



# 2 Diversity of Mechanical Architectures in Climbing Plants: An Ecological Perspective

Au: The chapter title is too long for the running head. Please advise.

*Nick Rowe, Sandrine Isnard, Friederike Gallenmüller, and Thomas Speck*

## CONTENTS

|       |  |    |
|-------|--|----|
| 2.1   | Introduction .....   | 36 |
| 2.1.1 | Importance of Climbers .....   | 36 |
| 2.1.2 | Mechanical Structure and Development of Climbers .....                                 | 36 |
| 2.1.3 | Attachment Modes of Climbers.....  | 37 |
| 2.1.4 | Mechanical Constraints and Types of Attachment.....                                    | 37 |
| 2.2   | Methods and Materials.....   | 40 |
| 2.2.1 | Experimental Protocols.....  | 40 |
| 2.2.2 | Calculation of structural Young's Modulus.....   | 43 |
| 2.2.3 | Sampling.....  | 44 |
| 2.3   | Results: Mechanical Properties and Type of Attachment .....                            | 44 |
| 2.3.1 | Twining Climbers.....  | 44 |
| 2.3.2 | Tendril Climbers .....   | 45 |
| 2.3.3 | Hook Climbers .....  | 46 |
| 2.3.4 | Branch-Angle Climbers .....  | 50 |
| 2.3.5 | Leaning Climbers.....  | 53 |
| 2.4   | Discussion .....   | 53 |
| 2.4.1 | Mechanical Properties and Attachment of Dicotyledonous Climbers .....                  | 53 |
| 2.4.2 | Climbing Growth Strategies in Monocots and Other Plants without Secondary Growth ..... | 55 |
| 2.4.3 | Ecological Diversity of Climbers among Different Groups .....                          | 56 |
| 2.5   | Conclusions .....  | 57 |
|       | References.....  | 57 |



## 2.1 INTRODUCTION

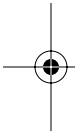
Many vines and lianas show extreme variations in mechanical properties during development from young to adult growth. These developmental trends differ from those observed in most self-supporting plants and have a significant effect on how climbing plants exploit the environment. Furthermore, different climbers show a wide range of attachment methods and may differ considerably in size as well as mechanical properties according to how they attach to host plants. To better understand how climbing habits differ, we investigate the mechanical properties of 43 species of tropical and temperate climbing plants according to their mode of attachment. The study includes stem twiners, tendril climbers, hook climbers, branch-angle climbers, and leaning climbers. Mechanical trends during growth are discussed in terms of mode of attachment, taxonomic affinity, and inherent developmental constraints (i.e., existence or lack of secondary growth) as well as approximate size and position of the climbing plant in the surrounding vegetation.

### 2.1.1 IMPORTANCE OF CLIMBERS

Climbing plants can differ considerably from self-supporting plants in terms of growth strategy and stem mechanics. Self-supporting plants can be understood to make up the overall primary mechanical structure of many terrestrial ecosystems, whereas climbers fill vacant space on and around their self-supporting hosts. Despite a number of commentators noting that the ecology of lianas is more poorly known compared with other plant growth forms such as trees, recent studies over the last decade, including biomechanical studies, have unequivocally demonstrated that lianas are extremely important constituents of many tropical ecosystems [1,2]. Furthermore, recent reports based on long-term censuses, particularly from the neotropics, have demonstrated that liana abundance is apparently increasing relative to tree species, possibly as a result of anthropogenic disturbance and/or climatic change [3,4]. Because climbing plants represent important elements as well as potential indicators of regional and possibly global vegetation change, there is much need for developing techniques and approaches to better understand their growth, development, and ecological significance, especially under natural conditions.

### 2.1.2 MECHANICAL STRUCTURE AND DEVELOPMENT OF CLIMBERS

Lianas are currently understood to have a range of important ecological functions in forest dynamics, of which a number are mechanical (Figure 2.1). Mature lianas climbing to the forest canopy can literally tie neighboring trees together (Figures 2.1c and 2.1d); they can weigh down and distort tree growth or even cause main branches or entire trees to fall. Young stages of liana growth can be particularly well adapted to spanning long distances even though they are composed of only narrow stems (Figures 2.1a and 2.1b), bridging host supports and exploring and filling open and disturbed areas, often to the detriment of self-supporting species. These specialized strategies are made possible in many climbing species by highly adapted mechanical properties of the stem. A number of recent studies have explored the developmental, ecological, and evolutionary significance of the transition from





relatively stiff young shoots to older more flexible stems [5–10]. This developmental trend differs from most self-supporting plants, which are normally composed of relatively compliant tissues when young and relatively stiff tissues when old. Many vine and liana stems show extreme changes in mechanical properties during development from young to adult plants (Figure 2.1), and these changes have a significant effect on how they exploit the environment. Climbers are particularly active in early successional and secondary forests as well as forest margins and disturbances within forests, including tree falls and tree fall gaps.

### 2.1.3 ATTACHMENT MODES OF CLIMBERS

Climbing plants can differ considerably in size, maximal diameter, mechanical properties of young and old stems, and exact ecological preference. Furthermore, they show a wide range of attachment organs connecting the climbing plant to its host plant or plants [11]. These attachment devices vary widely in mechanical function. Climbers, which attach themselves most firmly to host supports, are represented by twining stems, which can literally form knots around host trunks and branches. The main stem of the climber itself constitutes the connection with the host and such stems can be extremely firmly attached (Figure 2.1d). Climbers can also attach via tendrils and sensitive petioles or other touch-sensitive appendicular organs, which extend out and twine around relatively slender supports (Figure 5e and Figure 6f). These provide a relatively firm attachment for small-diameter searchers and for initial attachment to the host but are less strong than main twining axes that can provide extremely secure attachment after further woody secondary growth. Hooks, grapnels, recurved spines, and straight spines provide attachments, which are less secure than either twining leading stems or tendrils. Hooks and spines can be jolted loose from their attachment. Some hooks, such as the appendicular organs of the genus *Strychnos*, maintain woody growth after attachment and can eventually close the hook around the host support, providing a firmer attachment than when open (Figure 2.6d and 2.6e). Other climbers attain mechanical dependence on other host plants by even less secure and possibly less specialized attachment devices, including wide-angled, stiff branches, which can interlock with branches of neighboring plants (Figure 2.6a to 2.6c). Some climbing plants have roughened surfaces such as hairs, scales, or a roughened cuticular surface of the leaf that can increase frictional contact with potential host supports. Other climbers can generate friction or some degree of anchorage with the host plants via lobed or reflexed leaves.

TS: Ignore these figure citations. Insert figures in numerical order.

### 2.1.4 MECHANICAL CONSTRAINTS AND TYPES OF ATTACHMENT

The attachment of a climber to its support is a crucial aspect of its survival and ecology, and it can also mechanically influence its host plant. Climbers that twine via the main stem on host trees are less likely to fall than plants that deploy recurved hooks. An interesting question is whether the mechanical properties of the climbing plant stem differ according to the type of attachment device [5]. Climbers that deploy “weak” types of attachment might be expected to produce relatively stiffer stem materials than plants that are irreversibly twined onto the host support. If hook



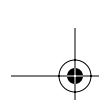
**FIGURE 2.1** (a) Juvenile stage of a twining liana. The plant is self-supporting and the stem below the circumnutating apex is relatively stiff and has a high  $E_{str}$  (French Guiana). This stage of development often has mechanical properties that are similar to those of the stiff terminal “searcher” twigs of adult climbing plants [see (b)]. (b) Apical, young stage of development of a mature twining liana (*Condylocarpon guyanense*) (French Guiana). Such axes are relatively stiff and span long distances to reach host supports. (c) Old stages of growth of a woody twining liana. The stems are firmly attached to the branches of the canopy, and the older basal portions are swinging freely from the canopy (French Guiana). Such stages have often very low values of  $E_{str}$ . (d) Old stage of growth of a twining liana stem traversing from one tree to another and forming a very firm attachment between the two (French Guiana). The stem was observed to be under significant tensile stress when the wind blew and the trees swayed violently in the wind. (e) Old stage of growth of *Bauhinia guianensis* (monkey ladder) (French Guiana). The mechanical properties of the old ribbonlike stem are characterized by low values of  $E_{str}$ , because this species attaches to the host tree by numerous tendrillar organs. The branch to the left is a reiterative branch with “young” development and circular cross section. These reiterative branches are very stiff.



attachment fails, a relatively stiff stem would prevent the stem from buckling and falling to the ground like a coil of rope; the relatively stiff stem would allow the plant to sway and perhaps secure attachment to another host. In this case, a good strategy would be to retain relatively stiff mechanical properties. Because climbing stems employing hooks and spines are more loosely attached to the host plant, swaying or movement of the host would also probably detach the climber from the support rather than constraining from being deformed and possibly becoming damaged during movement, especially if the host supports were massive. Climbers that are firmly attached, such as stem twiners possibly have rather different constraints between attachment type and stem mechanics. Although mature to aged twining stems can sometimes be observed to have loosened and fallen in coils from host trunks, many firmly secured twining connections that are reinforced by wood production will probably never disconnect from the stem unless by failure under extreme loading. In such cases, it is of no advantage of the climbing stem to invest in mechanically stiffening the older basal stem. In fact, with such types of connections, the host or climber will actually fail, possibly under the weight of the growing liana, before the twining attachment does. Failure of the host tree would probably result in catastrophic movement and stresses to the climbing plant stem; under such circumstances, a relatively slender stem is less likely to fail if it is flexible rather than relatively stiff. Furthermore, movement or swaying of host trees could exert extreme stresses and strains on the connected climbing stem, which if firmly twined or knotted to the host, would require high compliance to avoid failure [12]. Extreme movement of host trees might not occur often, but infrequent storm conditions with strong winds and large host movements could excessively load the stems of firmly attached climbers. Furthermore, tree falls and the formation of forest gaps are important elements of forest dynamics, particularly in the tropics. Plants that are firmly attached to trees and branches that fail are more likely to survive if compliant. Alternatively, more weakly attached climbers might avoid mechanical stresses by becoming unattached from the host.

In the following account, we investigate the bending elastic mechanical properties of 43 species of tropical and temperate climbing plants; we explore how mechanical properties of the stem vary with the type of attachment, overall height, size, and diameter of climbers ranging from woody lianas, which can extend to the canopy of the tropical rain forest, to more diminutive climbers or vines barely reaching a meter in height. The study has particular significance for understanding the likely ecological constraints on different climbing habits of different species. We have listed the species tested along with their type of attachment, taxonomic affinity, and approximate size and position of the mature climbing plant in the surrounding vegetation. We have differentiated between five types of attachment modes: stem twiners, tendrill climbers, hook climbers, branch-angle climbers, and leaning climbers. The categories of climber are somewhat generalized because, for example, both tendrill and hook climbers include plants with varying types of hooks and tendrils. An important omission in this study is root climbers, plants that climb on the host plant via roots produced from the stem. While these are an important element in many ecosystems, they are usually attached firmly along much of their entire length apart from the apex and as such differ from the majority of vines and lianas. In this





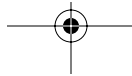
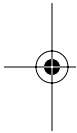
study, we compare plants that attach themselves to the host plant but do not “grow” directly on the host plant as do most root climbers.

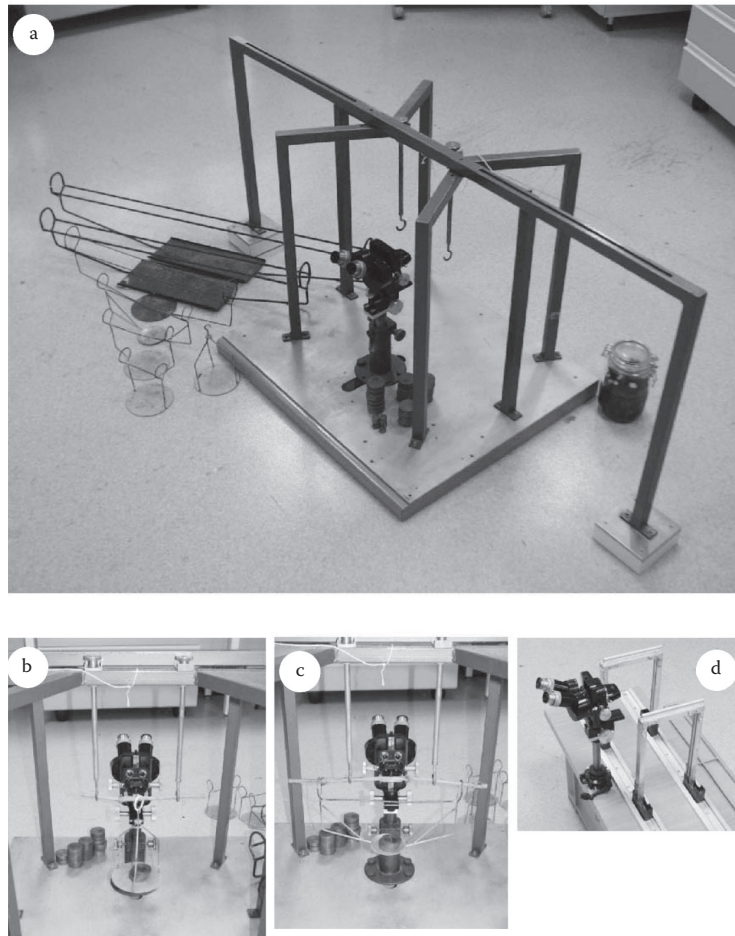
## 2.2 METHODS AND MATERIALS

A wide range of mechanical properties is relevant to the understanding of the extremely specialized stem structures found in some climbing stems. They include the stiffness in the elastic range of bending, torsion, and tension as well as other properties in the nonelastic range up to failure of the plant stem as well as toughness, extensibility, and critical strain — to mention a few [13,14]. Additional properties of interest and inextricably linked to stem mechanical properties are hydraulic conductance of the stem and the extent of mechanical deformation that can occur before the essential hydraulic supply of the stem is compromised. In the following account, we confine our attention to bending stiffness in the elastic range. We have chosen this single parameter because it can be measured relatively easily under field or laboratory conditions and because it gives a measure of the bending mechanical properties of the stem before irreversible deformation and damage outside the normal properties of living healthy plant tissues. Our objective is to compare a wide range of tested species with different climbing habits and, where possible, from plants sampled in their natural habitats. The inclusion of a wide range of mechanical parameters is not feasible with this view in mind. Bending mechanical properties can be measured in a number of ways and via a number of types of bending tests. In the following study, we include data from previous and ongoing research projects in which we use similar bending experimental protocols for a wide range of climbing species, in the laboratory, in relatively sophisticated “field laboratories,” and in remote field conditions.

### 2.2.1 EXPERIMENTAL PROTOCOLS

While bending tests are relatively straightforward in theory, the heterogeneity, geometry, combination of tissues contributing to the plant stem, and abrupt changes in development and anatomy provide a variety of practical and theoretical difficulties. A range of bending tests can be set up for the majority of climbing plant species, but the type of test depends on the diameter and resistance to bending of the material. A bending apparatus that we have used in many laboratory and field situations (Figure 2.2a) consists of a steel frame fixed to a solid base and equipped with adjustable holders that can be positioned at variable distances. A stereoscope binocular microscope equipped with an eyepiece graticule is attached to the base and can be adjusted vertically and focused in a horizontal plane to a fixed point on the plant specimen to critically observe deflection [7,15]. The apparatus can be configured for two types of bending tests: three-point (Figure 2.2b) and four-point (Figure 2.2c) bending. This kind of apparatus can be modified into more portable versions for making measurements in the field (Figure 2.2d). The principal aim of the bending experiment is to measure flexural stiffness,  $EI$ , of the stem, and from this quantity calculate the structural Young's modulus,  $E_{str}$ , of the plant stem [7].





**FIGURE 2.2** (a) Mechanical bending apparatus for use in field camps and field laboratories. The methods are entirely mechanical and do not require electricity. Plant stems are placed on supports suspended from a horizontal beam. Span distances can be adjusted to the size and bending resistance of the material. A range of panniers are used for tests in three- and four-point bending (left) as are a series of weights from 10 to 500 g (center). A series of up to six to eight weight increments is placed on the pannier, and the deflections are observed via a dissecting microscope equipped with an eyepiece graticule. The central part of each segment tested is stored in alcohol or FAA (right). (b) Configuration for three-point bending. The plant stem is placed on the two supports at a known distance, and the pannier is suspended from the exact center via a plastic ring, which can be turned obliquely to allow observation of the stem through the microscope. (c) Configuration for four-point bending. The plant stem is placed on the two supports at a known distance, and the two-armed pannier is placed on the specimen at equal distances from each central support. With this type of four-point bending, the weights applied to the pannier produce a deflection of the stem in an upward direction, and the influence of shear on the experiment is insignificant. (d) Portable, field bending apparatus. The plant specimen is placed on the two supports, and the span distance can be adjusted easily. Both three- and four-point bending tests are possible.

Au: Define  
FAA.

Plant stem segments are pruned from the plant body and placed in the apparatus configured for either three- or four-point bending. Stems are first checked for splits, fractures, or other damage that could affect their mechanical properties. Stems that taper significantly (more than 10%) and stems that include significantly thickened nodes or branch points are excluded from the study. Apical parts of some plant stems such as the leading searchers of lianas can show relatively abrupt changes in mechanical properties from immature tissue near the very apex to the mature, differentiated stem lower down. Tests of young axes should avoid this transition, which is not always obvious from external inspection.

There are a number of advantages and disadvantages to both three- and four-point bending. Three-point bending is relatively easy to apply because the weight is added centrally (Figure 2.2b) and the stem does not tend to move about and spoil the deflection reading when the weights are added. In four-point bending, however, the stem is loaded via a two-armed pannier (Figure 2.2c), and slightly irregular stems can twist or flip over after one or more weights are added. This means that it is sometimes difficult to study all of the stem segments of a sample. In three-point bending, because the force is applied and concentrated at one point at the center of the stem, the measurement can include deflection of the axis caused by shear of the plant tissues, thus such measurements would underestimate the flexural stiffness during the bending test [13,14,16,17]. In four-point bending, the force is distributed equally over the central portion of the tested stem, and the effect of shear is insignificant. Tests in three-point bending should be verified to find out the minimum span-to-depth ratio above which the effect of shear will be insignificant. A long length of plant stem is selected, and a series of tests at increasing span lengths is carried out until a span-to-depth ratio is reached at which the flexural stiffness becomes a constant value [15,18]. In a plant stem of, say, a liana, ideally such tests should be carried out prior to measuring stems with widely differing mechanical properties such as young and old developmental stages. Stiff combinations of plant tissues are less liable to shear than more compliant ones. Many references refer to a span-to-depth ratio of 20 as being suitable for three-point bending based on the properties of many industrially tested woods and timbers. This value, however, can change significantly. Some compliant plant materials we have observed require span-to-depth ratios of 40 or more. Four-point bending can also require the addition of quite substantial weight increments to obtain a reasonable deflection in the region of 1 to 3 mm for a range of stem diameters of 1 to 30 mm. Adding excessive weight in a four-point bending test can cause problems because the outer tissue of the plant stem resting on the fixed supports can indent and affect the deflection distance observed; this is especially the case when the deflection is small. Such problems can be addressed by carefully trimming soft bark tissue from around the of the stem's point of contact with the supports so that the support contacts harder wood beneath. But if the wood itself is compressible, the problem might be difficult to solve. In summary, three-point bending is somewhat easier and quicker to carry out, but the need for carrying out span tests can make the approach time-consuming, especially under field conditions. Four-point bending can be trickier to set up and carry out because of movement of the stem, and it might not be possible to measure all of the stem segments in a sample, resulting in a loss in continuity in the analysis. In





general, it is best to stick with one or the other types of test for a given analysis on a given plant. Having said that, it is also informative to first test a specimen in three-point bending and then repeat the test in four-point bending, combining this kind of verification with span tests; however, this takes time.

Successive weights are added during the bending experiment in three- or four-point bending at fixed time intervals of normally 1 min, which are sufficient for the plant stem to achieve its maximum deflection for a given weight. Creep is sometimes observed when the plant stem continues to deflect and is an indication that sufficient force is being applied to exceed the elastic range of the stem material. Some stems react extremely quickly to the force applied, while others react more slowly. The time increment should take this into account, but 1 min is normally enough to reach maximum deflection.

### 2.2.2 CALCULATION OF STRUCTURAL YOUNG'S MODULUS

The bending test results are plotted as the deflection (in millimeters) on the  $y$ -axis against the force applied (in Newtons) on the  $x$ -axis. The bending test was successful if the value of  $r^2$  for the force-deflection curve is greater than 0.98 (i.e., if the entire measurement is in the linear elastic range), the specimen has not moved or slipped during the test accidentally, and the experiment has remained within the elastic range. Immediately after the experiment, the diameter of the stem segment is measured in three to six positions along its length in the direction of the force applied and perpendicular to it. The mean axial second moment of area ( $I$ ) (in  $\text{mm}^4$ ) of the stem is then calculated from these measurements where the stem cross section is approximated as an ellipse:

$$I = (\pi/4) \cdot (r_1^3 \cdot r_2)$$

where  $r_1$  is the radial thickness of the stem in the direction of the applied force and  $r_2$  is the radial thickness in the perpendicular direction.

In three-point bending, the flexural stiffness ( $EI$ ) ( $\text{N mm}^2$ ) of the tested stem is calculated via:

$$EI = l^3/(48 \cdot b)$$

where  $l$  is the distance (mm) between the two supports (Figure 2b) and  $b$  is the slope of the force-deflection curve (deflection/force) (mm/N).

In four-point bending, the flexural stiffness ( $EI$ ) ( $\text{Nmm}^2$ ) of the tested stem is calculated via:

$$EI = l^2 \cdot a/(16 \cdot b)$$

where  $l$  is the distance between the two internal supports,  $a$  is the distance between the outside panner and the internal support (Figure 2c), and  $b$  is again the slope of the force-deflection curve (mm/N).



The structural Young's modulus of the stem ( $E_{str}$ ) ( $\text{N mm}^2$  or  $\text{MN m}^2$ ) is calculated via:

$$E_{str} = E/I/I$$

We use the term “structural Young's modulus” ( $E_{str}$ ) as the parameter to describe a structure consisting of different tissues, i.e., a plant stem [7,15].

### 2.2.3 SAMPLING

We present values of structural Young's modulus  $E_{str}$  for a wide taxonomic and morphological range of climbers; the results are presented as means and standard deviations for young and old developmental stages of climbing plants (Figure 2.3 and Figure 2.4; Table 2.1). Despite problems in assigning specific ages for young and old plant segments, young axes of the plant are generally positioned toward the apex and, often in climbing plants, represent “searchers” for reaching new hosts (Figures 2.1a and 2.1b). In general, older stages of development represent more basal and generally, but not always, more flexible parts of the climbing plant (Figures 2.1c and 2.1e) [10,19]. The object is to compare how mechanical properties vary with type of attachment among different plant groups. Attachment modes were summarized as:

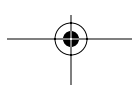
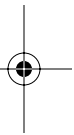
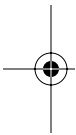
1. Twining or winding of the main leading axis and/or principal branches.
2. Attachment to the host plant via sensitive tendrils or tendril-like organs. There are a range of such types of organs derived from stem, leaf, or fertile axis. For simplicity, we have grouped these together. From a mechanical perspective and in terms of the growth form of the whole plant, we suspect that these types of attachment act similarly.
3. Attachment to host plants via hooks.
4. Attachment to host plants via wide-angled branches acting as anchors.
5. Leaning against the surrounding vegetation. The analysis includes 43 species from 18 vascular plant families, including 1 lycopsid, 3 gymnosperms, 8 monocotyledons, and 31 dicotyledons (Table 2.1).

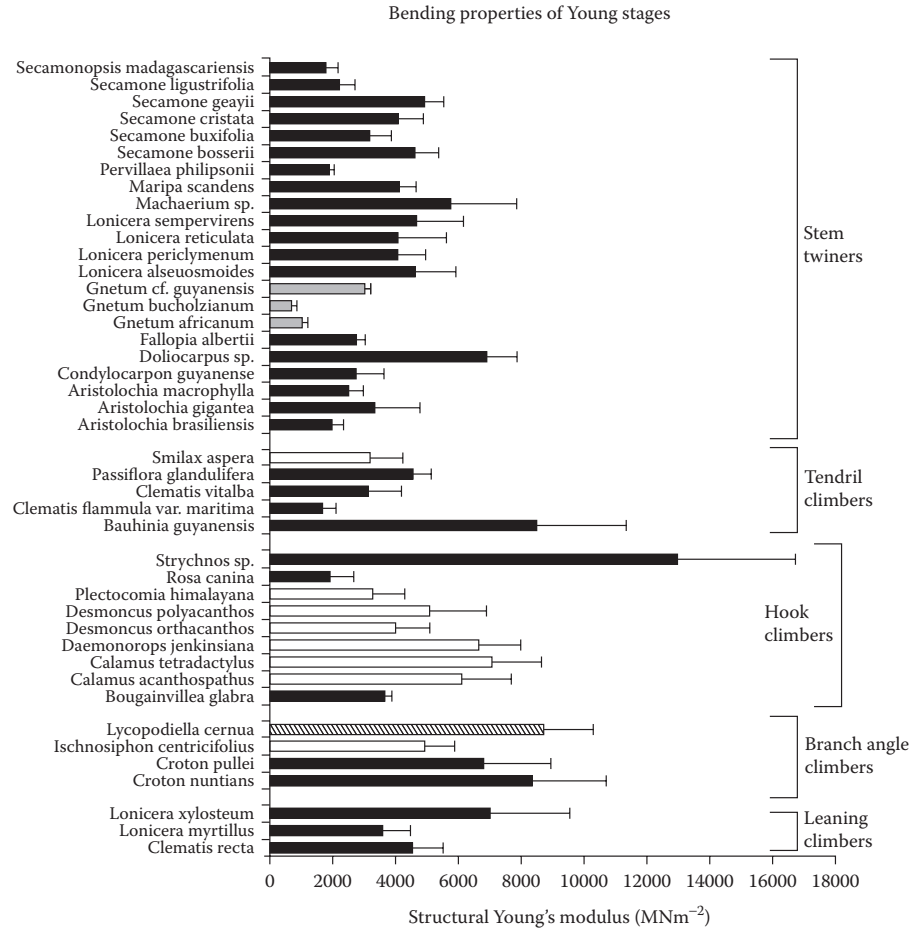
Au: Because there is no text below Results and because there is no other section on the level of 3.1, I combined the two heads and changed the levels of all the subsequent heads in this section.

## 2.3 RESULTS: MECHANICAL PROPERTIES AND TYPE OF ATTACHMENT

### 2.3.1 TWINING CLIMBERS

All twining climbers show a marked decrease in  $E_{str}$  from young to older stages of development (Table 2.1; Figure 2.3 and Figure 2.4). All but five twiners show relatively high values of  $E_{str}$  in young stages of development of 2000 to 6000  $\text{MN m}^2$ . The highest value for young stages occurs in *Doliocarpus* sp. at about 6900  $\text{MN m}^2$ . Except for the species of *Lonicera* and two species of *Secamone* (*S. bosserii*, *S. geayii*), values of older stages (Figure 2.4) are below 1200  $\text{MN m}^2$  and over half of these are less than 600  $\text{MN m}^2$ . All stem twiners tested are dicotyledonous



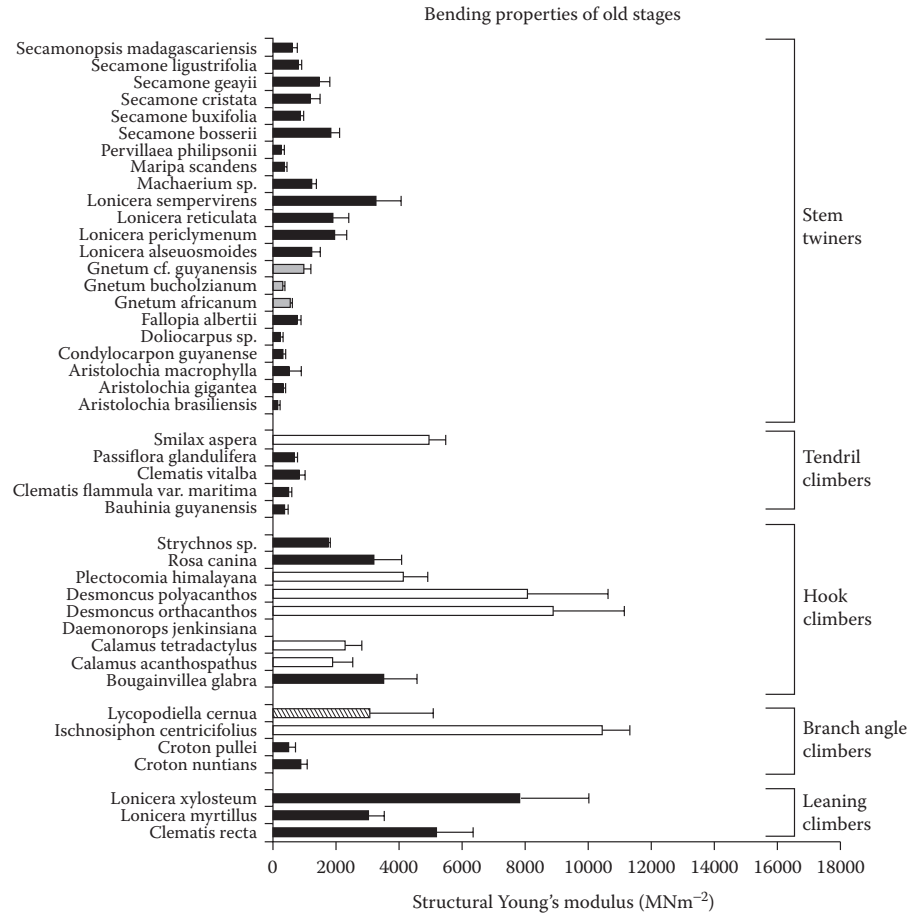


**FIGURE 2.3** Mean structural Young's modulus and one standard deviation of young stages of development of climbing plants with different modes of attachment. Black bars = dicotyledons, stippled bars = gymnosperms, white bars = monocotyledons, striped bar = lycopod.

angiosperms (Table 2.1) with the exception of the gymnosperm genus *Gnetum*. Interestingly, the two African species of *Gnetum* show markedly lower values of  $E_{str}$  in the young searcher shoots compared with all the other angiosperm twiners tested (Table 2.1; Figure 2.3 and Figure 2.4).

### 2.3.2 TENDRIL CLIMBERS

All dicotyledonous tendril climbers tested show a marked drop in  $E_{str}$  from young to older stages with final values of  $E_{str}$  in the range of below 1000 MN m<sup>2</sup> (Table 2.1; Figure 2.3 and Figure 2.4). The species of *Bauhinia* (monkey ladder) shows an extreme drop in mechanical properties from young stages of over 8000 MN m<sup>2</sup> (Table 2.1). This varies from one of the highest tested of all categories (8480 MN m<sup>2</sup>)



**FIGURE 2.4** Mean structural Young's modulus and one standard deviation of old stages of development of climbing plants with different modes of attachment. Black bars = dicotyledons, stippled bars = gymnosperms, white bars = monocotyledons, striped bar = lycopod.

to one of the lowest (350 MN m<sup>2</sup>). The species shows a marked change in both material properties of the stem (Figure 2.3 and Figure 2.4) as well as a profound change in stem geometry leading to ribbonlike, highly flexible stems (Figure 2.1e). In contrast to the dicotyledonous twiners, the small monocotyledonous climber *Smilax aspera*, which generally grows on herbs, shrubs, and small trees, shows an increase in  $E_{str}$  from younger parts of the plant to older basal parts (Table 2.1).

### 2.3.3 HOOK CLIMBERS

The hook climbers show a more variable range of shifts in mechanical properties compared with twiners and tendril climbers (Table 2.1; Figure 2.3 and Figure 2.4). The woody dicotyledonous liana *Strychnos* (Figure 2.6d and 2.6e) shows the highest value of  $E_{str}$  of all plants tested in young stages of development, i.e., over 12,000

**TABLE 2.1**  
**Structural Young's Modulus, Attachment Type, Size, Diameter, and Taxonomic Group of 43 Tested Climbing Plants from 18 Different Vascular Plant Families**

| Species                            | Notes | $E_{st}$ [MNm <sup>-2</sup> ]<br>Young Stages | $E_{st}$ [MNm <sup>-2</sup> ]<br>Old Stages | Climbing to:                                |                   | Diameter<br>Of Widest<br>Stem<br>Tested<br>[Mm] | No. of<br>Samples<br>(Young<br>Stages) | No. of<br>Samples<br>(Old Stages) | Family         | Group    |
|------------------------------------|-------|---|---|---|-------------------|---|--|-----------------------------------|----------------|----------|
|                                    |       |   |   | Forest Understory<br>Herb to Shrub<br>Level | Herb Level        |   |  |                                   |                |          |
| <b>Leaning</b>                     |       |   |   |   |                   |   |  |                                   |                |          |
| <i>Clematis recta</i>              | **    | 4521 ± 980                                    | 5132 ± 1200                                 | Herb to shrub                               | Herb to shrub     | 6   | 20                                     | 33                                | Ranunculaceae  | Dicot    |
| <i>Lonicera myrtillus</i>          | **    | 3560 ± 939                                    | 2978 ± 560                                  | Forest understory                           | Forest understory | 10  | 3                                      | 7                                 | Caprifoliaceae | Dicot    |
| <i>Lonicera xylosteum</i>          | *     | 7022 ± 2497                                   | 7790 ± 2222                                 | Forest understory                           | Forest understory | 18  | 4                                      | 5                                 | Caprifoliaceae | Dicot    |
| <b>Angled Branch</b>               |       |   |   |   |                   |   |  |                                   |                |          |
| <i>Croton nuntians</i>             | *     | 8318 ± 2401                                   | 849 ± 211                                   | Forest canopy                               | Forest canopy     | 49  | 14                                     | 5                                 | Euphorbiaceae  | Dicot    |
| <i>Croton pulliei</i>              | *     | 6741 ± 2206                                   | 490 ± 203                                   | Forest canopy                               | Forest canopy     | 102   | 38                                     | 8                                 | Euphorbiaceae  | Dicot    |
| <i>Ischnosiphon centricifolius</i> | *     | 4956 ± 921                                    | 10427 ± 921                                 | Forest understory                           | Forest understory | 15  | 5                                      | 8                                 | Marantaceae    | Monocot  |
| <i>Lycopodiella cernua</i>         | *     | 8719 ± 1571                                   | 3031 ± 2054                                 | Herb to shrub                               | Herb to shrub     | 4   | 10                                     | 10                                | Lycopodiaceae  | Lycopsid |
| <b>Hook</b>                        |       |   |   |   |                   |   |  |                                   |                |          |
| <i>Bougainvillea glabra</i>        | **    | 3640 ± 219                                    | 3460 ± 1113                                 | Forest canopy                               | Forest canopy     | 11  | 41                                     | 20                                | Nyctaginaceae  | Dicot    |
| <i>Calamus acanthospathus</i>      | *     | 6110 ± 1560                                   | 1830 ± 670                                  | Forest canopy                               | Forest canopy     | 15  | 3                                      | 2                                 | Areaceae       | Monocot  |
| <i>Calamus terradactylus</i>       | **    | 7070 ± 1560                                   | 2300 ± 500                                  | Forest canopy                               | Forest canopy     | 13  | 13                                     | 40                                | Areaceae       | Monocot  |
| <i>Daemonorops jenkinsiana</i>     | **    | 6630 ± 1330                                   | -   | Forest canopy                               | Forest canopy     | 33  | 8                                      | 4                                 | Areaceae       | Monocot  |
| <i>Desmoncus orthacanthos</i>      | *     | 4000 ± 1070                                   | 8906 ± 2240                                 | Forest canopy                               | Forest canopy     | 30  | 17                                     | 9                                 | Areaceae       | Monocot  |
| <i>Desmoncus polyacanthos</i>      | *     | 5074 ± 1782                                   | 8091 ± 2546                                 | Forest understory                           | Forest understory | 10  | 16                                     | 11                                | Areaceae       | Monocot  |
| <i>Plectocomia himalayana</i>      | *     | 3250 ± 1030                                   | 4120 ± 780                                  | Forest canopy                               | Forest canopy     | 40  | 3                                      | 3                                 | Areaceae       | Monocot  |
| <i>Rosa canina</i>                 | *     | 1848 ± 787                                    | 3155 ± 954                                  | Herb to shrub                               | Herb to shrub     | 13  | 12                                     | 23                                | Rosaceae       | Dicot    |
| <i>Strychnos</i> sp.               | *     | 12920 ± 3790                                  | 1750 ± 40                                   | Forest canopy                               | Forest canopy     | 49  | 14                                     | 2                                 | Loganiaceae    | Dicot    |

(continued)

Au: Ed'in  
 Table 11  
 deleted the  
 Attach-  
 ment type  
 column and  
 added sub-  
 heads to  
 indicate  
 that infor-  
 mation  
 since  
 everything  
 was  
 arranged  
 that way  
 anyway.  
 This makes  
 the table a  
 little  
 smaller and  
 conveys  
 the same  
 informa-  
 tion.



**TABLE 2.2 (CONTINUED)**  
**Structural Young's Modulus, Attachment Type, Size, Diameter, and Taxonomic Group of 43 Tested Climbing Plants from 18 Different Vascular Plant Families**

| Species  | Notes | $E_{st}$ [MNm <sup>-2</sup> ]<br>Young Stages | $E_{st}$ [MNm <sup>-2</sup> ]<br>Old Stages | Climbing to:                                |                   | Diameter<br>Of Widest<br>Stem<br>Tested<br>[Mm] | No. of<br>Samples<br>(Young<br>Stages) | No. of<br>Samples<br>(Old Stages) | Family           | Group      |
|--|-------|---|---|---|-------------------|---|--|-----------------------------------|------------------|------------|
|  |       |   |   | Forest Understory<br>Herb to Shrub<br>Level | Herb Level        |   |  |                                   |                  |            |
| <b>Tendrils</b>                                  |       |   |   |   |                   |   |  |                                   |                  |            |
| <i>Bauhinia guyanensis</i>                       | *     | 8480 ± 2820                                   | 350 ± 100                                   | Forest canopy                               | Forest canopy     | 18  | 3                                      | 3                                 | Fabaceae         | Dicot      |
| <i>Clematis flammula</i> var.<br><i>maritima</i> | *     | 1619 ± 492                                    | 470 ± 113                                   | Herb to shrub                               | Herb to shrub     | 10  | 21                                     | 10                                | Ranunculaceae    | Dicot      |
| <i>Clematis vitalba</i>                          | *     | 3074 ± 1083                                   | 772 ± 261                                   | Forest canopy                               | Forest canopy     | 18  | 18                                     | 17                                | Ranunculaceae    | Dicot      |
| <i>Passiflora glandulifera</i>                   | *     | 4540 ± 620                                    | 630 ± 130                                   | Forest canopy                               | Forest canopy     | 21  | 3                                      | 3                                 | Passifloraceae   | Dicot      |
| <i>Smilax aspera</i>                             | *     | 3178 ± 1057                                   | 4937 ± 529                                  | Herb to shrub                               | Herb to shrub     | 6   | 7                                      | 7                                 | Smilacaceae      | Monocot    |
| <b>Stem Twiner</b>                               |       |   |   |   |                   |   |  |                                   |                  |            |
| <i>Aristolochia brasiliensis</i>                 | **    | 1955 ± 411                                    | 104 ± 72                                    | Forest canopy                               | Forest canopy     | 35  | 6                                      | 8                                 | Aristolochiaceae | Dicot      |
| <i>Aristolochia gigantea</i>                     | **    | 3343 ± 1405                                   | 294 ± 89                                    | Forest canopy                               | Forest canopy     | 23  | 6                                      | 5                                 | Aristolochiaceae | Dicot      |
| <i>Aristolochia macrophylla</i>                  | **    | 2465 ± 479                                    | 497 ± 385                                   | Forest understory                           | Forest understory | 28  | 40                                     | 45                                | Aristolochiaceae | Dicot      |
| <i>Conylocarpus guyanense</i>                    | *     | 2720 ± 900                                    | 310 ± 50                                    | Forest canopy                               | Forest canopy     | 38  | 36                                     | 11                                | Apocynaceae      | Dicot      |
| <i>Dolioscarpus</i> sp.                          | *     | 6870 ± 980                                    | 290 ± 30                                    | Forest canopy                               | Forest canopy     | 33  | 3                                      | 3                                 | Dilleniaceae     | Dicot      |
| <i>Fallopia albertii</i>                         | **    | 2740 ± 290                                    | 730 ± 150                                   | Forest canopy                               | Forest canopy     | 13  | 10                                     | 3                                 | Polygonaceae     | Dicot      |
| <i>Gnetum africanum</i>                          | *     | 1036 ± 176                                    | 560 ± 64                                    | Forest canopy                               | Forest canopy     | 24  | 2                                      | 4                                 | Gnetaceae        | Gymnosperm |
| <i>Gnetum buchholzianum</i>                      | *     | 683 ± 180                                     | 293 ± 90                                    | Forest canopy                               | Forest canopy     | 17  | 11                                     | 7                                 | Gnetaceae        | Gymnosperm |
| <i>Gnetum</i> cf. <i>guyanensis</i>              | *     | 3037 ± 126                                    | 961 ± 222                                   | Forest canopy                               | Forest canopy     | 17  | 2                                      | 3                                 | Gnetaceae        | Gymnosperm |
| <i>Lonicera albeo-smoides</i>                    | **    | 4561 ± 1330                                   | 1170 ± 342                                  | Forest understory                           | Forest understory | 7   | 10                                     | 2                                 | Caprifoliaceae   | Dicot      |
| <i>Lonicera periclymenum</i>                     | *     | 4050 ± 894                                    | 1912 ± 444                                  | Forest understory                           | Forest understory | 24  | 3                                      | 6                                 | Caprifoliaceae   | Dicot      |
| <i>Lonicera reticulata</i>                       | **    | 4028 ± 1589                                   | 1876 ± 528                                  | Forest understory                           | Forest understory | 9   | 8                                      | 5                                 | Caprifoliaceae   | Dicot      |
| <i>Lonicera sempervirens</i>                     | **    | 4666 ± 1516                                   | 3262 ± 796                                  | Forest understory                           | Forest understory | 12  | 8                                      | 3                                 | Caprifoliaceae   | Dicot      |

Au: Ed:in  
 Table 11  
 deleted the  
 Attach-  
 ment type  
 column and  
 added sub-  
 heads to  
 indicate  
 that infor-  
 mation since  
 everything  
 was  
 arranged  
 that way  
 anyway.  
 This makes  
 the table a  
 little  
 smaller and  
 conveys  
 the same  
 informa-  
 tion.

## Diversity of Mechanical Architectures in Climbing Plants

|                                      |   |   |             |            |                 |    |    |    |                |       |
|--------------------------------------|---|---|-------------|------------|-----------------|----|----|----|----------------|-------|
| <i>Machaerium</i> sp.                | * | a | 5750 ± 2110 | 1200 ± 150 | Forest canopy   | 29 | 3  | 3  | Fabaceae       | Dicot |
| <i>Maripa scandens</i>               | * | a | 4111 ± 510  | 390 ± 30   | Forest canopy   | 32 | 5  | 3  | Convolvulaceae | Dicot |
| <i>Pervillaea philipponii</i>        | * |   | 1851 ± 232  | 266 ± 79   | Forest canopy   | 15 | 12 | 11 | Apocynaceae    | Dicot |
| <i>Secamone bosserii</i>             | * |   | 4573 ± 818  | 1793 ± 305 | Herb to shrub   | 12 | 12 | 6  | Apocynaceae    | Dicot |
| <i>Secamone buxifolia</i>            | * |   | 3145 ± 693  | 850 ± 85   | Forest canopy   | 17 | 12 | 6  | Apocynaceae    | Dicot |
| <i>Secamone cristata</i>             | * |   | 4057 ± 851  | 1158 ± 357 | Forest to shrub | 11 | 9  | 2  | Apocynaceae    | Dicot |
| <i>Secamone geayii</i>               | * |   | 4909 ± 647  | 1415 ± 396 | Herb to shrub   | 11 | 8  | 6  | Apocynaceae    | Dicot |
| <i>Secamone ligustrifolia</i>        | * |   | 1976 ± 544  | 767 ± 105  | Forest canopy   | 29 | 12 | 7  | Apocynaceae    | Dicot |
| <i>Secanomopsis madagascariensis</i> | * |   | 1734 ± 413  | 570 ± 192  | Forest canopy   | 23 | 12 | 4  | Apocynaceae    | Dicot |

Note: The species are listed according to type of attachment. Values of  $E_{ar}$  are based on means and 1 standard deviation.

\* Plant measured in natural habitat

\*\* Plant measured in botanical gardens or greenhouses.

a See ref. [8]

b See ref. [27]

c See ref. [7]

d See ref. [21]

e See ref. [15]

f See ref. [25]

g Old stems of *Bauhinia guyanensis* are ribbon-shaped; the maximum diameter given here corresponds to the diameter of a circular surface equal in area to the ribbon-shaped stem in cross section.

h Measurements of *Rosa camina* are confined to leaning or climbing stems up to 1 year old.

i Data for these climbing palms include measurements based on old stages in which the outer leaf sheath has been lost via natural aging. The other species are all based on older portions of climbing stems in which the leaf sheath is still attached but usually, at least, partially senescent.

MN m<sup>2</sup>, followed by a large reduction in  $E_{\text{str}}$  (Table 2.1). In older stages, its value of  $E_{\text{str}}$  is also rather higher than most twining and tendril-climbing species. The two woody hook-climbers *Bougainvillea* and *Rosa* do not show a noticeable drop in  $E_{\text{str}}$  during development; rather, they retain relatively high values in old stages.

Monocotyledonous hook climbers (Figure 2.5) also show variable trends, depending on the taxonomic group they belong to. Species of *Calamus* (Calaminae, Calamoideae) (Figure 2.5b) show decreases in  $E_{\text{str}}$  to values of 1663 and 2297 MN m<sup>2</sup>, equivalent to the highest values of old twining species (*Lonicera* and *Secamone*) (Table 2.1; Figure 2.3 and Figure 2.4). Old stages of these *Calamus* species are canelike and have lost the leaf sheath that contributed to relatively high values of  $E_{\text{str}}$  in young stages of growth. In *Daemonorops jenkinsiana*, old stages included stems, which are still surrounded by leaf sheaths. For this species, very old and long stems were not available in the studied area. In *Plectocomia himalayana* (subtribe Plectocominae), the older stages measured show no changes in mechanical properties compared with young stages (Table 2.1; Figure 2.3 and Figure 2.4). For this species, values of  $E_{\text{str}}$  remain high, around 3000 to 4000 MN m<sup>2</sup> (Table 2.1). The South American climbing palm *Desmoncus* (Arecoideae) (Figure 2.5a and 2.5f) shows a quite different trend. Interestingly, both species show a marked increase in  $E_{\text{str}}$  in older stages of development, for which the leaf sheath has senesced and, in the case of *D. orthacanthos*, was finally lost. Values in young stages of around 4000 to 5000 MN m<sup>2</sup> are in the similar range, with higher values found among twiners and tendril climbers, whereas values in older stages of 8000 to 9000 MN m<sup>2</sup> are higher than all other plants tested with the exception of the monocotyledon *Ischnosiphon* and the leaning species *Lonicera xylosteum* (Table 2.1).

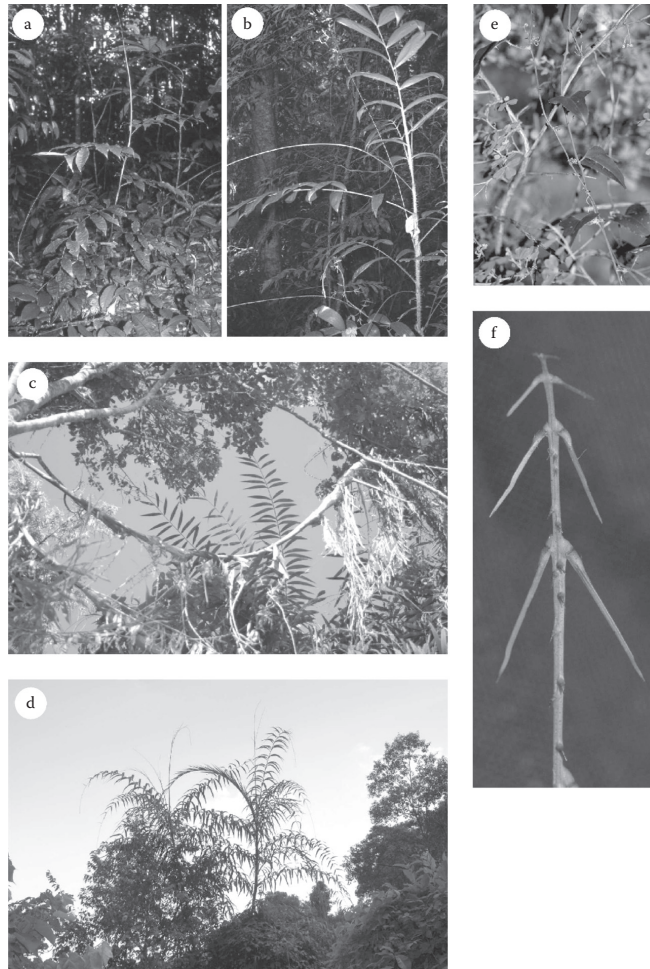
Au: The Calamus species in Table 2.1 do not have these values. It's not clear what these numbers represent.

### 2.3.4 BRANCH-ANGLE CLIMBERS

Plants forming attachments via wide-angled branching also show widely differing patterns of change in  $E_{\text{str}}$ . The species of *Croton*, representing a woody dicotyledon (Figure 2.6a), shows a similar trend as the majority of twiners and tendril-climbers (Table 2.1; Figure 2.3 and Figure 2.4). The young parts of climbing stems have high values of  $E_{\text{str}}$  and above the general range of nearly all twiners and most of the hook climbers and tendril climbers. The older parts show a marked drop in  $E_{\text{str}}$  with values of less than 1000 MN m<sup>2</sup>, approaching that of many tendril climbers and twiners and, interestingly, well below that of all of the other hook climbers.

Stems of *Lycopodiella cernua* interlock with the surrounding vegetation via lateral branches. The younger parts of the plant show relatively stiff mechanical properties of over 8000 MN m<sup>2</sup>, in the range of woody rigid species like *Bauhinia* and *Strychnos* (Table 2.1; Figure 2.3 and Figure 2.4). The older stage at the base of the plant is more flexible but still retains high values of around 3000 MN m<sup>2</sup>.

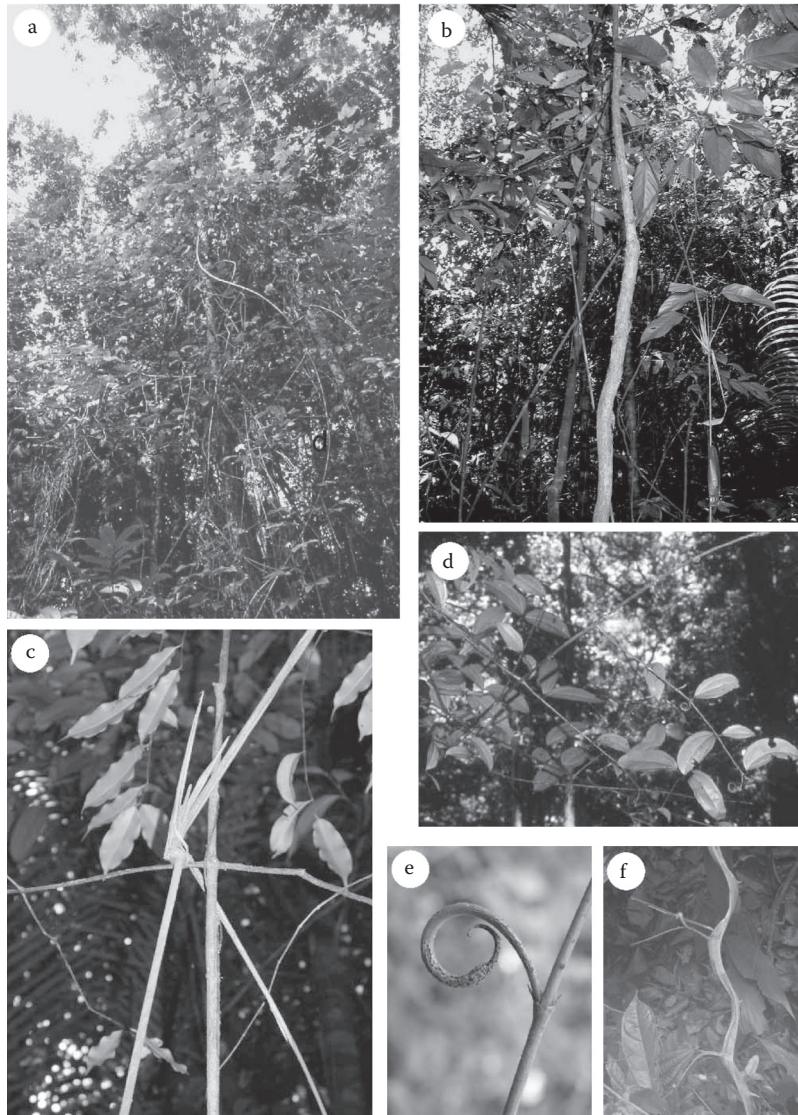
Finally, the monocotyledonous branch climber, *Ischnosiphon centricifolius* (Marantaceae) has highly characteristic “pencil-like” stems, which produce rosettes of leaves at nodes along the stem (Figure 2.6b and 2.6c). Both the leaves and the angle formed by the insertion of the next internode can anchor the plant stem onto surrounding host plants in the forest understory. Younger distal parts of the climbing stem show relatively high values of  $E_{\text{str}}$  of around 5000 MN m<sup>2</sup>, which is in the



**FIGURE 2.5** (a) Young phase of growth of the understory climbing palm *Desmoncus polyacanthos* (French Guiana). When the plant becomes mechanically unstable, it produces leaves equipped with distal hooks and grapnel-bearing cirri (left). (b) Young phase of growth of *Calamus acanthospathus* (Yunnan Province, China). When the plant becomes unstable, long modified inflorescences bearing recurved hooks (flagellae) are produced, and the plant can reach the canopy, producing stems over 30 m in length. (c) The calamoid rattan palm *Plectocomia himalayana* (Yunnan Province, China), old stage of development in which the young part of the plant is firmly attached in the canopy and the older part of the axis is spanning a wide space between supports. The leaves and leaf sheaths of this part of the stem are senescing and lose their attachment with the original supports. (d) Apical parts of *P. himalayana* emerge from the forest canopy (Yunnan Province, China) and bear many cirrus-bearing leaves and many potential attachment points with the surrounding canopy vegetation. (e) The small-bodied *Smilax aspera* (southern France) uses both apendicular tendrils and recurved hooks for attaching to host plants. Tendrils firmly connect the plant to the host. (f) Apex of the attachment organ (cirrus) of *Desmoncus polyacanthos* (French Guiana) produce laterally deployed grapnel-like modified leaflets (acanthophylls) and abaxially placed recurved spines.

Au: Plecto-  
comia hima-  
layana  
correct spell-  
ing





**FIGURE 2.6** The branch-angle climber *Croton nuntians* (French Guiana) shows a well attached apex and flexible older stems descending to ground level. (b) The climbing monocotyledon *Ischnosiphon centricifolius* (French Guiana). Its narrow pencil-like stems ascend into the understory. (c) The angles formed between successive nodes and internodes in stems of *Ischnosiphon centricifolius* provide effective points of attachment. (d) Stiff distal branches and sensitive hooks of *Strychnos* sp. (French Guiana). (e) Unattached hook of *Strychnos* sp. When hooks locate a host branch, they can develop a more secure attachment by tendril-like growth and woody development (French Guiana). (f) Appendicular woody tendrils produced from *Bauhinia guianensis*. Such structures can form firm attachments to narrow diameter host branches (French Guiana).





upper range of values for twiners and hook climbers. Interestingly older, more basal parts of the plant show very high values of  $E_{\text{str}}$  of over 10,000 MN m<sup>2</sup> (Table 2.1; Figure 2.3 and Figure 2.4).

### 2.3.5 LEANING CLIMBERS

This final category includes plants that simply lean against the surrounding vegetation without any specialized attachment, often showing a limited range of development and small body size. Species tested do not show significant changes in mechanical properties from young to old stages (Table 2.1; Figure 2.3 and Figure 2.4). The two woody dicotyledons, *L. xylosteum* and *L. myrtilus*, which resemble “unstable shrubs” show high values of  $E_{\text{str}}$  in old stages with values of *L. xylosteum* among the five stiffest stems tested of older stages. The small statured *Clematis recta* also shows very similar values of  $E_{\text{str}}$  in both younger apical parts of the plant and older basal stages of development.

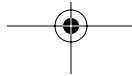
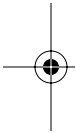
## 2.4 DISCUSSION

### 2.4.1 MECHANICAL PROPERTIES AND ATTACHMENT OF DICOTYLEDONOUS CLIMBERS

All twiners, tendrill climbers, and branch-angle climbers of dicotyledons show a drop of  $E_{\text{str}}$  from young to old stages of growth. These changes in mechanical properties probably reflect a need for twining and tendrill plants to be protected against extreme forces generated by movement of the host trees. Climbers that twine from one tree to another risk experiencing extremely high forces during high winds and after failure of branches and trunks. The twining strategy therefore requires highly compliant older stems that can withstand severe stresses and strains. Being strongly attached to a support also means that once the stem is attached, the part of the stem that is below the point of attachment has little need of stem stiffness to partially support the stem or lean against surrounding vegetation to retain its position. Mature trunks of large-bodied twining species are often so compliant that they hang in tension from the point of attachment above. Such stems can have very low structural Young's moduli as reflected in some of the values presented among twiners.

Tendrils can also form an extremely firm attachment to the host supports, but the attachment is usually weaker than for stem twiners because the tendrillar organs are often derived from modified stipules, leaves, or fertile axes, which have narrow diameters. Like stem twiners, tendrill climbers also have little need of stem stiffness in basal parts of the plant once they are firmly attached at many points.

Hook climbers are generally less firmly attached to the host plant than either stem twiners or tendrill climbers. Hooks and curved spines can be effective means of attaching to host supports, but attachment is constrained by the internal angle and length of the hook. They can also be dislodged by movement of the host branches. Compared with twiners, hook climbers are considerably less firmly attached to the host plant, particularly in young stages. Movement and swaying of the host plant could potentially dislodge the climber from the support rather than exert extreme



stresses on the main stem as in twiners. Furthermore, relatively stiff, older parts would ensure that the plant stem would maintain its position in the vegetation even though one or more hooks had become unattached. After detachment, the young apical part of the plant would remain in the vicinity of potential supports. This is quite different from the effect of removing the attachment from a mature or aging stem twiner because such stems can buckle and collapse in coils of their own weight. A hook-climbing strategy with relatively stiff older stems is probably adopted by many different plant groups and with different developmental constraints [20]. Among the plants tested, two of the three woody plants, *Bougainvillea* and *Rosa*, retain relatively high Young's moduli in older stages of development, with even higher values found in **yet** older stages of *Rosa*. Interestingly, both climb via less specialized curved spines rather than acutely angled hooks. In species of *Strychnos* tested from French Guiana, early growth of apical branches bear open hooks that are green and sensitive to touch (Figure 2.6e). They can engage small-diameter supports, and the limb of the hook eventually thickens and closes around the supporting host branch. *Strychnos*, like all the dicotyledons that produce active attachment organs, shows a large reduction in  $E_{\text{str}}$  to just below 2000 MN m<sup>2</sup> from relatively large values of over 12,000 MN m<sup>2</sup> found in young stages.

Au: Addition of "yet OK in sentence beginning "Among the plants tested..."? Otherwise the meaning is unclear.

Plants climbing via wide-angled branches show high values of  $E_{\text{str}}$  in young stages, generally higher than those of twiners and consistent with the idea that young stages of growth require stem stiffness for attachment. Wide-angled branches can interlock with the branches of neighboring trees and provide very firm anchorage. It is important that young stages of growth be stiff and not deflect when the plant has established its climbing phase. The branch-angle climbers of *Croton* also show marked drops in  $E_{\text{str}}$  toward the base of the plant. Even though the attachment is not as active as in tendrils and twining species, branch anchorage can be very effective and can be coupled with very low values of  $E_{\text{str}}$  in old stems [21].

For the three plants grouped as leaning climbers, general observations indicate that branches and leaves do not anchor the plant in the vegetation. We saw previously that the adult stems of *Croton* that were tested can be suspended from the host canopy via their wide-angled attachment and finally produce highly compliant wood. Unlike climbing species of *Clematis*, the petioles of *C. recta* do not twine extensively around supports. Similarly the two leaning species of *Lonicera* tested differ from the more typical climbing species in that they do not twine around neighboring stems. All three plants produce little change in  $E_{\text{str}}$  from young to old stages of development and from near the apex to the base. The values do remain relatively high, and this kind of pattern has been termed "semi-self-supporting" [10]. Such growth forms retain relatively stiff mechanical properties through their growth trajectory. They form little attachment with host vegetation apart from simply leaning.

Most dicotyledonous species that show a marked decrease in  $E_{\text{str}}$  during development, such as stem twiners and tendril climbers, have active attachment organs. The data also indicate that some species (e.g., *Croton*) that climb by wide-angled branches are also capable of producing compliant wood. The production of branches with many potential points of anchorage might finally permit a firm connection with the surrounding vegetation, but twining stems are always more firmly bound. Interestingly, both *Strychnos* and *Croton* eventually produce older stages of growth with

relatively low values of  $E_{\text{str}}$ . Recent studies have shown that these plants have relatively extended “stiff” phases of development, and this is possibly linked to their type of attachment as well as other potential environmental factors such as light availability [9,20]. The type of attachment shown by these plants via many potential points of attachment and the degree of security this affords to the climbing plant differs considerably from the mechanical constraints imposed by firmly twining or attaching via tendrils.

#### 2.4.2 CLIMBING GROWTH STRATEGIES IN MONOCOTS AND OTHER PLANTS WITHOUT SECONDARY GROWTH

In dicotyledonous species, the secondary growth leads to an increase in the second moment of area ( $I$ ) and stem flexural stiffness ( $EI$ ). The reduction of  $E_{\text{str}}$  during development can be interpreted as a mechanical strategy that “compensates” for this increase in  $I$  and confers relative stem compliance. Despite the diversity of attachment modes, all the monocots tested, except for species of the rattan *Calamus*, show high values of  $E_{\text{str}}$  in old stages and otherwise little change in mechanical properties during development. The latter can be explained by the structural constraints inherent to monocotyledons as a result of the absence of secondary growth. By retaining relatively small stem diameters (i.e., a small  $I$ ) in old stems, the monocots escape this constraint and can, even with a high value of  $E_{\text{str}}$  remain compliant in older stems, i.e., have a relatively small  $EI$  in old developmental stages [20,22]. The tendril-climbing species *Smilax aspera* also lacks secondary growth and shows an opposite trend to other dicotyledonous tendril climbers, with an increase in structural Young’s modulus. *Smilax aspera* is a relatively lightly built, small-bodied plant rarely exceeding shrub level in its natural habitat (Figure 2.5e), and may therefore not be exposed to high stresses caused by the swaying of the host plants as would be the case for large tendril climbers. The branch-angle climber *Ischnosiphon* with its pencil-like stem has a peculiar growth form that relies largely on stem stiffness to maintain the plant in position between points at which leaf-bearing nodes catch onto branches of host plants. High stiffness from top to bottom is used throughout the life history of the plant to ensure a weakly attached, partially leaning growth form. A similar strategy is observed in the more diminutive lycopsid *Lycopodiella cernua*, which has very high values of  $E_{\text{str}}$  in near apical portions of their small stems that are only loosely supported by the wide-angled branches [9,23]. This plant also lacks secondary tissues, but the primary tissues toward the base of the stem are more compliant. The developmental and ecological significance of the basal compliancy in *Lycopodiella* is not clear [9,20,23]. This herbaceous plant is self-supporting with climbing and horizontal or trailing axes. It is possible that the basal compliancy observed may permit the plant to occupy a procumbent orientation by bending at the base if it becomes detached from the surrounding herbs and shrubs. Many formerly upright or leaning individuals end up as procumbent stems. If true, this is an interesting variant of how herbaceous plants might use stem compliancy to avoid damage via mechanical stresses after movement and falling from host supports.

The palms tested climb via hooklike organs placed on modified frond tips (cirri) or modified inflorescence stalks (flagellae) that emerge from the leaf sheath. Two

species of the South American genus *Desmoncus* show an actual increase in  $E_{\text{str}}$  toward the base of the plant [22]. In the larger species, *D. orthacanthos*, old stages have shed the outer leaf sheath and resemble canes. This stage of development does nevertheless show relatively high values of  $E_{\text{str}}$ . With the exception of the two tested *Calamus* species, the other climbing palms in the Calamoideae, *P. himalayana* (Plectocominae) [24] also show high values of  $E_{\text{str}}$  in old stages. This is consistent with the idea that hook climbers that are not firmly bound to host supports do not need to develop high compliancy to survive movement of host branches. Instead, the relatively high stiffness of the stem ensures that the stems can retain their orientation in the surrounding vegetation when movement of the host branches moves or detaches any hooks and grappels from their points of attachment. Rattans are wonderful examples of how monocots can escape the structural constraints to develop a comparable mechanical architecture as dicotyledonous lianas. Species of *Calamus* can show a decrease in  $E_{\text{str}}$  toward the base, a trend typical of many dicotyledonous lianas. However, the values of old stages of *Calamus* measured are in the range of the highest values of old stages of dicotyledonous twiners but do not approach the highly compliant properties of many others.

Au: In the sentence beginning "However, the values..." "many other" what?

Au: Is this Ref. 29 or 25? If it's 29, then Ref. 25 is not cited in the text and the sequence of the references is out of order.

Finally, future studies should incorporate studies based on hydraulic and mechanical properties of the stem. Many climbers show a reduction in structural Young's modulus during ontogeny, and this might be consistent with a relative increase in large-diameter vessels and increased hydraulic conductivity at the expense of relatively stiff tissues in the wood. The developmental and ecological trade-offs between mechanical functioning (stem stiffness and support) and hydraulic conductivity are complex [29]. While increased vessel diameter might influence stem stiffness in some climbers, many dicotyledonous climbers show relative increases in other compliant tissues during ontogeny such as rays and development of thinner-walled wood fibers. Such tissues are more easily interpreted as structural modifications that increase compliancy, resistance to fracture, and stem repair in vines and lianas.

#### 2.4.3 ECOLOGICAL DIVERSITY OF CLIMBERS AMONG DIFFERENT GROUPS

Climbing growth forms are common among woody families of angiosperms, relatively common among monocots, but much rarer in other groups, including gymnosperms and ferns. The mechanical properties of climbing stems as well as the type of attachment are undoubtedly coupled to a wide range of evolutionary constraints among different plant groups [19,20,26–29]. Most monocot climbers tested so far retain the relatively stiff properties of host location and initial stiff phase of growth. Such plants without secondary growth are unable to make the developmentally complex, though ecologically important, transition from high stiffness to high compliance of tissues. However, because of their small axial second moment of area, flexural stiffness also remains relatively low in old stems. Such climbing forms nevertheless occupy both small-bodied and large-bodied climbing niches and an important diverse modes of climbing attachment. Only species of *Calamus*, arguably the most diverse and specialized group of climbing monocots, show relatively low values of  $E_{\text{str}}$  of the inner stem, which produces flexible canes after the loss of the



leaf sheath. This particular mechanical architecture in *Calamus* could have been an important innovation in the group and might explain its ecological success in South-east Asia.

## 2.5 CONCLUSIONS

Twining climbers that attach firmly to the host support eventually require substantial compliance to escape stresses. Most of the climbing strategies require a stiff initial development to (a) get off the ground, (b) locate host supports, and (c) span distances between host supports. A twining strategy would therefore require an initial phase of stiff development followed by a later stage of compliant development. This requires a relatively sophisticated change in stem development and is mostly observed among dicotyledonous angiosperms that possess a bifacial vascular cambium and produce a specialized type of highly compliant wood during later growth. Many of these wood types have been termed “anomalous wood” (or more recently, variant cambia), and produce a wide range of vascular configurations that often incorporate enhanced hydraulic conductance, wound repair, and mechanical compliance properties. Is high compliance necessary for all climbing habits? For firmly attached twining plants that produce large diameter climbing axes, the answer is probably yes. However, some kinds of hook climbing may require relatively stiff stems so that the plant stem will be more likely to sway onto another neighboring support rather than buckle and collapse.

In summary, climbing plants can show many types of attachment from firmly attached twiners to less well attached hook climbers and to leaning plants. Bending mechanical properties of the stem and its change during development can differ between these categories: Twining climbers tend to produce lower values of  $E_{str}$  in older stages of development than other more loosely attached climbers. This is probably because firm attachment to host plants requires high compliancy to survive movement of the host plant. Other niches linked to more loosely attached climbing modes are open to a wider range of plant groups and do not require high compliancy in older growth stages. This type of climbing strategy has been adopted by a wide range of plant groups, notably monocotyledons.

## REFERENCES

1. Schnitzer, S.A. and Bongers, F., The ecology of lianas and their role in forests, *TREE*, 17, 223, 2002.
2. Rowe, N.P. and Speck T. Plant growth forms: an ecological and evolutionary perspective, *New Phytol.*, 166, 61, 2005.
3. Phillips, O.L. et al., Increasing dominance of large lianas in Amazonian forests, *Nature*, 418, 770, 2002.
4. Wright, S.J., Calderón, O., Hernández, A., and Paton, S., Are lianas increasing in importance in tropical forests? A 17 year record from Panama, *Ecology*, 85, 484, 2004.
5. Putz, F.E. and Mooney, H. A. (Eds.), *The Biology of Vines*, Cambridge University Press, Cambridge, 1991.



6. Speck, T., Bending stability of plant stems: ontogenetical, ecological, and phylogenetical aspects, *Biomimetics* 2, 109, 1994.
7. Rowe, N.P. and Speck T., Biomechanical characteristics of the ontogeny and growth habit of the tropical liana *Condylocarpon guianense* (Apocynaceae), *Int. J. Plant Sci.* 157, 406, 1996.
8. Speck T. et al., How plants adjust the “material properties” of their stems according to differing mechanical constraints during growth: an example of smart design in nature, in *Bioengineering. Proceedings of the 1996 Engineering Systems Design and Analysis Conference*, Engin, A.E., Ed., PD-volume 77, volume 5. The American Society of Mechanical Engineers, New York, 1996, p. 233,.
9. Rowe, N.P. and Speck T., Biomechanics of plant growth forms: the trouble with fossil plants. *Rev. Palaeobot. Palynol.*, 102, 43, 1998.
10. Speck, T. and Rowe, N.P., A quantitative approach to analytically defining size, form and habit in living and fossil plants, in *The Evolution of Plant Architecture*, Hemsley, A.R. and Kurmann, M., Eds., Royal Botanical Gardens, Kew, UK, 1999, p. 447.
11. Hegarty E.E., Vine-host interactions, in *The Biology of Vines*, Putz, F.E. and Mooney, H.A., Eds., Cambridge University Press, Cambridge, 73, 1991.
12. Fisher, B. and Ewers, F.W., Structural responses to stem injury in vines, in *The Biology of Vines*, in Putz, F.E. and Mooney, H.A., Eds., Cambridge University Press, Cambridge, 99, 1991.
13. Wainwright, S.A., Biggs, W.D., Currey, J.D., and Gosline, J.M., *Mechanical Design in Organisms*. John Wiley, New York. 1976.
14. Niklas, K.J., *Plant Biomechanics, an Engineering Approach to Plant Form and Function*, The University of Chicago Press, Chicago, 1992.
15. Gallenmüller, F., Müller, U., Rowe, N.P., and Speck, T., The growth form of *Croton pullei* (Euphorbiaceae) — Functional morphology and biomechanics of a neotropical liana. *Pl. Biol.*, 3, 50, 2001.
16. Vincent, J.F.V., *Structural Biomaterials*, Princeton University Press, London, 1990.
17. Vincent, J.F.V., Plants, in *Biomechanics — Material: A practical approach*, Vincent, J.F.V., ed., IRL Press, Oxford, 1992, p. 165.
18. Bodig, J. and Jayne, B.A., *Mechanics of Wood and Wood Composites*,. Krieger Publishing Company, Malabar, FL, 1993.
19. Speck, T. et al., The potential of plant biomechanics in functional biology and systematics, in *Deep Morphology: Toward a Renaissance of Morphology in Plant Systematics*, Stuessy, T.F., Mayer, V., and Hörandl, E, Eds., Koeltz, Königstein, 2003, p. 241,.
20. Rowe, N.P., Isnard, S., and Speck, T., Diversity of mechanical architectures in climbing plants: an evolutionary perspective, *J.P.G.R.*, 108, 205.
21. Gallenmüller, F., Rowe, N.P. and Speck, T., Development and growth form of the neotropical liana *Croton nuntians*: the effect of light and mode of attachment on the biomechanics of the stem, *J.P.G.R.*, 83, 2005.
22. Isnard, S., Speck, T., and Rowe, N.P., Biomechanics and development of the climbing habit in two species of the South American palm genus *Desmoncus* (Arecaceae). *Am. J. Bot.*, (in press) 2005
23. Rowe, N.P. and Speck, T., Biomechanics of *Lycopodiella cernua* and *Huperzia squarrosa*: implications for inferring growth habits of fossil small-bodied Lycopsiads. *Med. Ned. Ins. Toeg. Geo. TNO.*, 58, 290, 1997.
24. Isnard, S., Biomechanics and development of rattans: What is special about *P. himalayana*? *Bot. J. Linn. Soc.*, (in press) 2005.

Au: Please spell out J.P.G.R. Please also provide a page or volume no. Please provide updated publication information.

Ref. 21. Please provide updated publication information.



25. Traiser, C., Reidelstrüz, P., and Speck, T., Biomechanische, anatomische und morphologische Untersuchungen verschiedener Wuchsformtypen der Gattung *Lonicera* L. *Mitt. Bad. Landesver. Naturkunde u. Naturschutz N.F.*,17, 123, 1998.
26. Civeyrel, L. and Rowe, N.P., Phylogenetic relationships of Secamonoideae based on the plastid gene matK, morphology and biomechanics. *Ann. Missouri Bot. Gard.*, 88, 583, 2001.
27. Isnard, S., Speck, T., and Rowe, N.P. Mechanical architecture and development in *Clematis*: implications for canalised evolution of growth forms, *New Phytol.*, 158, 543, 2003.
28. Lahaye, R., Civeyrel, L., Speck, T., and Rowe, N.P., Evolution of shrub-like growth forms in the lianoid sub family Secamonoideae (Apocynaceae s.l.) of Madagascar: phylogeny, biomechanics and development. *Am. J. Bot.* (in press), 2005.
29. Rowe, N.P. and Speck, T., Hydraulics and mechanics of plants: novelty, innovation and evolution, in *The Evolution of Plant Physiology*. Poole, I. and Hemsley, A.R., Eds., Elsevier Academic Press, Kew, 2003, p. 297.

Au: Ref. 28.  
Please provide updated publication information.

