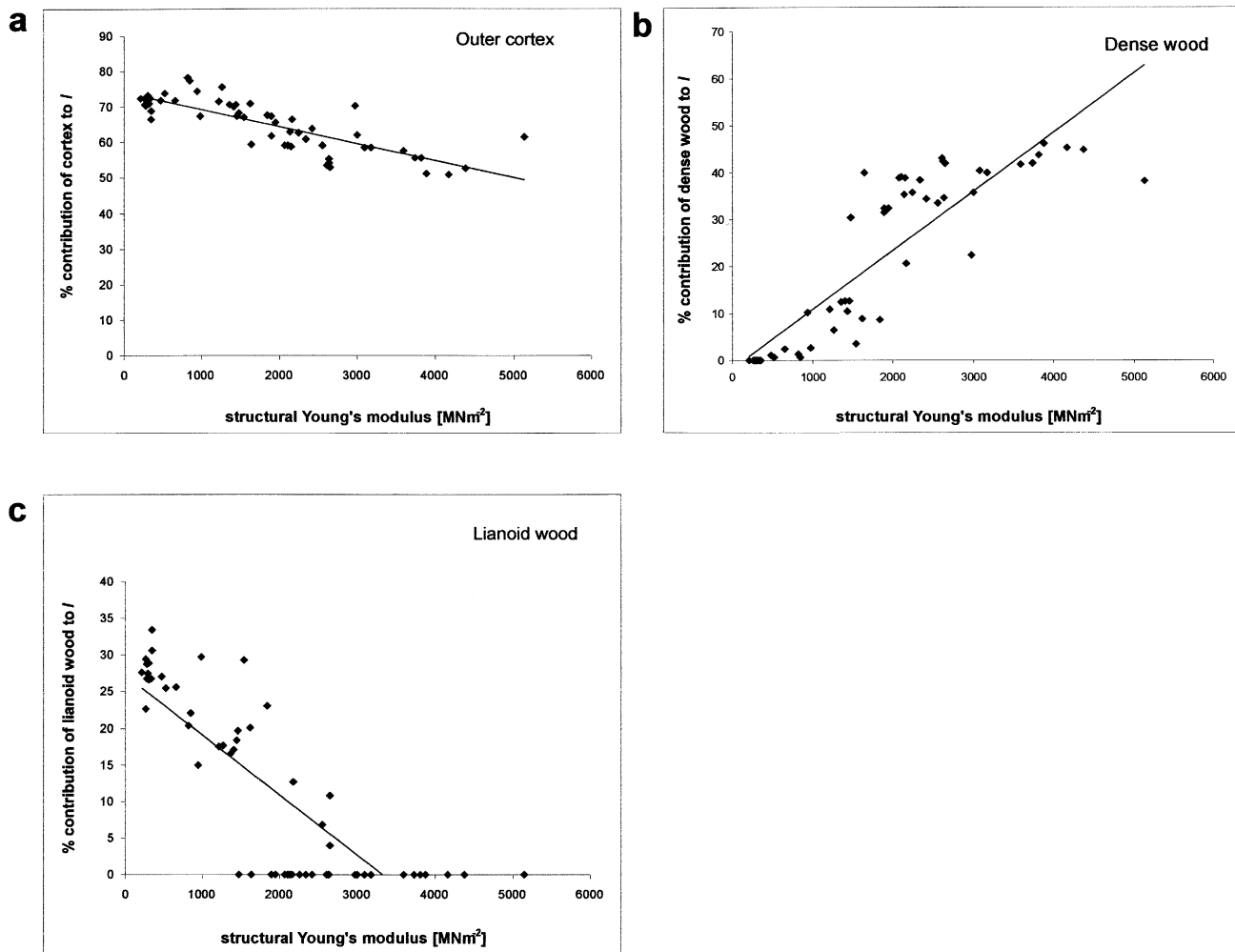


**Figure 3.** *Lycopodiella cernua*, contributions of main tissues to axial second moment of area I and structural Young's modulus  $E_{\text{str}}$  along (a) an unstable vertical axis (c) a longer axis scrambling into the surrounding vegetation. Both plants show an increase in from the base coupled with an increase in % contribution of sclerenchyma tissue and reductions in other cortical tissues. Relatively high levels of  $E_{\text{str}}$  and sclerenchyma contribution are retained during the "climbing phase" in the median to upper part of the scrambling plant, (b) Plot of % contribution of cell wall to cross-sectional area of tissue (measured as mean area of cell wall/total area of sampled tissue in 10 samples of approx. 5-10 individual cells per mean value) of sclerenchyma tissue and structural Young's modulus along an unstable vertical axis. The trend in density of the main mechanical tissue follows that of the contribution to axial second moment of area and increases and decreases with  $E_{\text{str}}$ .

### Phylogenetic Constraints and Canalization of Growth Forms in Ranunculaceae

The majority of species in the Ranunculaceae are herbaceous perennials (Judd and others 2002). Many include herbaceous aerial stems emerging from a perennial underground tuber or rhizome. Above-ground woody stems only appear in the

genus *Clematis* and in the monospecific genus *Xanthorhiza*. Observations of these woody forms reveal that all of them are not entirely self-supporting; they include lianas, creeping plants and small statured, semi-self-supporting or procumbent shrubs. According to recent phylogenetic reconstructions, basal members are herbaceous with perennial underground stems (Johansson and Jansen 1993;



**Figure 4.** *Condylocarpon guianense*, bivariate plots of contributions of main tissues to axial second moment of area  $I$  and structural Young's modulus  $E_{\text{str}}$ . (a) Outer cortical tissues show a negative correlation with structural Young's modulus. (b) The development of dense wood during the early phases of development are strongly positively correlated with the trend in structural Young's modulus. (c) Development of non-dense lianoid wood shows a negative correlation and relatively large scatter (all regressions are significant at the 0.001 level).

Hoot 1995; Johansson 1995) and woodiness is secondary in the family (Judd and others 2002).

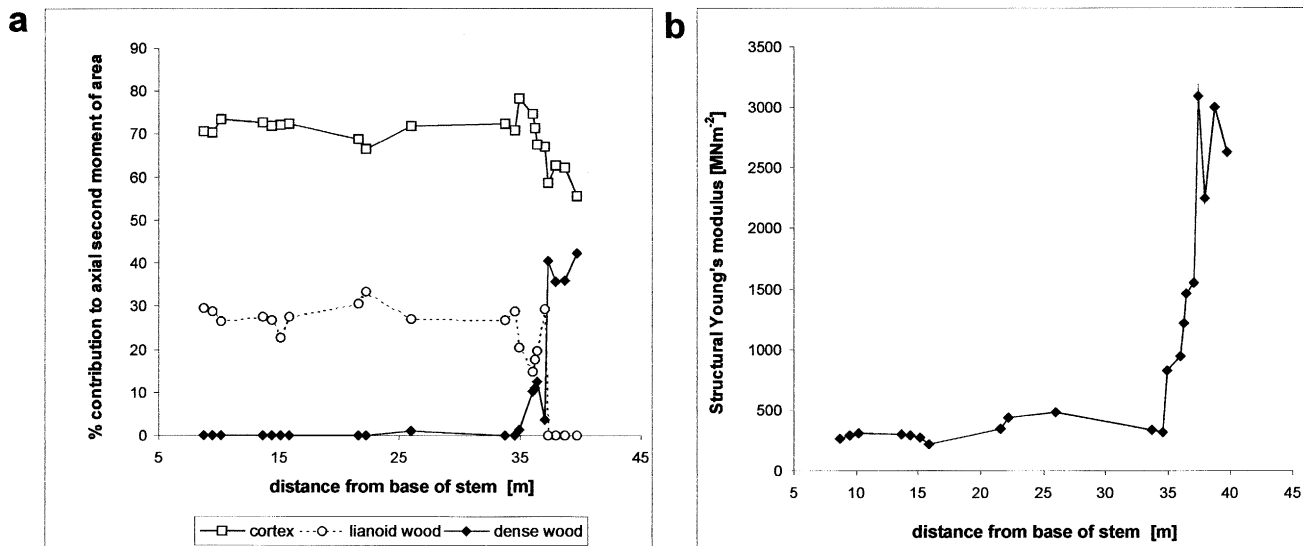
This review of recent studies on *Clematis* (Isnard and others 2003a, b) concerns three species with different growth forms. *Clematis vitalba* is a woody liana growing in woodland; *Clematis maritima* establishes itself on the Mediterranean coast with annual herbaceous axes forming a trellis on the sand dune surface with older, largely underground woody stems. *Clematis recta* is a rhizomatous herb, where secondary growth is nearly entirely confined to an underground rhizome and the very basal parts of annual aerial stems. Stems of this semi-self-supporting species become rapidly unstable under their own weight and lean on the surrounding vegetation. The small shrub-like and partly procumbent

species *Xanthorrhiza simplicissima* grows in thickets under shaded moist conditions. The sparsely branched stems do not exceed 1 m in length.

### Mechanical Architecture

For the two woody species of *Clematis*, the structural Young's modulus drops by 71% for *C. maritima* and 75% for *C. vitalba* between the first and oldest stages of growth (Figures 7a,b). This pattern is typical of non-self-supporting plants. In *C. maritima*, there is a marked transition from the first to second developmental stages (Figure 7a) and there is a significant drop in mean structural Young's modulus from  $1619 \pm 492$  [ $\text{MNm}^{-2}$ ] ( $n=21$ ) to  $855 \pm 253$  [ $\text{MNm}^{-2}$ ] ( $n=9$ ) ( $F=17.06$ ,  $P<0.01$ ). This drop corresponds





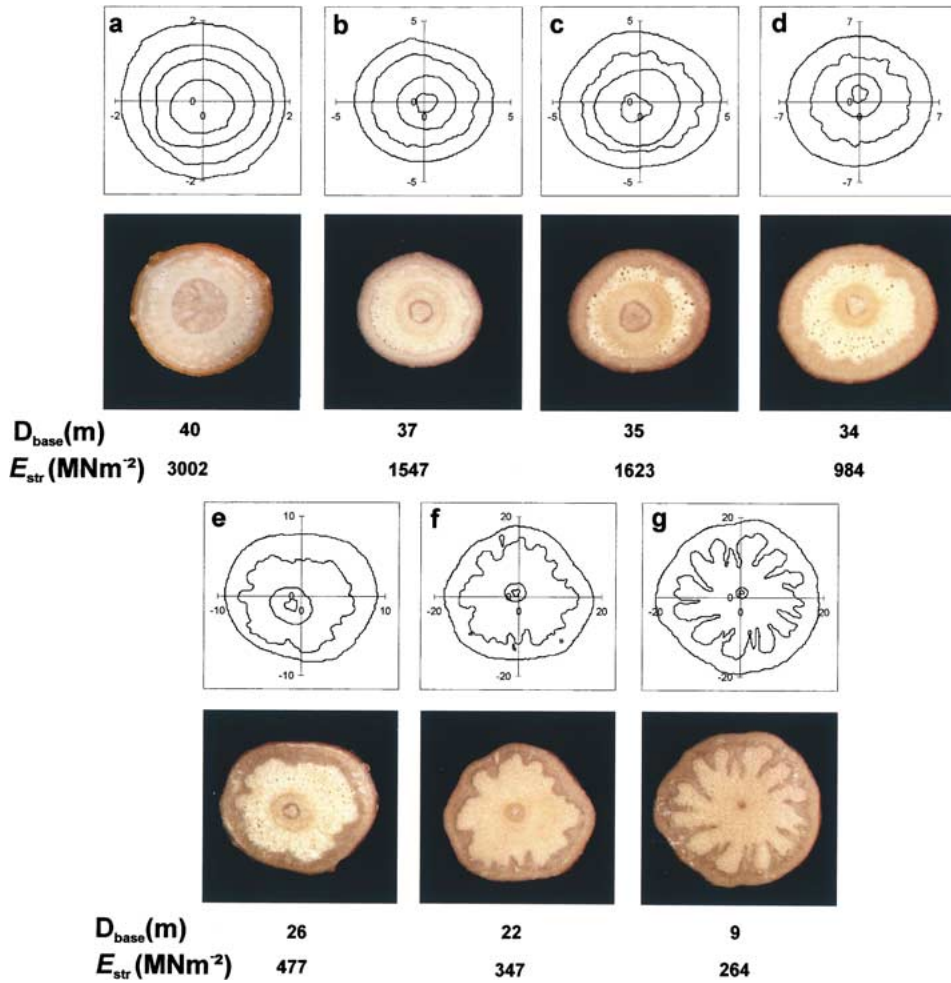
**Figure 5.** *Condylocarpon guianense*, (a) positional data showing trends in contributions of each tissue to axial second moment of area from the base to the apex of the plant. There is a relatively abrupt and profound transition in anatomical and biomechanical properties just below the apex of the plant. The contribution of dense wood falls abruptly and this is concomitant with an increase in the contribution of outer cortical tissues. At the same time, the contribution of lianoid, compliant wood to the stem increases significantly from 0 to approximately 30%. (b). Trend in change of Young's modulus along length of stem, the initial variation in  $E_{str}$  is concomitant with changes in contribution of dense wood in the apical part of the liana "trellis", the basal drop in  $E_{str}$  is sudden and follows the changes in tissue contributions from dense wood to lianoid wood and cortex (mechanical data based on Rowe and Speck 1996, and Rowe and Speck 1998).

exactly to the emergence of the stem at ground level with the decrease occurring in the underground part of the plant (Isnard and others 2003a). In *C. vitalba* the drop in  $E_{str}$  occurs further from apical branches (Figure 7b) and remains relatively stable between stage I [ $E_{str} = 3074 \pm 1083 \text{ MNm}^{-2}$  ( $n=18$ )] and stage II [ $E_{str} = 3126 \pm 784 \text{ MNm}^{-2}$  ( $n=14$ )] but decreases in stage III [ $E_{str} = 979 \pm 478 \text{ MNm}^{-2}$  ( $n=20$ )]. The mechanical pattern in herbaceous aerial stems of *C. recta* is typical of semi-self-supporting plants with values remaining stable during development (Figure 7c) and showing no significant variation of  $E_{str}$  between stages I [ $E_{str} = 4522 \pm 979 \text{ MNm}^{-2}$  ( $n=20$ )] and II [ $E_{str} = 5132 \pm 1206 \text{ MNm}^{-2}$  ( $n=33$ )].

Anatomical investigation of these three species reveals a similar mechanical architecture in young stages where all three species are characterized by bundles or a ring of primary fibers near the periphery of the stem section (Figures 8a,c,e). Contributions of the primary fibers to axial second moment of area are high in *C. vitalba* and vary between 31 and 22% in stages I and stage II with corresponding high values of  $E_{str}$  (Figure 7b). In *C. maritima*,  $E_{str}$  is lower and the contribution of fibers varies from only 4.1 to 2.2% (Fig. 7a). The contribution of fibers to axial second moment of area is stable in the two first stages of *C. recta* as are values of  $E_{str}$ .

In the two woody species, *C. vitalba* and *C. maritima*, the initial (primary) periderm initiated in the primary phloem tissue isolates outer tissues and causes their disruption and death. Primary phloem fibers and collenchyma are displaced outwards by the development and this is believed to disrupt their mechanical integrity in stage II (Isnard and others 2003a, b). Such changes are not observed in upright stems of *C. recta*, which lack secondary growth except at the very base of the stems and in the rhizome (Figure 8f). A compliant wood with large vessels and large parenchyma rays is produced later in aerial stems of *C. vitalba* and the older mostly underground stages of growth of *C. maritima* (Figures 8b,d) with significantly lower values of  $E_{str}$ . A compliant wood type also comprises the underground rhizome of *C. recta* (Figure 8f).

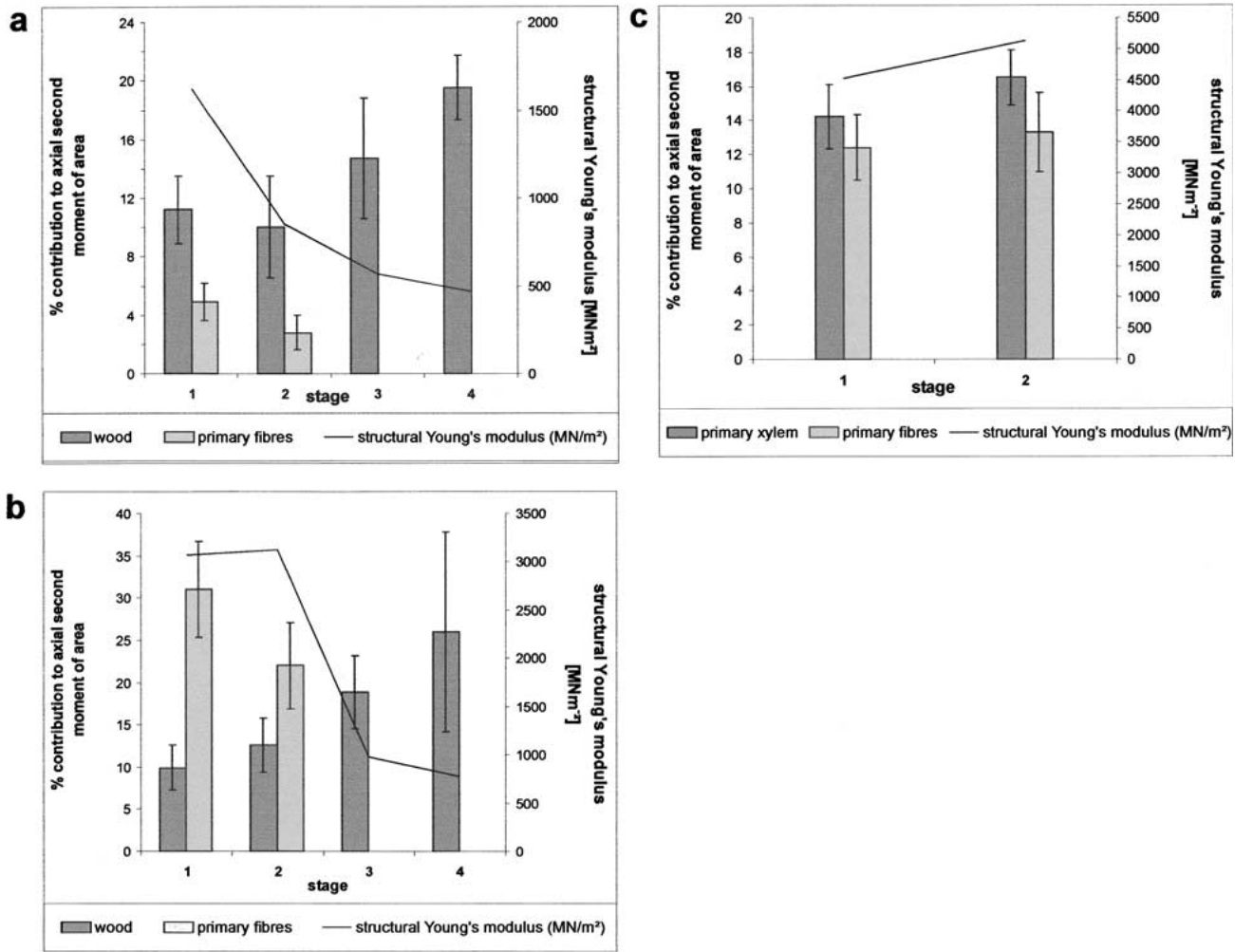
The overall mechanical pattern of aerial stems of *Xanthorrhiza* is similar to that of self-supporting shrubs (Figure 9), with an increase of  $E_{str}$  during development occurring between the herbaceous and above-ground woody stems. Values of  $E_{str}$  level off in older, larger stems. Aerial stems remain relatively short and slender, never exceeding 1 m in height and limited to a diameter of 3-10 mm (Figures 10a,c). The underground rhizome shows relatively low structural Young's moduli ( $E_{str} = 850 \pm 52 \text{ MNm}^{-2}$ ), which are similar to old stages of *C.*



**Figure 6.** *Condylocarpon guianense*, anatomical development along entire length of the liana.  $D_{\text{base}}$  (m), distance from the base in meters;  $E_{\text{str}}$  ( $\text{MNm}^{-2}$ ), structural Young's modulus. Plotted tissue outlines are those used for measuring axial second moment of area with tissues from inside to outside represented by pith, dense wood, lianoid wood and cortex; the scales are depicted on the values plotted on the graph axes in mm. (a) Young searcher, of canopy trellis showing significant proportion of dense stiff wood in small diameter stem, (b) Slightly older searcher stem showing early development of vessels and outer band of less dense wood, (c) Stem development near base of liana crown showing clearly demarcated transition between dense wood and compliant lianoid wood with large diameter vessels. (d-e) Increasing contribution of lianoid wood with increasing vessel size, these stages show a marked drop in  $E_{\text{str}}$  compared with more distal stages and this corresponds to relatively free parts of the liana stem between the crown and twining phases on the main host trunk, (f) The outer perimeter of the lianoid wood development begins to show variant cambial development. (g) Variant cambial growth has advanced and produced conspicuous lobes of outer compliant wood separated by compliant cortical tissues, these stages show some of the lowest and most compliant values of  $E_{\text{str}}$  measured for dicotyledonous lianas.

*vitalba* and *C. maritima*. During the growing season, new herbaceous shoots are produced bearing inflorescences, and stems often bend significantly under their own weight (Figure 10b). Even though the structural Young's modulus is relatively high in older woody aerial stems, they appear to reach their critical height rapidly and become unstable. Lower values of  $E_{\text{str}}$  in rhizomes compared with aerial stems can be explained by an increase in parenchyma rays, wider diameter vessels and thinner-walled wood fibers (Figure 11).

A marked feature of the lianoid development in *Clematis* is that mechanical support is provided by a primary structure composed of fibers and collenchyma localized at the outside of the stem, it is termed a mechanical hypoderm. It provides mechanical support in above-ground stems of *C. recta* and the young stages of the climber and sand dune species. A comparison of *Clematis* and *Xanthorhiza* with basal members of the Ranunculaceae suggests that rhizomatous specialization coupled with secondary growth producing compliant wood



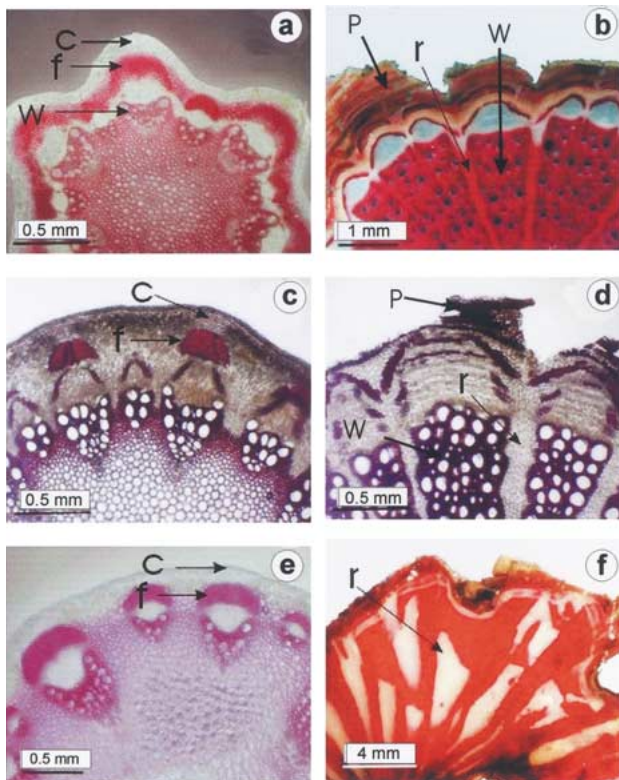
**Figure 7.** *Clematis*, plots of contributions of wood (primary xylem - *C. recta*) and primary fibers to the axial second moment of area with structural Young's modulus based on defined development stages for three species (Isnard and others 2003a). (a) *Clematis maritima* and (b) *Clematis vitalba* both showing non-self-supporting patterns with a drop of  $E_{str}$  from stage I to stage IV. Decrease in  $E_{str}$  is concomitant with increase of compliant wood contribution during development. Primary fibers are largely separated or lost from the stem by stage III. (c) *Clematis recta*, semi-self-supporting signal with  $E_{str}$  remaining stable between stages I and II and following the unchanging contribution of primary fibers.

led to a biomechanical constraint on the production of self-supporting growth forms (Isnard and others 2003a). This might explain the abundance of lianoid growth forms in *Clematis* and the rarity of self-supporting forms, which are confined to small statured and unstable shrub-like rhizomatous growth forms of *Xanthorrhiza*. In *Clematis*, the stiff hypodermal architecture of young stages might be homologous with the herbaceous architecture of short-lived aerial stems of basal members of the Ranunculaceae (Isnard and others 2003a). Perennation of aerial stems in *Xanthorrhiza* results from a limited secondary growth, similar to that of the rhizome development but with modification of the relative contributions of compliant wood and parenchyma

rays, resulting in a relatively dense and stiff type of wood. This secondary growth does not significantly increase the diameter of aerial stems and the mechanical architecture of the plant is limited to small, unstable upright growth and procumbent woody axes.

### CLIMBING GROWTH FORMS IN MONOCOTS: MECHANICAL ARCHITECTURE AND EVOLUTION OF THE SCANDENT HABIT IN PALMS

Climbing growth forms have appeared several times independently during palm evolution (Baker and



**Figure 8.** Early and latest defined developmental stages for the three species of *Clematis* based on Isnard and others 2003a. (a-b): *C. vitalba*; (c-d) *C. maritima*; (e-f) *C. recta*. (a, c, e) All stems show a conspicuous hypodermal sterome of primary fibers in the outer part of the cortex in the earliest developmental stages. This imparts high stiffness to young searchers of climbers and the erect herbaceous growth phase in *C. recta*. Older development in the two woody aerial climbers (b,d) shows sloughing of the entire primary hypoderm and production of compliant wood. Unlike predominantly woody lianas (see Figure 6) secondary wood does not show an initial phase of dense wood production. Secondary growth is almost entirely confined to the underground rhizome in *C. recta* (f), which is highly compliant and shows high levels of parenchyma and large diameter vessels (c = collenchyma, f = primary fibers, p = periderm, r = rays, w = wood)

others 2000; Tomlinson and Fisher 2000). Three subfamilies include climbing species (Ceroxyloideae, Calamoideae, Arecoideae) (Uhl and Dransfield 1987) with an overall total of approximately 580 species (16% of all palms species) belonging to 16 genera (7% of Arecaceae). The species richness of climbing forms in palms within a single family is one of the most important in the plant kingdom and is probably only exceeded by some of the large dicot families such as Asclepiadaceae, Convolvulaceae and Fabaceae (Gentry 1991). This success of the climbing habit has developed within groups lacking

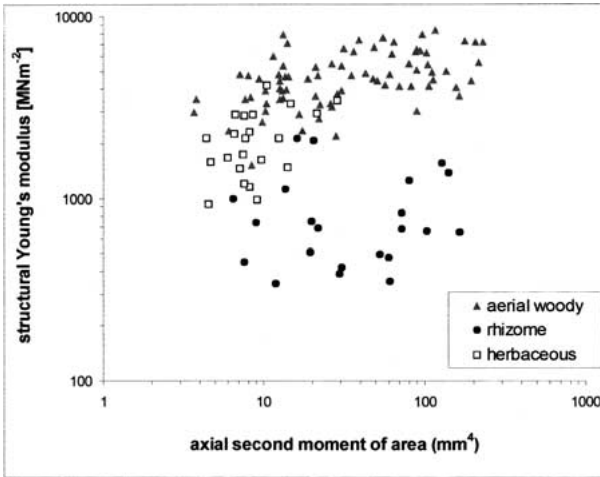
secondary growth, which is otherwise an essential mechanical and hydraulic feature in the success of many dicotyledonous climbers. More surprising is the length of the stem reached by some species, especially within the Calamoideae, which are reported to reach up to 200 m (Burkill 1966 in Tomlinson and Spangler 2002) and commonly between 10 and 50 m.

By lacking secondary growth, climbing palms retain the primary anatomical architecture of the stem for their entire life span and are unable to produce new vascular bundles after establishing growth. For these reasons mechanical or hydraulic failure of slender climbing stems cannot be countered via secondary growth. Climbing palms have developed adaptive modifications such as the reduction of the establishment growth phase, specialized attachment devices (modified leaf or inflorescence) (Dransfield 1978; Tomlinson 1990), long leaf sheaths and a distribution of leaves along relatively large parts of the stem. Climbing palms also possess larger vessels than their self-supporting counterparts and in this sense share some characteristics of dicotyledonous lianas (Fisher and others 2002; Tomlinson and Zimmermann 2003).

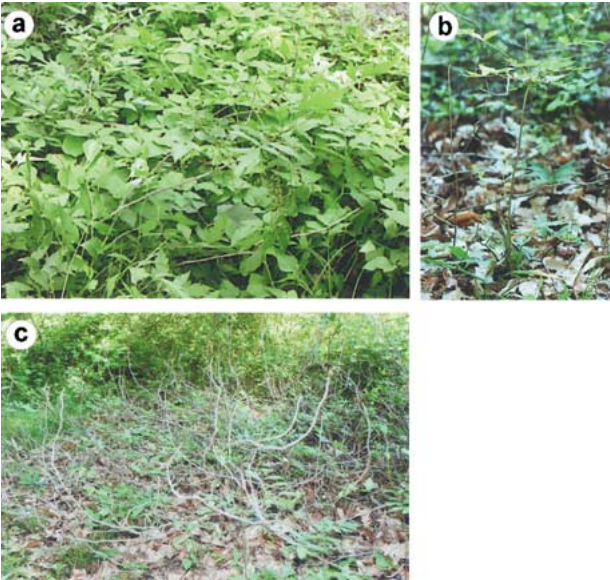
A better knowledge of the mechanical properties of the stems of climbing palms should help us understand which characters and mechanical adaptations permit a scandent habit in these plants. Since the climbing habit has appeared independently several times in the family, do they show a diversity of mechanical architectures? Are there any parallels or comparisons with the kinds of mechanical trends observed in dicotyledonous lianas? We present some preliminary results from a project focussed on the mechanical architecture and evolution of the climbing form in the two palm subfamilies: Calamoideae (*Plectocomia*, *Daemonorops* and *Calamus*) and Arecoideae (*Desmoncus*). Two representative species investigated in this paper include *Calamus tetradactylus* (Calamoideae) and *Desmoncus orthacanthos* (Arecoideae).

*Desmoncus orthacanthos* is widespread and distributed from the Atlantic coast of South Mexico to Central South America (Henderson and others 1995). It is common in French Guyana where it grows in open and disturbed areas along rivers and streams. Stems are 0.6-3 cm in diameter and grow in clusters reaching up to 30 m in length by climbing on the surrounding vegetation. Stems are attached to supports by specialized organs known as *cirri*, which bear modified hook-like leaflets known as acanthophylls (Figure 12a).

*Calamus tetradactylus* is distributed in Vietnam, Laos and Yunnan province in Southeast China



**Figure 9.** *Xanthorhiza simplicissima*. Double logarithmic plots of structural Young's modulus  $E_{\text{str}}$  and axial second moment of area  $I$  of herbaceous, woody and rhizomatous stems.  $E_{\text{str}}$  increases from herbaceous to young aerial woody stems and then remains stable in older perennial woody (more basal) axes. Low values of  $E_{\text{str}}$  for the rhizome are similar to those of old stages in *Clematis*.



**Figure 10.** *Xanthorhiza simplicissima*. (Botanical Garden, Freiburg), (a) Aerial axes of small-bodied shrub-like growth form (b) Young stages are relatively erect, (c) Older woody stages become unstable and are partly pro-cumbent.

(Evans 2001). It is known as a high quality source of small diameter cane and widely planted in Vietnam and China. Stems grow in clusters and reach up to 6 m long and 0.3 to 1 cm in diameter (Figure 12b).

The species climbs on the surrounding vegetation by a modified inflorescence via hook-like spines attached to a long whip-like axis known as a "flagellum."

## Mechanical Architecture

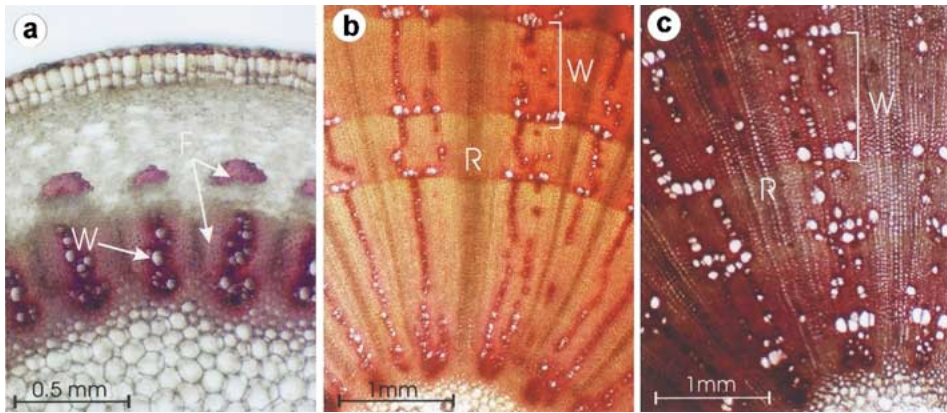
Values of structural Young's modulus ( $E_{\text{str}}$ ) are shown from bending measurements carried out on axes of the plants before and after removal of the leaf sheath (Figures 13, 14).

In *D. orthacanthos* (Figure 13) values of  $E_{\text{str}}$  of stems alone are higher than those of stems with the leaf sheath. Because the structural Young's modulus can be considered as a mean of  $E_{\text{str}}$  of all tissue components of the stem, this result demonstrates that in terms of material properties the leaf sheath is less stiff than the inner stem. The composite structure is different in *Calamus* where values of the stem alone are lower than measurements with the leaf sheath (Figure 14). In this case, the material properties of the stem are less resistant to bending than those of the leaf sheath.

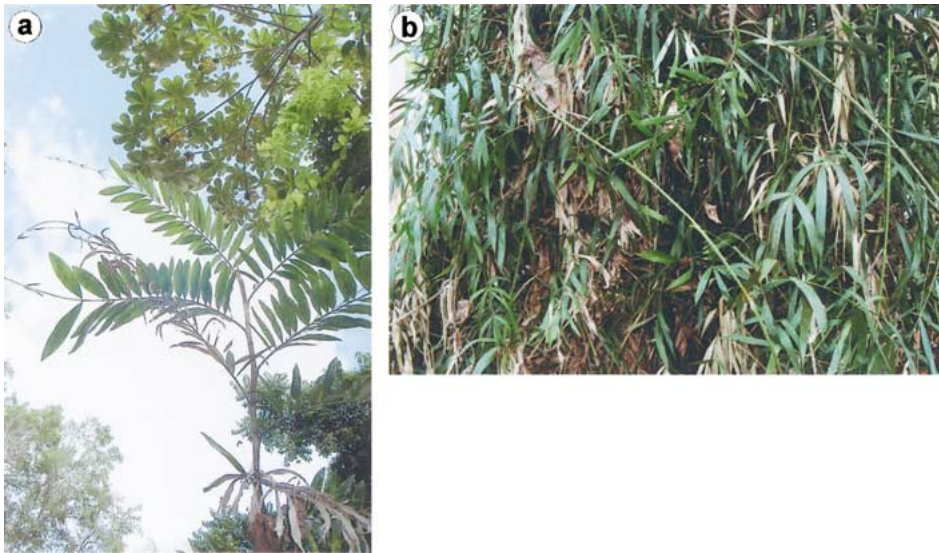
The overall values of structural Young's modulus for *Desmoncus orthacanthos* are relatively high for the entire axis (2400-8500  $\text{MNm}^{-2}$ ) and for the stems alone (3800-15300  $\text{MNm}^{-2}$ ), particularly toward the base of the plant. This differs markedly from the range and variation of values seen in typical dicotyledonous lianas, which show drastic drops in Young's modulus during development and towards the base of the plant. In *Calamus tetradactylus* the structural Young's modulus of the entire axis (5400-10000  $\text{MNm}^{-2}$ ) is also high but those of the stems alone (715-2700  $\text{MNm}^{-2}$ ) are relatively low and remain stable along the stem. The lower range of these values approaches the  $E_{\text{str}}$  of old and flexible parts of some dicot lianas (Speck and Rowe 1999).

Differences in the mechanical properties of the stem and leaf sheath of both species are readily observed by differences in anatomical organization. In *D. orthacanthos*, very dense bundles with thick-walled fibers are distributed at the periphery of the stem (Figure 15a, b). The number of bundles and their density decrease toward the center of the stem cross-section. This kind of organization has been observed in arborescent palms, where stiffness is concentrated at the periphery of the stems and increases towards the base of the stem (Rich 1986, 1987). In *C. tetradactylus* fibers sheaths are smaller and less concentrated at the outside of the stem (Figure 15c, d).

The contribution of the leaf sheath to flexural stiffness has an important mechanical role in *C. tetradactylus* where it contributes more than 90% of



**Figure 11.** *Xanthorhiza simplicissima*. (a) Transverse section of stem; the mechanical architecture includes a ring of lignified primary fiber bundles similar to the organization in species of *Clematis*, (b) Dense wood of aerial stems with relatively small groups of relatively narrow diameter vessels and conspicuous, large unclignified rays. This dense wood type is rare among Ranunculaceae. (c) Compliant wood of underground rhizome, the wood type is less dense than that of the aerial stems, with more numerous, larger diameter vessels and less dense wood fibers and large unclignified rays (F = fibers, R = rays, W = wood).

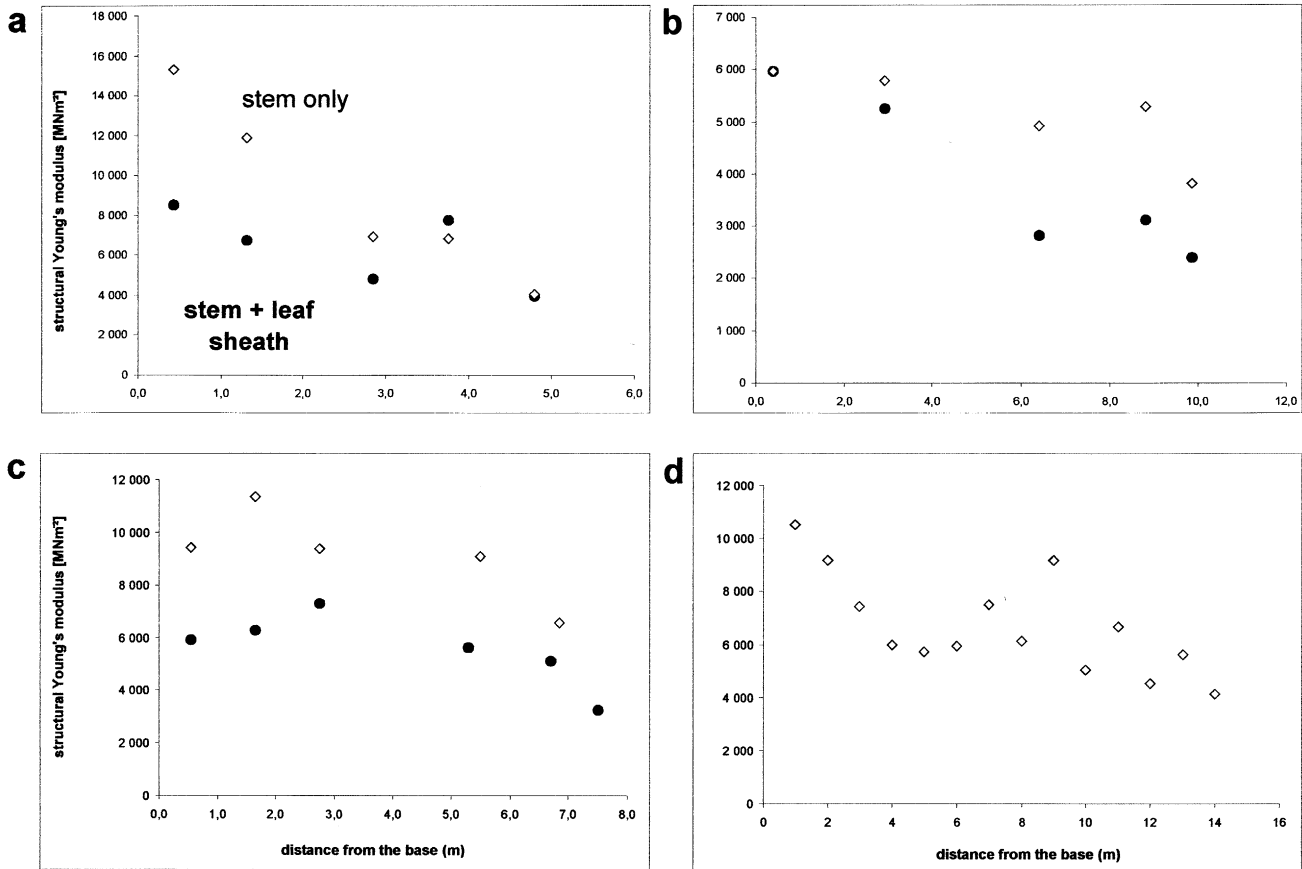


**Figure 12.** (a) *Desmoncus orthacanthos* growth habit of relatively young stem deploying cirri with hook-like acanthophylls and climbing into surrounding vegetation (Piste de l'Anse, French Guyana), (b) *Calamus tetradactylus*, climbing axes growing from a cluster and climbing via spines on the surface of the leaf sheath and hooks on the flagellae (Xishuangbanna Tropical Botanical Garden, Yunnan Province, China).

the stiffness (Figure 16). In *D. orthacanthos* the contribution is lower and less than 90%. The lower contributions near the base of the plant correspond to areas where the leaf sheath has senesced and partly or entirely fallen away from the stem. In these parts of the plant the stem alone provides mechanical support. In this species of *Calamus* the sheath provides almost all of the stem stiffness. If the sheath is removed in apical parts of the plant the axis is mechanically unstable and bends significantly under its own weight.

In many climbing palms that we have observed, the leaf sheath may break locally under excessive

bending or torsional loads resulting from slipping or falling of the main axis from its supports. This has been observed in several species of Calamoideae and *Desmoncus orthacanthos* (Figure 17a). The inner stem often shows evidence of surviving these traumatic effects. Splitting and breakage of the leaf sheath at a given point permits local flexibility of the inner compliant stem. Curvature of the surviving inner stem permits a repositioning of the fallen stem, but as the fractured leaf sheath is only broken locally, the rest of the stem and leaf sheath remains intact and sufficiently rigid to retain its overall climbing position.

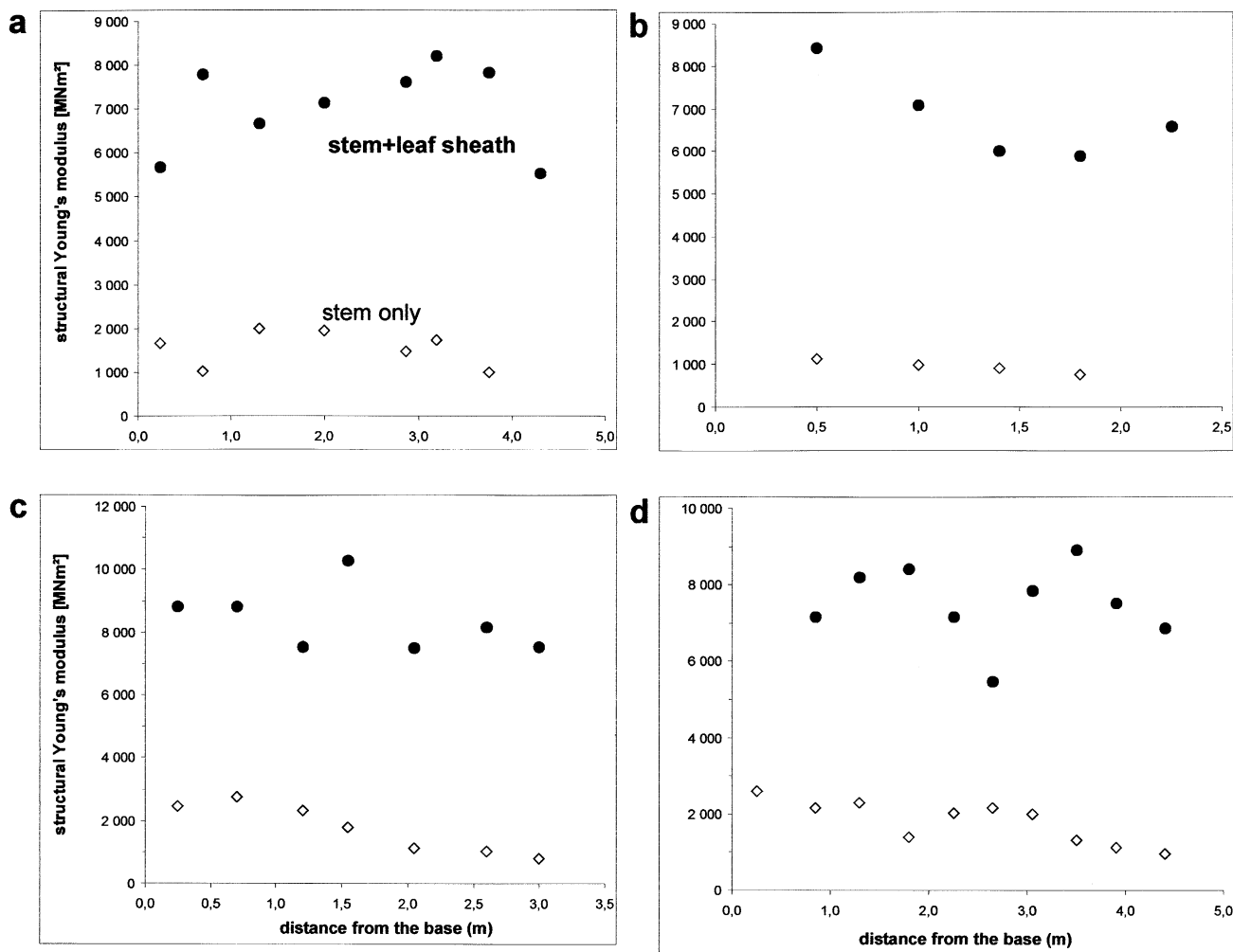


**Figure 13.** Structural Young's modulus along four representative axes of *Desmoncus orthacanthos*. (a-c) Values of axes measured with the leaf sheath are lower than values of the stem only. (d) Older stem in which the leaf sheath has senesced and been shed. Most stems with and without the leaf sheath including the mature stem show a general increase in  $E_{ST}$  towards the base of the plant.

This preliminary analysis suggests different mechanical architectures in *Desmoncus orthacanthos* and *Calamus tetradactylus*. Both species are characterized by a composite mechanical structure comprising stem and leaf sheaths but differ in the relative mechanical contribution of the leaf sheath and the stem. Mechanical architecture of the stem seems to be more adapted to a specialized climbing habit in the calamoid palm where a greater flexibility of stems protects the plant from irreversible breakage.

A mechanical innovation shared by both scandent palm subfamilies is the mechanical role of the leaf sheath and its function and modification during development of the growth form. The leaf sheath contributes significantly to flexural stiffness during young phases of growth and enables the climbing stems to span gaps between host supports prior to deployment of the cirri and flagellae. The composite structure can also permit local stem flexibility via leaf sheath breakage when the stem is

exposed to excessive external stresses. In *D. orthacanthos* and certain species of the Calamoideae, the leaves and leaf sheath senesce and are lost from the stem. Long and heavy stems are then only attached to the support via relatively few existing apical leaves and many species slip downwards from their previously attached supports (Corner 1966; Putz 1990). Loss of the leaf sheath more readily allows curvature of the stem, which can form wide loops of cane on or near the ground (Figure 17b). This kind of growth appears to result from a continuous apical growth of the stem where new leaves become attached to the surrounding vegetation as older leaves senesce and fall away. This mechanism thus retains the climbing position of the plant in the host vegetation and could explain why some of these plants produce extremely long axes, most particularly in some species of *Calamus*, which have some of the longest stems in the plant kingdom (Burkill 1966 in Tomlinson and Spangler 2002).



**Figure 14.** Structural Young's modulus along four representative axes of *Calamus tetradactylus*. (a-d) Values of axes with the leaf sheath are always higher than those of the stem only (compare with Figure 13). The overall trends along the stem do not show a marked increase in  $E_{str}$  as observed in *D. orthacanthos*.

It is possible that at least this species of *Calamus* shows a more specialized climbing mechanical architecture than the species of *Desmoncus* studied, which appears to have retained a similar anatomical organization of arborescent palms. A mechanical innovation in *Calamus* leading to flexible stems could explain, if shared by other members of the group, the evolutionary success of this taxa and the great diversity of species.

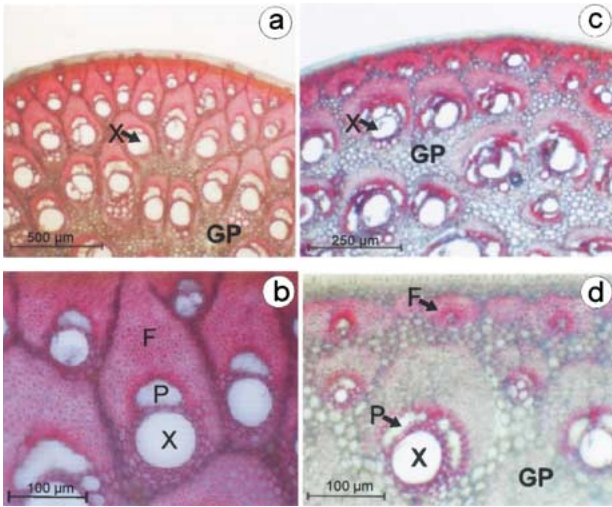
## DISCUSSION

### Constrained Archetypal Bauplans and the Mechanical Hypoderm

The types of development underlying the biomechanical changes of the stem are produced by quite

different types of development and are strongly constrained by evolutionary contingency. The least derived plant, *Lycopodiella cernua*, shows a mechanical stem architecture that is modulated by varying amounts of thick-walled fiber elements in the cortex. Changes in mechanical properties are made only via primary differentiation of the thickness of the sclerenchyma band and the thickness of the fiber element walls constituting it. This shows little difference from archetypal organizations of early lycopsids and other early land plants in which the appearance of a mechanical hypoderm represented a major mechanical innovation in land plant diversity (Speck and Vogellehner 1994; Bateman and others 1998; Rowe and Speck 2003). Lycopodiaceae show relatively little variation of growth form types including notably a widespread shift to epiphytism during the mid Cretaceous angiosperm





**Figure 15.** (a-b) *Desmoncus orthacanthos*. (a) Large interlocking vascular bundles and fiber sheaths are densely arranged at the periphery of the stem, (b) Bundle sheaths consist mostly of thick-walled fiber tissue. (c-d) *Calamus tetradactylus*, vascular bundles are less densely arranged in a parenchymatous cortex of the stem. (d) Bundle sheaths consist of thick-walled fiber cells but are less extensive around each vascular bundle.

forest formation (Wikstrom and Kenrick 1999; Wikstrom and others 1999). Despite a very simple overall bauplan and limited potential for forming diverse growth form types, plants can produce climbing growth forms from highly constrained plesiomorphic organizations.

### Derived Woody Lianas

The lianoid organization observed in *Condylocarpon* deploys a number of mechanical novelties peculiar to angiosperms, most significantly the partitioning of mechanical and hydraulic functioning of the secondary tissues of the wood including dense fiber-rich wood and hydraulically efficient vessel-rich wood. These different tissues are developed for different functional demands during different phases of growth. The timing, ontogeny and combination of tissue types is complex and combines at least four active, mechanically significant processes involving dense wood, lianoid wood, lobed (variant) growth of lianoid wood and significant variations of outer compliant cortex. The species comes from a highly derived family of dicotyledons of over 2000 species with over 350 lianoid species. The organization observed is highly specialized to form large-bodied, woody, long-lived climbing forest lianas. Despite overall differences in size, scale, mode of development and probable resistance to fracture and

capacity for wound healing (Fisher and Ewers 1991) the 40 m long plant shows an overall similar trend, as seen in climbing specimens of *Lycopodiella* using relatively high stiffness to traverse spaces as searchers and higher compliancy below the point of attachment with the host.

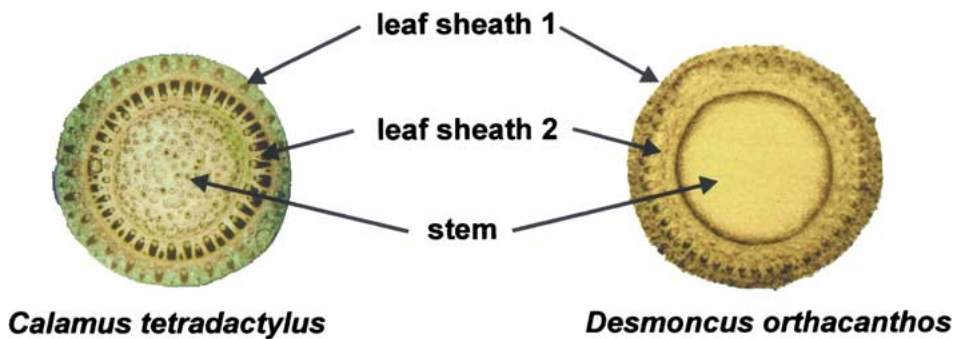
### “Herbaceous” Aerial Architectures and “Rhizomatous” Secondary Growth

The climbing architectures observed in the tested species of *Clematis* (Ranunculaceae) include a semi-self-supporting form, a woody climber and a scrambling sand dune plant. All three show young stages of development that are relatively rigid and correspond to types of “searchers” (*C. vitalba*, *C. maritima*) or to relatively stiff stems spanning points of contact with the host (*C. recta*). This rigid phase of development is mechanically dominated by primary tissues (primary fiber bundles) and thus differs considerably from the stiff young ontogenetic stages of lianas with a dominantly woody bauplan such as *Condylocarpon*.

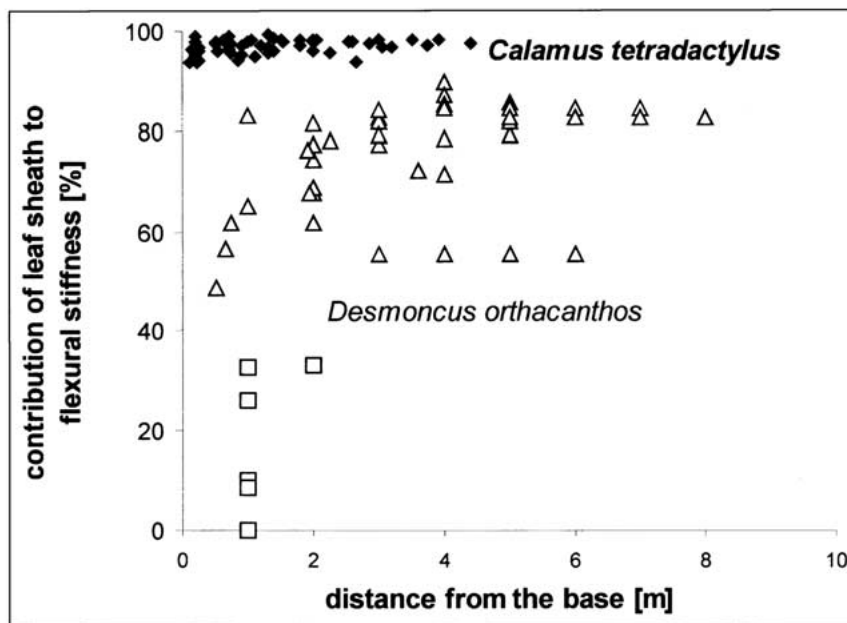
This initial rigid phase is more similar to primary hypodermal steromes such as found in *Lycopodiella* and probably linked to the herbaceous organization of aerial stems of basal members of the Ranunculaceae. The Ranunculaceae represent a group that has at some point in its history undergone a profound change in growth form organization to herbaceous annuals or herbaceous perennials (Isnard and others 2003a). This might explain why the lianoid features of development within *Clematis* (primary tissue hypoderm = stiffness; single type of rhizome-like wood = compliancy) might be derived from an ancestral bauplan quite different from other types of liana such as *Condylocarpon*. The mechanical architecture of *Xanthorhiza* represents a rare element within the family that can produce a denser, stiffer wood type in aerial stems. The underground rhizome comprises highly compliant wood with a low stiffness similar to mature *Clematis* wood. The rarity of these types of growth form within the family suggest that such “escapes” from the herbaceous-rhizomatous-lianoid developmental plan are possible but as in the case of *Xanthorhiza*, appear to be constrained to relatively small-bodied or procumbent shrubs.

### The Loss of the Secondary Vascular Cambium

The loss of an entire bifacial vascular cambium characterizing monocotyledons had a profound effect on the subsequent radiation of the group.

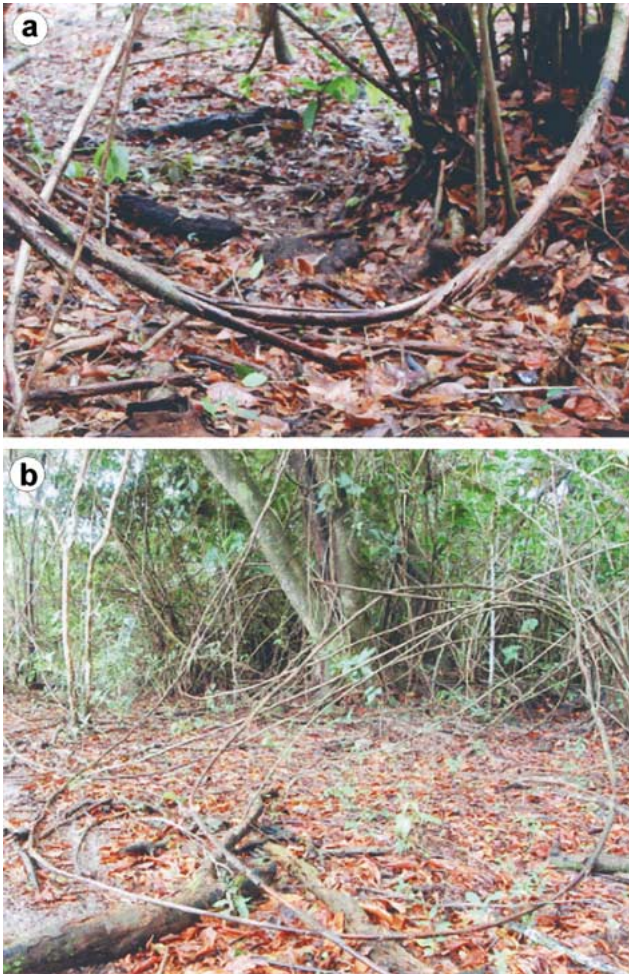


**Figure 16.** Transverse sections of entire axes (stems and leaf sheaths) of *Calamus tetradactylus* and *Desmoncus orthacanthos*. Relative contribution of the leaf sheath to flexural stiffness is plotted for representative stems. In *Calamus tetradactylus* the leaf sheath always contributes more than 90% of the flexural stiffness of the stem. This contribution is less in *Desmoncus orthacanthos*. Square symbols correspond to older stems of *Desmoncus orthacanthos* that have partially or entirely lost the leaf sheath.



Whatever the selective advantages operating on this simplification and reduction of the body plan, monocotyledons radiated into a wide range of mechanical architectures. Those observed in the two representative climbing palms from the New and Old World tropics show no evidence of secondary tissue formation or prolonged primary meristem activity as characterizing some other large-bodied monocotyledons or the lianoid dicotyledons discussed here. Both species show mechanical architectures, which employ modified leaves or reproductive organs as ephemeral modes of attachment via hook-like structures. Biomechanical changes in the stem are modified by and confined to primary differentiation and maturation. Biomechanical adaptation of the axial system for these climbing forms concerns a combination of the central stem and the outer leaf sheath but differs in detail between the two species. Further biomechanical changes of the stem are “accidental” or result from senescence. Higher compliance can fol-

low local stress concentration after fracture of the leaf sheath. Furthermore, higher compliance can characterize older cane-like parts of the stem system, particularly in the calamoid palm tested, when the outer leaf sheath has naturally senesced and fallen away from the stem. It is possible, but remains to be tested, whether there is a significant difference between the mechanical architectures of the climbing cocosoid palms of the New World and the calamoid rattans in the Old world. These preliminary observations suggest that the *Desmoncus* species tested is relatively similar in anatomy and biomechanics of the stem to the nearest sister group of predominantly self-supporting palms. It is possible that the mechanical differences between climbing axes of the two groups might reflect a longer radiation of calamoid palms as climbers, a fact suggested by their species richness of 530 spp in 15 genera and our observations of the inner stem showing higher compliance, which is possibly closer to the highly compliant “strategies” observed in



**Figure 17.** *Desmoncus orthacanthos*, Piste de l'Anse, French Guyana. Long axes, up to 30 m in length reach the canopy with an average height of 12 m. **(a)** Many of the stems have partially slipped from their supports and lost their leaves and leaf sheaths towards the base. Local stresses can produce localized splitting of the outer leaf sheath with the inner stem remaining intact. **(b)** Such stems can form large arcs and loops on the ground.

many dicotyledonous lianas. This overview of climbing palms does at least highlight the fact that such forms can develop relatively sophisticated mechanical architectures via a combination of developmental innovations based only on primary growth, differentiation and aging. The result is a mechanical architecture, which differs fundamentally from many woody dicotyledonous lianas whether compared with the predominantly woody organization of *Condylocarpon* or the hypodermal stiffness and then woody compliance found in *Clematis*.

Biomechanical analyses combined with anatomical and developmental studies can be a powerful

method for understanding the underlying innovations and constraints contributing to the evolution of different growth forms (Rowe and Speck 2003; Speck and others 2003). Such studies are of particular interest in determining the transitions of self-supporting to non-self-supporting growth forms in widely related plants and widely differing bauplans. This brief review has highlighted some of the biomechanical features found in differing climbing plants and how fundamentally different developmental processes have adapted to produce relative stiffness and compliance for the different phases inherent to climbing growth habits. The climbing habit is a highly persistent and iterative type of growth form in land plants, and biomechanical specialization of the stem appears to have been selected despite a wide range of evolutionary contingencies.

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