

BIOMECHANICS AND DEVELOPMENT OF THE CLIMBING HABIT IN TWO SPECIES OF THE SOUTH AMERICAN PALM GENUS *DESMONCUS* (ARECACEAE)¹

SANDRINE ISNARD,^{2,4} THOMAS SPECK,³ AND NICK P. ROWE²

²Botanique et Bioinformatique de l'Architecture des Plantes, UMR 5120 CNRS, TA40/PS2, Boulevard de la Lironde, F-34398 Montpellier cedex 5, France; and

³Plant Biomechanics Group, Institut für Biologie 2 and Botanischer Garten, Universität Freiburg, Schänzlestr. 1, D-79104 Freiburg, Germany

Mechanical properties are investigated in *Desmoncus orthacanthos* and *D. polyacanthos* from French Guiana, South America. Differences in size and axis stiffness are related to different trellis requirements and habitats. The leaf sheath surrounds the stem, increasing stiffness of young self-supporting stages and apical parts of older climbing plants. Senescence of the leaf sheath reduces stiffness of older climbing axes of both species. Its eventual loss in *D. orthacanthos* facilitates deformation into coils and loops when plants slip from their supports following senescence of leaves bearing attachment organs. In smaller climbing axes of *D. polyacanthos*, the senescent leaf sheath remains attached and axes rarely form loops and coils below attachment. An increase in stiff mechanical properties toward the base of both species is radically different from that of many dicotyledonous lianas. Besides the presence of attachment organs, stem mechanical properties of *Desmoncus* are similar to those of erect though not fully self-supporting stems of *Bactris major*, a sympatric species of the sister group genus to *Desmoncus*. The climbing habit in *Desmoncus* may have evolved via (1) heterochronic processes including early elongation of internodes relative to increase in stem diameter (reduction of the establishment phase) and (2) increased persistence of leaf sheaths.

Key words: *Bactris major*; climbing palms; *Desmoncus orthacanthos*; *Desmoncus polyacanthos*; growth form; leaf sheath; lianas; mechanical architecture.

Climbers are relatively common among monocotyledons (Tomlinson and Fisher, 2000). They vary greatly in size from climbing herbs such as *Scleria secans* (Cyperaceae) to liana-sized rattans (Calamoideae) of southeast Asia, Australia, and West Africa, and the morphologically similar *Desmoncus* (Arecoideae) of the New World tropics. Climbing palms lack secondary growth and rely on primary tissues for their entire life history. Extreme mechanical stresses applied to these stems might be potentially fatal because they apparently lack the high compliance, toughness, and potential for self-repair attributed to vines and lianas having secondary vascular cambial growth. Furthermore, most climbing palms do not develop aboveground branching, so recovery from mechanical damage via aerial branching is also limited. Despite these apparent constraints, the abundance and diversity of climbing palms suggests a considerable evolutionary success of this type of growth form.

This investigation follows recent studies into the biomechanics of plant growth forms, particularly climbers. These have demonstrated how changes in cambial development can drastically modify mechanical properties of the stem during development (Rowe and Speck, 1996, 1998, 2004; Speck et al., 1996; Gallenmüller et al., 2001; Isnard et al., 2003a, b). In lianas, modifications of mechanical properties between

young self-supporting and older non-self-supporting stages of growth commonly show a significant drop in structural Young's modulus—a measure of the flexibility of the stem and its constituent tissues (Speck, 1994; Rowe and Speck, 1998; Speck and Rowe, 1999). In dicotyledonous lianas, this is highly adapted to the mechanical constraints where growth relies on “mechanical parasitism” (Caballé, 1980; Putz, 1984; Fisher and Ewers, 1991; Putz and Holbrook, 1991; Rowe and Speck, 2004).

Other groups besides dicotyledons have evolved climbing growth forms, though not much attention has been paid to these in terms of their biomechanics or the evolution of this specialized growth form (Rowe and Speck, 2004; Rowe et al., 2004). Climbers have also evolved among plants that lack secondary growth including ferns and monocotyledons. Scandent habits are known even among plants with an archaic stem organization such as *Lycopodiella cernua* (Lycopodiaceae). Recent biomechanical studies have shown that mechanical properties of climbers can nevertheless be modified via strategically modulating the stiffness of primary tissues along self-supporting, procumbent, or climbing stems (Rowe and Speck, 1997, 1998, 2004; Rowe et al., 2004).

Climbers have evolved in two subfamilies Arecoideae and Calamoideae (including true rattans) among the five now recognized in palms (Dransfield et al., in press). They occur in 16 genera (7% of all palm genera) and 580 species (22% of all palm species) (Baker et al., 2000a, b). Most climbing palms have developed a range of adaptive novelties including modified leaves and inflorescences forming organs of attachment (Figs. 1C, 2B) and leaf sheaths, which remain attached to the stem along extensive segments of the plant (Fig. 1A). Like many climbing dicotyledons, they also have larger vessel diameters (c. 150–180 μm in *Desmoncus* and up to 350 μm in *Calamus*) than related nonclimbers (Tomlinson and Zimmer-

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⁴ Author for correspondence (e-mail: sisnard@cirad.fr) phone: +33 (0) 467617553, fax: +33 (0) 467615668.

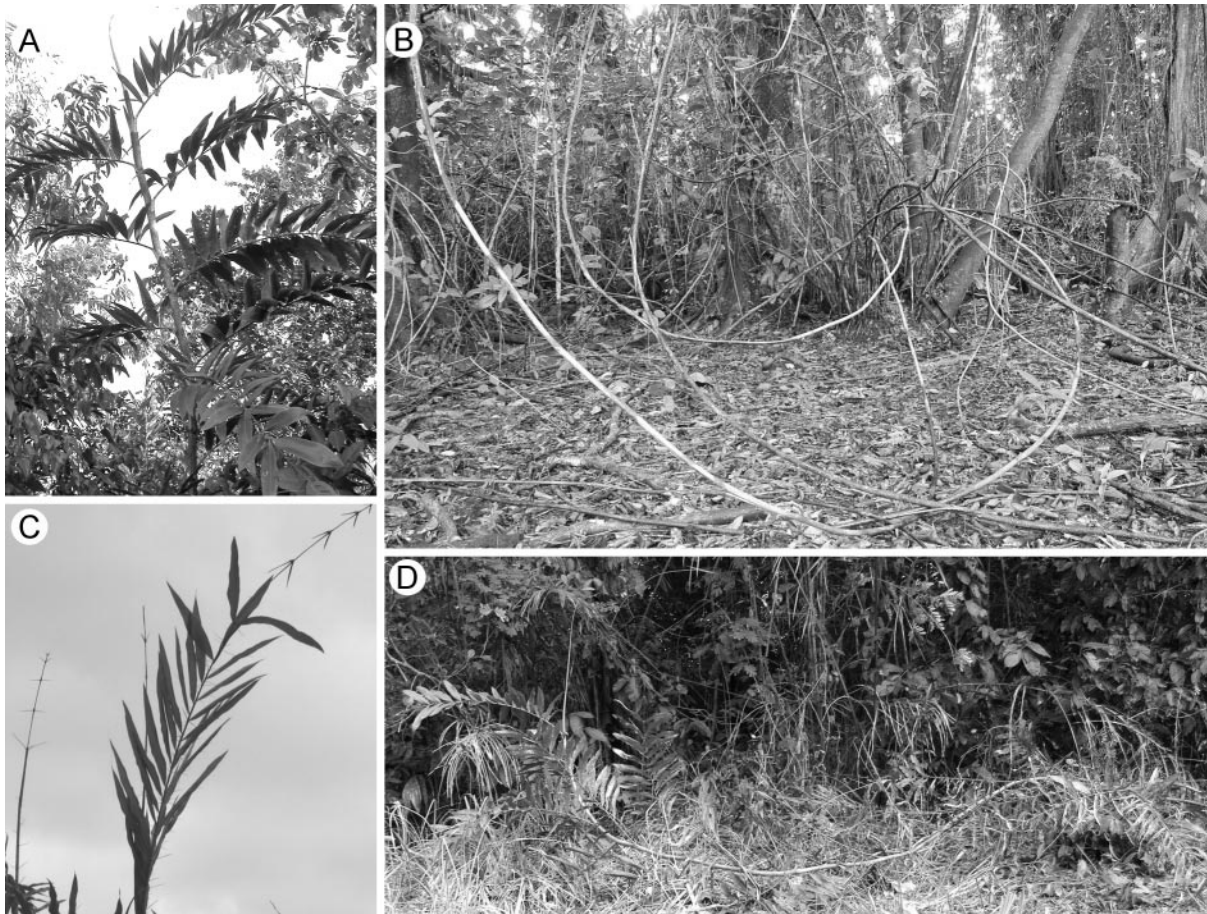


Fig. 1. *Desmoncus orthacanthos*. (A) Upright young axis. Leaves bearing cirri are distributed along its length and attached to the surrounding vegetation. (B) Basal parts of older climbing plants. Cane-like stems are growing in clusters in a disturbed wooded area; canes descend toward the ground, forming loops. (C) Extension of the rachis into a cirrus with pairs of reflexed hook-like leaflets (acanthophylls); younger cirrus (left) with developing acanthophylls becoming reflexed. (D) Procumbent plant growing in open habitat with S-shaped axis and ascending apex.

mann, 2003). In both *Desmoncus* and *Calamus*, the vascular architecture lacks direct connection between protoxylem and metaxylem and thus differs from that found in the tree-palm model *Rhapis excelsa*. This has been interpreted as a possible protection against cavitation and hydraulic dysfunction (Tomlinson and Zimmermann, 2003). Tomlinson (1962) emphasized the persistent, tube-like leaf sheaths in climbing palms compared with the shorter, more ephemeral, and partially encircling leaf bases of nonclimbers. In many climbing palms, leaf sheaths probably contribute to the mechanics of the climbing axis for at least part of the growth trajectory, as well as form a mechanical connection with host vegetation via hooks on leaves and inflorescences. A potential constraining feature in such plants is the ultimately ephemeral nature of the leaves and leaf sheath and the effects of their senescence and breakage on the mechanical architecture, growth form, and life history in general.

Species of *Desmoncus* are not as economically important as their Asian counterparts, the rattans, though they are used locally for a range of uses including furniture (Henderson and Chavez, 1993; Siebert, 2000). Interest has focused recently on some species to better understand ecological requirements and impact of harvesting (Troy et al., 1997; Siebert, 2000; Escalante et al., 2004).

In this study, we investigated the mechanical architecture of

Desmoncus orthacanthos and *D. polyacanthos*. Each species occupies a different habitat in French Guiana and differs in overall size, leaf size, type and size of attachment organs, height, ramet diameter, and type of trellis. We also compared their axial mechanical properties with those of *Bactris major*, an upright, though ultimately unstable, species of the sister group genus *Bactris*. We also compared the mechanical design of these climbing palms with dicotyledonous lianas. Because radically increased flexibility during ontogeny is such a prevalent feature among climbing dicotyledons, we wished to find out how plants lacking secondary growth can maintain similar growth forms in both large- and small-bodied species of the genus.

MATERIALS AND METHODS

Taxonomy and distribution of *Desmoncus*—The genus is placed in the tribe Bactridinae, subfamily Arecoideae (Uhl and Dransfield, 1987; Hahn, 2002). It is distributed widely in Central and South America from Mexico to Brazil and Bolivia and in the Caribbean except Trinidad and Tobago (Henderson et al., 1995). The systematics and taxonomy of the genus is in need of revision with estimates of the number of species ranging from six (Henderson et al., 1995) to 61 (Uhl and Dransfield, 1987). The genus is distinguished from true rattans of southeast Asia by its reflexed, thickened leaflets (acanthophylls) on the modified frond apex (cirrus) acting as hook-like grapnels. Strangely, the geographically intermediate, calamoid rattans of West Af-

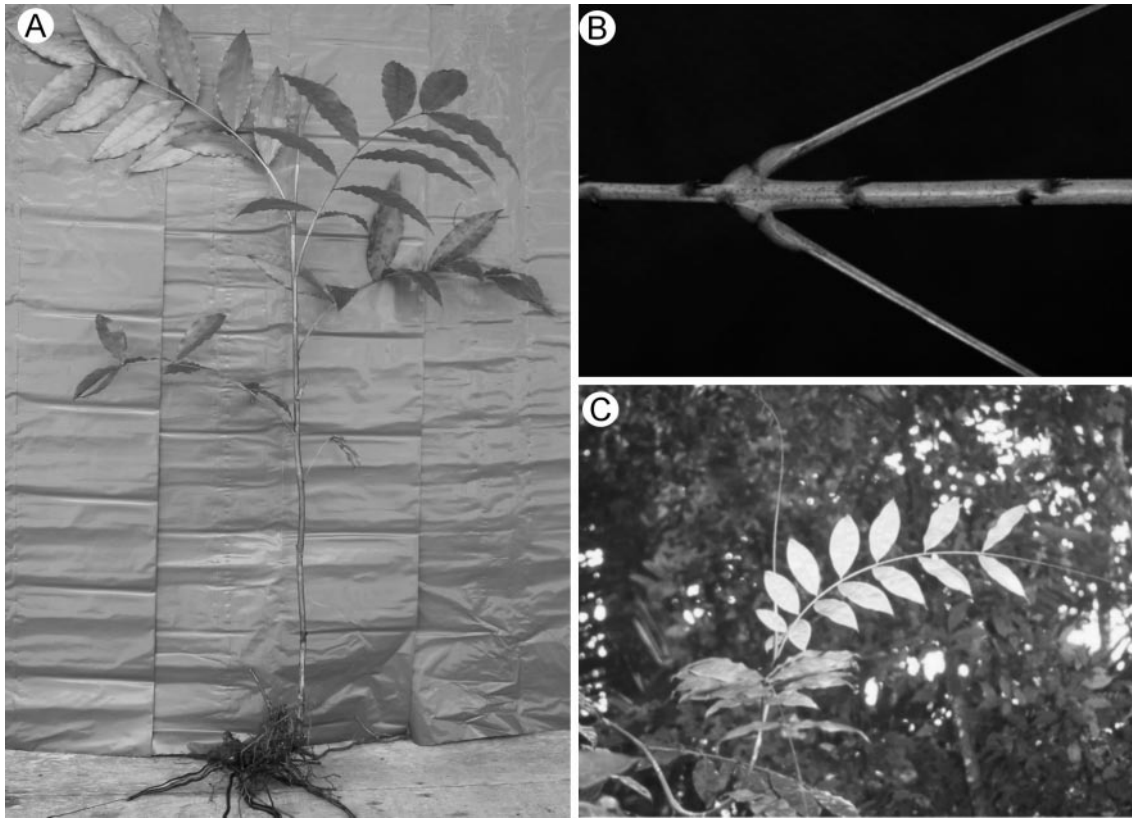


Fig. 2. *Desmoncus polyacanthos*. (A) Young self-supporting axis bearing leaves without cirri, emerging from rhizome bearing leaves without cirri. (B) Abaxial surface of cirrus bearing recurved hooks and a pair of acanthophylls. (C) Apical part of a climbing plant, emerging from its host support in the understory. The axis has slipped to a horizontal position and then produced an S-shaped, ascending apex deploying new leaves with cirri.

rica (*Eremospatha*, *Laccosperma*, and *Oncocalamus*) also possess these structures (Corner, 1966; Dransfield, 1978). This study is based on material collected in the field in French Guiana. *Desmoncus polyacanthos* Mart. was collected from an understory forest habitat at the research station known as "Piste de St. Elie" (5°17' N, 53°03' W); specimens of *D. orthacanthos* Mart. and *B. major* Jacq. were collected from disturbed open and wooded sites near mangroves along the "route de l'Anse" near the village of Sinnamary (5°39' N, 52°95' W).

Habitat, growth form, and morphology—The species differ in habitat and morphology. *Desmoncus orthacanthos* can be very common alongside rivers and is considered a generalist species with a preference for high light and vigorous vegetative propagation (Siebert, 2000). *Desmoncus polyacanthos* is sparsely distributed in forest understory and has a preference for patchy light environments with diffuse shade (Troy et al., 1997). It tends to grow alongside paths, beside tree-fall gaps, along creeks, and in temporarily flooded areas. The species develop and climb in basically similar ways. Individual ramets are produced from underground rhizomes lying just below the soil surface. Young axes are composed of an inner stem and an outer leaf sheath bearing leaves. In both species, shoots grow upwards, become mechanically unstable, and then climb into the surrounding vegetation via effectively deployed hooks borne on leaves. In this account, the plant axis is defined as the stem and leaf sheath combined. The true stem is defined as the axial parts of the plant that have naturally shed the leaf sheath, or parts from which the leaf sheath has been removed prior to mechanical tests.

Desmoncus orthacanthos is a clustering species producing clumps of tens of upright and climbing axes from extensive rhizomes. Young axes remain self-supporting to a height of about 2.5 m. Cirri are produced only after the plant becomes unstable and these specialized grapnel-bearing leaf tips increase in length toward the apex of the climbing axis (Fig. 1A, C). Climbing

axes with intact leaf sheaths are 0.6–3 cm wide. In open areas where supports are rare, axes become procumbent but can eventually produce ascending apices, which can develop into climbing axes if they grow near an appropriate host (Fig. 1D). The species can reach canopy heights of nearly 20 m and total axis lengths of about 30 m. Mature climbing axes remain attached to host trees by up to 20 leaves below the apex.

Desmoncus polyacanthos is much smaller and delicate, producing fewer (1–4) axes per rhizome at any one time. Young axes remain upright to about 1.5 m in height (Fig. 2A) and as in *D. orthacanthos*, produce attachment organs only when unstable. Climbing axes are slender (0.4–1 cm in diameter) and differ from *D. orthacanthos* by having recurved hooks on both leaf rachis and cirrus (Fig. 2B). When unstable, axes climb on the surrounding vegetation via extremely "catchy" cirri and often show "S-shaped" growth resulting from partial falls of the growing apex and later ascending growth (Fig. 2C). In the area examined, stems do not exceed 12 m in total length and rarely climb higher than 7–8 m.

Canopy openings were estimated at 20 stations of *D. polyacanthos* along 2.7 km of forest trail and adjacent areas. Photographs with a digital camera and fish-eye lens were taken in diffuse light conditions just before and after sunrise. The lens was pointed vertically upwards at three locations (north, west, and east) at 1 m around the rhizome and at 1 m from the ground. Percentages of canopy openings were then calculated using standard image analysis software. The measurements provided an approximate measure of the canopy gap above rhizomes bearing upright axes.

Bactris major is sympatric with *D. orthacanthos* and typically occurs beside mangroves forming dense monospecific stands. Axes are produced from large rhizomes and young axes are self-supporting, while older, longer stems lean against each other (Fig. 3A). Axes remain relatively short (1–10 m; Henderson et al., 1995) and mature stems, though not fully self-supporting, do not develop specialized attachment devices. Leaf sheaths senesce rapidly along self-



Fig. 3. *Bactris major*. (A) Old unstable stems growing in a monospecific stand. Some are leaning on each other and supplying mutual support. (B) Apical part of a young axis showing rapid senescence of the leaf sheath below the apex.

supporting plants and are thus only intact at the apex (Fig. 3B). A fibrous sheath surrounds the stem after the decay of the leaf lamina (Fig. 4).

Mechanical tests—Specimens selected for mechanical tests among young self-supporting to older climbing axes were healthy and had no external damage or decay apart from natural senescence or fracture of the outer leaf sheath. Senescence was considered a natural and integral part of axis development; therefore, older axes with leaf sheaths that were dry or partially so were tested in bending. Axes were carefully pruned just above contact with the rhizome, carefully stripped of leaves, and then carefully detached from surrounding vegetation without exerting undue force. Plants were cut into lengths for transport and stored in humid conditions before mechanical tests. Axes are compound structures comprising stem and leaf sheath; the diameter and bending mechanical properties were measured along entire lengths and then remeasured after removal of the leaf sheath. The difference in measured flexural



Fig. 4. Fibrous leaf sheath of *Bactris major* surrounding the stem after the decay of the leaf lamina.

rigidity of the entire axis and isolated stem was used to calculate the relative contributions of the leaf sheath and stem in young to old plants.

The total number of axes studied included: *D. orthacanthos* (entire axes, $N = 15$; leaf sheath removed, $N = 15$), *D. polyacanthos* (entire axes, $N = 11$; leaf sheath removed, $N = 6$), *B. major* (entire axes, $N = 4$; leaf sheath removed, $N = 2$). Older axes of *D. orthacanthos* and *B. major* were selected that had naturally lost the leaf sheath and were measured in bending. Apical segments of all species were comprised of highly flexible, immature stems and immature leaf sheath and could not be reliably tested in bending. Axes were cut into segments suitable for three-point bending tests so that the span-to-depth ratio of tested segments was always greater than 20 (mean = 43 ± 11 for *D. orthacanthos*, 38 ± 9 for *D. polyacanthos*, and 41 ± 7 for *B. major*). This minimum ratio was empirically established after conducting bending tests at a range of span distances; a value of 20 was found to be sufficient to minimize the influence of shear during bending to a negligible degree.

The principal aim of the bending tests was to measure the flexural stiffness, EI of the entire axis and that of the stem without the leaf sheath. Bending test protocols followed those of recent analyses on woody plants (Vincent, 1990; Rowe and Speck, 1996; Gallenmüller et al., 2001; Rowe et al., in press). Axes were placed on a steel frame apparatus at two supporting points at a precise span distance. Consecutive weights were added to a pannier suspended from the exact center of the stem segment. Deflection of the axis was measured via a dissecting microscope equipped with an eyepiece graticule and the resulting force-deflection curve used to calculate flexural stiffness:

$$EI_{\text{axis}} = L^3/48R$$

where L represents the span of the axis on the apparatus, and R is the slope of the force deflection curve where the deflection observed in (mm) at the center of the tested axis is plotted against the force applied (N).

All three species have a conspicuous node/internode structure and wherever possible, the same positions of nodes and internodes were set up during each bending experiment. Axial diameters along each segment were used to calculate the mean axial second moment of area (I) of each tested segment via the formula for an ellipse, which approximates closely the shape of the axes in cross-section:

$$I_{\text{axis}} = (\pi/4)a^3b,$$

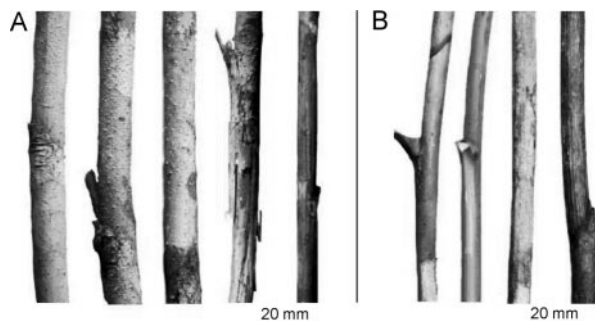


Fig. 5. Aging and senescence (left to right) of the leaf sheath (LS) during development. The LS is green and tightly encircles young stems of both species. (A) *Desmoncus orthacanthos*. Note that the LS is entirely lost in older parts of the plant (right) leading to exposure of the cane-like stem. (B) *D. polyacanthos*. The leaf sheath is dried and senescent but still encircles the stem in the oldest part of older climbing plants (right).

where a and b represent the radial widths in the direction of the force applied and perpendicular to it, respectively.

After measuring flexural stiffness (EI) and axial second moment of area (I) of each axis segment, structural Young's modulus (E_{str}) was calculated:

$$E_{entire\ axis} = EI_{entire\ axis} / I_{entire\ axis}$$

The same protocols were used to measure EI , I , and E_{str} of the stem after removal of the leaf sheath. Since I and EI of the entire axis must equal that of the leaf sheath and the stem:

$$I_{entire\ axis} = I_{leaf\ sheath} + I_{stem}$$

$$EI_{entire\ axis} = EI_{leaf\ sheath} + EI_{stem}$$

Values of I and EI of the leaf sheath were calculated by subtracting values of I and EI of the stem from those of the entire axis. Values of E_{str} of the leaf sheath were then deduced via

$$E_{leaf\ sheath} = (EI_{entire\ axis} - EI_{stem}) / (I_{entire\ axis} - I_{stem})$$

RESULTS

Mechanical architecture of entire axis (stem and leaf sheath)—In young self-supporting and unstable plants of both species, leaf sheaths were intact, green, and tightly surround the stem along most of the length (Fig. 5A, B). Senescence occurs at the base of young plants of *D. polyacanthos* and in both species occurs progressively towards the apex in older climbing axes. In *D. polyacanthos*, the leaf sheath remains on the stem after prolonged senescence (Fig. 5B, right). In *D. orthacanthos*, the leaf sheath is progressively loosened below the apex and is finally lost (Fig. 5A, right) in cane-like older stems (Fig. 1B). Among younger procumbent axes of *D. orthacanthos* that have fallen from their support, leaf sheaths are often already fractured, dried, and loosened toward at the base.

Flexural stiffness (EI), the tangible resistance to bending forces of intact axes, differs widely between the two species (Fig. 6A, C). Axes of *D. orthacanthos* are much more resistant to bending because they are larger with values around a hundred times higher than in *D. polyacanthos*. This is explained by the large difference in axial second moment of area (Fig. 6B, D). Variation of EI is also large within each species (Fig. 6A, C), particularly in *D. orthacanthos* (4–184 N·m²). This also reflects wide variation of axial second moment of area (I) in each species. In *Desmoncus*, older and larger rhizomes produce larger diameter aerial shoots (Putz, 1983). Initial diameter and I and EI can vary widely from one axis to another de-

pending on the size of the rhizome and the timing of the production of axes. In *D. orthacanthos*, young self-supporting and unstable axes have higher values for both EI and I than older climbing axes in which the leaf sheath is still present (Fig. 6A, B) because of the presence of a thick, intact leaf sheath surrounding the stem during these stages. This trend is more marked in *D. orthacanthos* than in the relatively diminutive *D. polyacanthos*. Despite differences in EI , trends along axes generally follow shifts in size as represented by axial second moment of area (Fig. 6A–D).

In both species, EI strongly increases towards the base of young self-supporting and unstable axes (Fig. 6A, C). Later senescence of the leaf sheath from the base modifies both geometry and mechanical properties. Somewhat older procumbent axes of *D. orthacanthos* can markedly decrease in I and EI toward the base (Fig. 6A, B) resulting from senescence, loosening, and partial loss of the leaf sheath. At this stage of development, both the mechanical pattern and actual growth form are consistent with a non-self-supporting architecture. In older climbing axes of *D. orthacanthos*, EI remains relatively stable along the middle part, but three climbing axes measured increase toward the very basal segment (Fig. 6A), following the trends in I . Variation of flexural stiffness along young self-supporting, procumbent, and older climbing axes largely results from different degrees of senescence, thinning, loosening, and partial loss of the leaf sheath.

A rather different pattern is observed in *D. polyacanthos*; older climbing axes consistently increase in EI toward the base whatever the age and orientation. Relatively lower and constant values extend toward the apex. Both trends in EI follow the shifts in values of I (Fig. 6C, D). Senescence of the leaf sheath base appears to affect the mechanical properties less than in *D. orthacanthos*.

Some self-supporting to climbing individuals of *D. polyacanthos* increased in height up to a maximum of 1.8 m over a period of 5 months, while other axes had little or no increase. Measurements of canopy opening above stations of *D. polyacanthos* ranged from 5.7–9% with an overall mean value of $7.3 \pm 1.1\%$. The range of values observed did not correlate with or explain differences in axis elongation over the period studied.

Mechanical architecture of the stem—In both species, trends in EI along young self-supporting and young unstable stems following removal of the leaf sheath, do not differ from overall trends of axes measured with their leaf sheaths (Fig. 7A, C). Stems increase in EI toward the base, following trends in I (Fig. 7B, D). In *D. orthacanthos*, the increase in EI of intact axes toward the apex of long procumbent axes (up to 5.5–10 m; Fig. 6A) is not observed after removal of leaf sheaths (Fig. 7A). This highlights the importance of the leaf sheath in resisting bending forces toward the apex of the plant.

Older climbing stems of *D. orthacanthos* show relatively unchanged trends along stems but a slight increase of both EI and I at the base (Fig. 7A, B). One climbing stem (25 m), like many similarly aged axes in the vicinity (Fig. 1B), had climbed into the canopy (12 m) and lost the leaf sheath along nearly its entire length. The cane-like older stem deformed into wide arcs and loops on or near the ground; interestingly, the stem has relatively low and stable values of EI and I along most of the length but increases in both parameters at the very base (Fig. 7A, B, insets). In *D. polyacanthos*, older climbing stems have a more consistent increase in EI toward the base

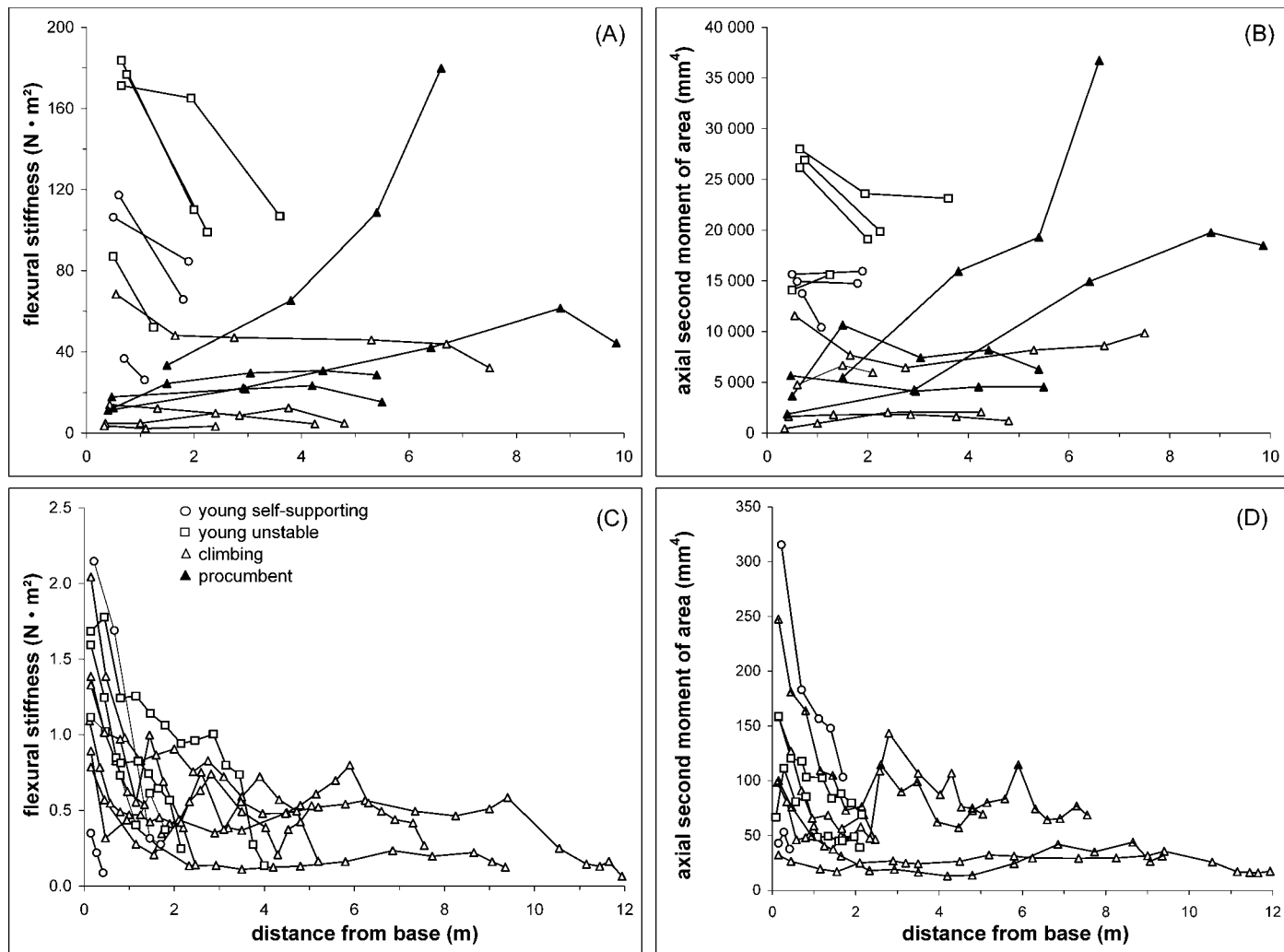


Fig. 6. Variation of flexural stiffness, EI ($N \cdot m^2$) and axial second moment of area, I (mm^4) of stems with leaf sheath plotted against distance from the base (m) for (A, B) *Desmoncus orthacanthos* and (C, D) *D. polyacanthos*.

with a concomitant increase in I (Fig. 7B, D); values vary little in median parts of the plant and follow trends in I .

Mechanical roles of the stem and leaf sheath—Leaf sheath thickness differs between species (Fig. 8); in *D. polyacanthos* it rarely exceeds 1 mm but in *D. orthacanthos* it can reach up to 6 mm in apical parts of old plants. In both species, it varies little along young self-supporting to unstable axes (Fig. 8A) but decreases significantly towards the base in older plants (*D. orthacanthos*: $R^2 = 0.43$, $R = 0.656$, $N = 27$, $P < 0.01$; *D. polyacanthos*: $R^2 = 0.5$, $R = 0.705$, $N = 45$, $P < 0.01$; Fig. 8B). Features of the leaf sheath and stem were explored via bivariate plots where data above the isometric relationship x (contribution of stem) = y (contribution of leaf sheath) indicate greater contribution by the leaf sheath. The parameters investigated included I (Fig. 9A, B) and EI (Fig. 9C, D). Similar bivariate plots were used to compare the relative calculated values of structural Young's modulus (E_{str}) of leaf sheath and stem (Fig. 9E, F). Since leaf sheaths progressively senesce and are lost from bases of old axes of *D. orthacanthos*, we include only plants with entire leaf sheaths, tested before and after removal of the leaf sheath.

Relative contribution of leaf sheaths to I differ between species. In *D. orthacanthos* contribution is over 50% in both young and old plants (Fig. 9A). Basal segments tend to fall closer to the isometric line but contribution to I is still generally higher than 50%. In *D. polyacanthos*, leaf sheaths contribute over 50% in median to apical segments of young and older axes but are closer to the isometric line (Fig. 9B). Contribution to basal segments is less clearly differentiated than in *D. orthacanthos*, often dropping below 50%.

In both species, the contribution of the leaf sheath to EI is often lower in basal segments but cannot be distinguished between self-supporting, young unstable, and climbing axes (Fig. 9C, D). In *D. orthacanthos*, the contribution of the leaf sheath to EI is generally greater than 50% apart from basal segments of older climbing stages (Fig. 9C). In *D. polyacanthos*, the leaf sheath generally contributes to about 50% of total flexural stiffness. Basal segments of both young self-supporting and older climbing axes show contributions less than that of the stem and noticeably less than that of *D. orthacanthos* (Fig. 9D).

In both species, values of E_{str} for the leaf sheath are generally lower than those of the inner stem with the vast majority of points falling beneath the isometric line (Fig. 9E, F). In *D.*

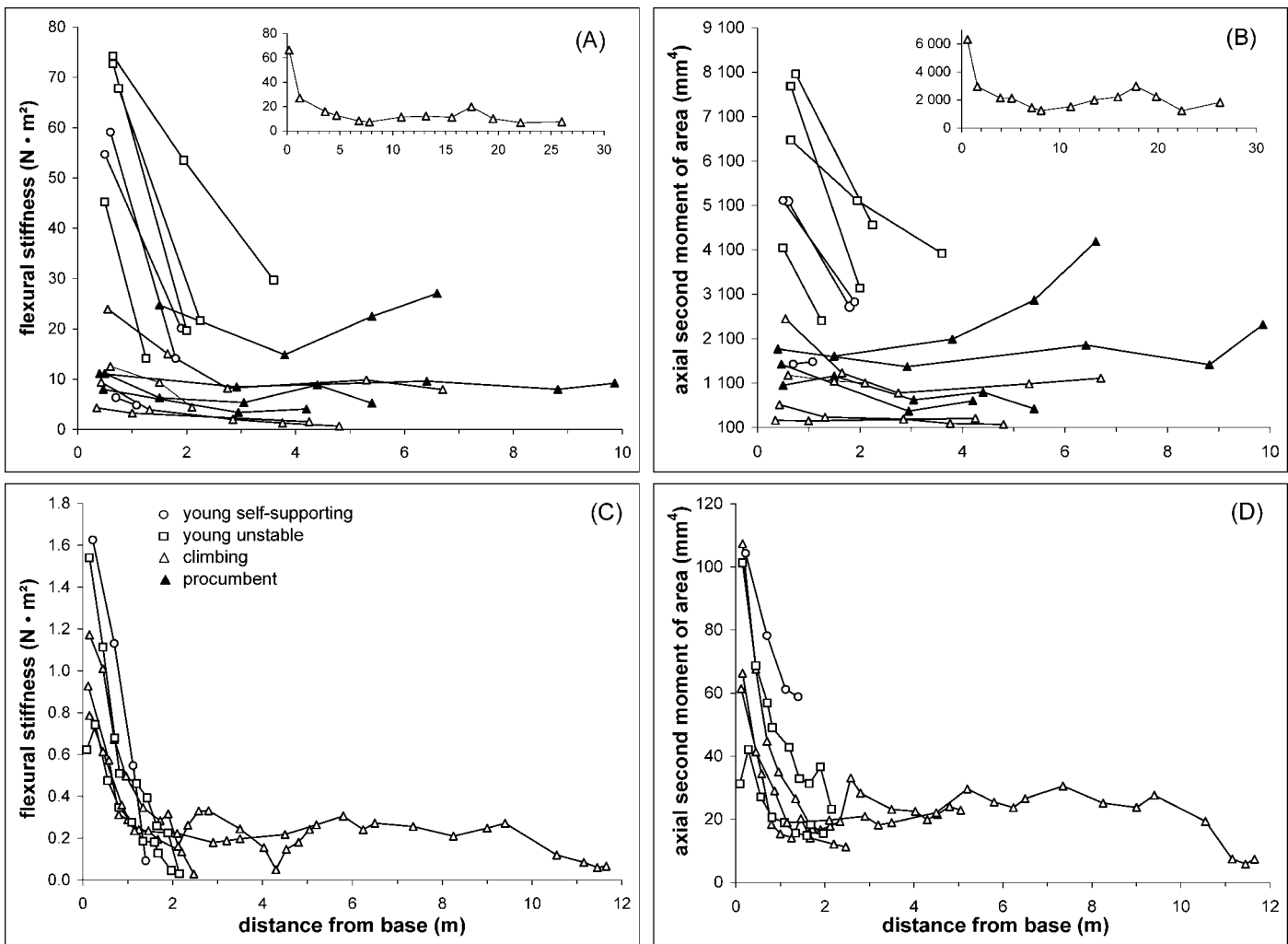


Fig. 7. Variation of flexural stiffness, EI ($N \cdot m^2$) and axial second moment of area, I (mm^4) plotted against distance from the base of stems (m) after manually removing the leaf sheath for (A, B) *Desmoncus orthacanthos* and (C, D) *D. polyacanthos*. Inset graphs represent an old climbing stem of *D. orthacanthos* in which the leaf sheath has been naturally lost along the length measured below the apex.

orthacanthos, values range from just below 2000 to 7800 MN/m^2 (Fig. 9E), with one value close to zero representing the dried and senescent basal portion of an old axis. In *D. polyacanthos*, the upper limit is somewhat higher, 10–11 000 MN/m^2 (Fig. 9F). Outlying values (Fig. 9F) represent basal and senescent parts of young unstable and older climbing axes as well as median parts of young-self-supporting axes for which leaf sheaths have senesced and E_{str} is consequently low.

In young axes of *D. orthacanthos*, E_{str} values of the leaf sheath are similar in basal and median parts of the plant. In young plants of *D. polyacanthos*, however, E_{str} tends to be lower in basal segments. Overall values of E_{str} for the stems of both species range between c. 3000 and 17 000 MN/m^2 for *D. orthacanthos*, with rather higher upper limits of between 1300 and 19 000 MN/m^2 for *D. polyacanthos*. For both species, a few points are distributed above the isometric line and correspond to apical segments for which the immature and mainly parenchymatous stem has a lower E_{str} , thus increasing the mechanical role of the leaf sheath near the apex (Fig. 9E, F). In both species, structural Young's modulus of the stem increases significantly toward the base in both young self-sup-

porting (*D. orthacanthos*: $R^2 = 0.65$, $N = 6$; $P < 0.05$; *D. polyacanthos*: $R^2 = 0.87$, $N = 6$; $P < 0.01$), to unstable stems (*D. orthacanthos*: $R^2 = 0.97$, $N = 14$; $P < 0.01$; *D. polyacanthos*: $R^2 = 0.79$, $N = 19$; $P < 0.01$; Fig. 10A). This increase, though still significant (*D. orthacanthos*: $R^2 = 0.21$, $N = 62$; $P < 0.01$; *D. polyacanthos*: $R^2 = 0.36$, $N = 74$, $P < 0.01$), is less marked in older climbing stems of both species (Fig. 10B). For both basal and middle segments of *D. polyacanthos*, mean values of E_{str} are noticeably higher than in *D. orthacanthos* (Fig. 11).

Mechanical properties of *Bactris major*— EI increases toward the base of young and old axes (Fig. 12A). Stems are stiffer than those of *Desmoncus* and range from 100–1000 $N \cdot m^2$. In young self-supporting plants, there is almost no difference in values of EI between stems alone and stems plus leaf sheaths. Leaf sheaths do not contribute to axis stiffness except for the very apical part of the plant as in many other palms (Niklas, 1992). Structural Young's moduli of young self-supporting stems without leaf sheaths varies from 5000 to 10 000 MN/m^2 towards the base (Fig. 12B) and are similar to

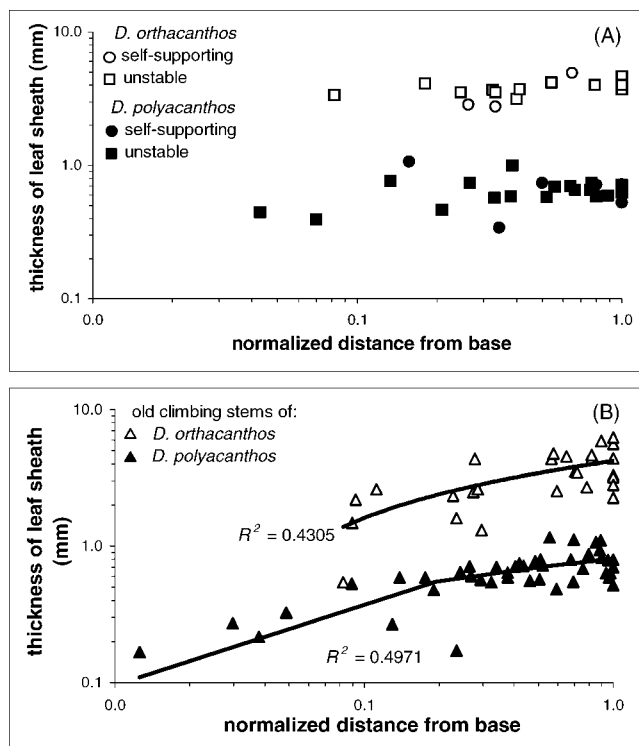


Fig. 8. Leaf sheath thickness (mm) as a function of normalized distance from the base for *Desmoncus orthacanthos* and *D. polyacanthos*. (A) Young self-supporting and unstable axes. (B) Old climbing axes.

values in *Desmoncus*. Two older unstable stems, which have naturally lost their leaf sheaths, have relatively stable values for E_{str} ($16013 \pm 1810 \text{ MN/m}^2$) and are thus somewhat stiffer than the two species of *Desmoncus*.

DISCUSSION

Variation of mechanical architecture in *Desmoncus*—Mechanical roles of stem and leaf sheath differ in each species during ontogeny. In the larger *D. orthacanthos*, the leaf sheath contributes more to resisting bending forces than in the smaller *D. polyacanthos*. This is clear in younger self-supporting plants of *D. polyacanthos*, in which leaf sheaths contribute less and senescence occurs earlier. In this species, mechanical support is mainly provided by the stem. In both species, the leaf sheath has a lower calculated E_{str} than the stem. The fact that the leaf sheath is comprised of a more compliant material than the stem, yet nevertheless contributes significantly to bending resistance, highlights its geometrical role (high value of I) in contributing to axis stiffness. In both species, the leaf sheath contributes significantly to axis stiffness near the apex of older climbing plants.

In *D. orthacanthos*, loss of the leaf sheath confers an ob-conical geometry and relatively low values of EI toward the base of procumbent and climbing axes. In the oldest stage of development, canes are more compliant than the entire stem/leaf sheath of younger parts and readily form loops on or near the ground. These appear to result from slippage of the plant from host supports when apically attached leaves either lose their connection or senesce and break away from the supports. The effect of senescence of the leaf sheath on the ability of the axis to resist bending forces is less in *D. polyacanthos*.

While this smaller-bodied climbing species had been observed to fall from its supports, it did not form the wide loops and arcs linked to the possibly continual slipping of the larger species.

Body size, growth habit, and attachment—Differences in body size and mechanical architecture are characteristic of different habitats and trellis requirements. Large basal diameter and relatively high axis stiffness enable young plants of *D. orthacanthos* to remain upright for up to 2–3 m in clonal groups, even in relatively open environments. Narrow basal diameter and relatively low values of axis stiffness in *D. polyacanthos* are more consistent with strategies of rapidly locating a support in more closed conditions or “pausing” apical growth and entering a waiting phase as observed in many dicotyledonous lianas (Putz, 1984; Caballé, 1986; Lee and Richards, 1991).

In *D. orthacanthos*, acanthophylls on the cirrus and robust spines of the leaf sheath and petioles assure attachment between ramets as well as other neighboring plants. Large leaves (mean length of 1 m with cirrus) provide large “search and attachment” ranges for relatively distant supports. Large size and wide angle of acanthophylls in *D. orthacanthos* can furthermore ensure attachment to host branches up to 1.5 cm in diameter. Initial pulling/fracture tests have shown that a single acanthophyll can withstand forces of up to 200–250 N before breaking. This suggests that a single grapnel can suspend a significant portion of otherwise unattached axis. In summary, large and stiffer axes are heavier but can span larger distances in self-supporting and searcher phases of growth. Such larger axes require a more robust attachment, which can interlock with sturdier and larger diameter host branches during the climbing phase.

In *D. polyacanthos*, small acanthophylls on the cirrus and recurved spines on both cirrus and leaf rachis only interlock with supports one to several millimeters in diameter. Climbing individuals were mainly attached to palm leaves or woody branches under 10 mm in diameter. Initial pulling/fracture tests indicate that the largest hooks and grapnels of *D. polyacanthos* can sustain loads of 3–9 and 20 N, respectively. The height of the self-supporting phase is more limited before becoming unstable, and the climbing strategy relies on attaching smaller lighter axes to relatively small supports across smaller distances.

In *D. orthacanthos*, senescence of primary tissues probably plays a decisive role in the climbing strategy and life history processes. Leaves and leaf sheath senesce from the base of the plant upwards so that both the attachment of the climber by any given leaf and the stiffness imparted by the leaf sheath are limited over time. To remain attached to supports during and after the loss of leaves beneath the apex, the plant must continue to grow and produce new leaves and new points of attachment. This explains why the overall length of plants (20–30 m) is greater than the overall height. This type of growth form is similar to that observed among rattans from southeast Asia (Corner, 1966; Putz, 1990). Observations suggest that senescence of leaves and leaf sheath and slipping or ratcheting of the mature climbing stem in the surrounding vegetation might have important implications on other aspects of the plants life history. The fact that the plant crown might be under almost constant tensile strain from the weight of the suspended cane below might limit its lateral growth to new supports of the canopy. Furthermore, the production of new

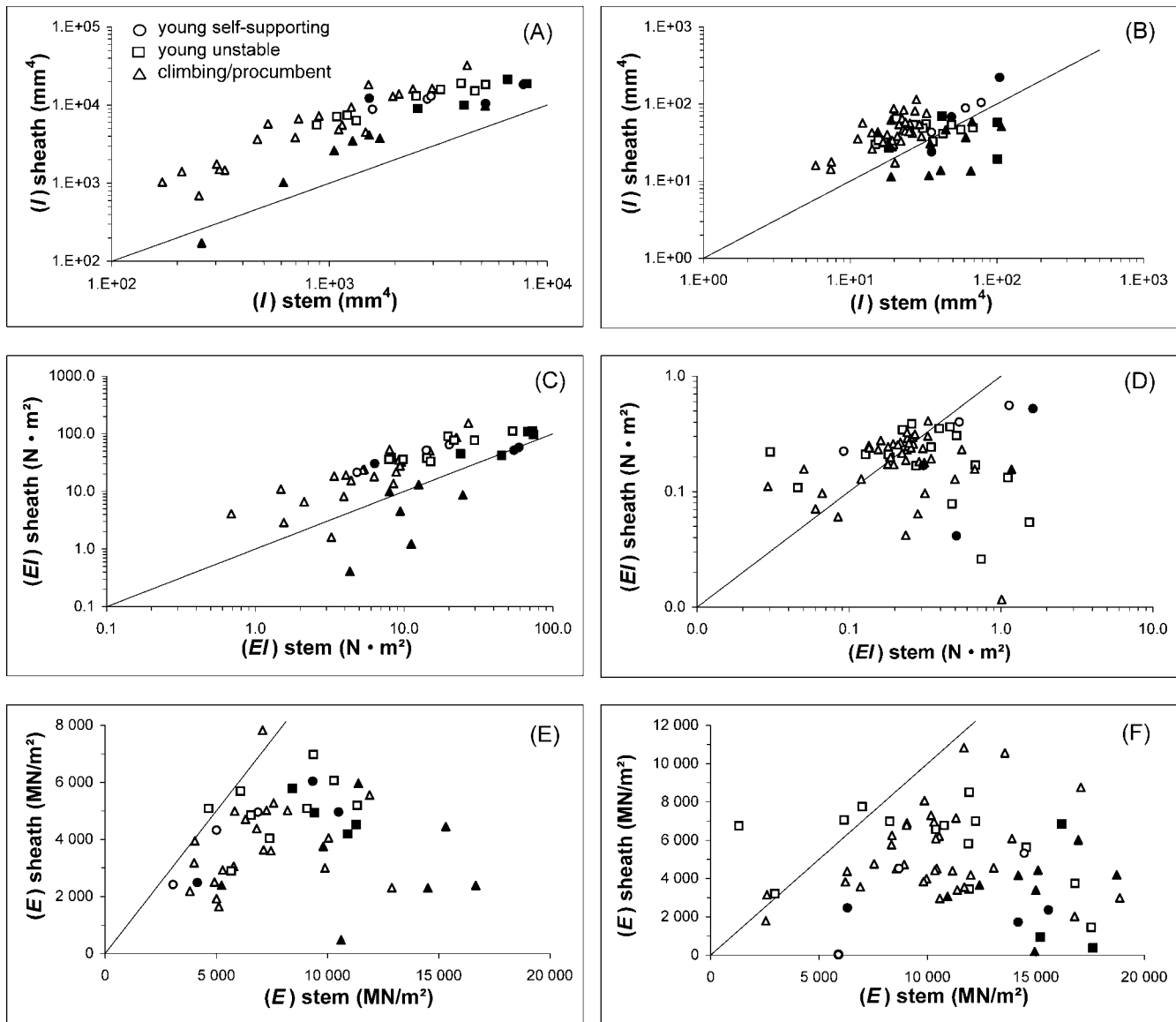


Fig. 9. Geometric and mechanical parameters of the leaf sheath and stem. The isometric relationship x (contribution of stem) = y (contribution of leaf sheath) is represented by a line. Data points scattered above this line indicate that the contribution of the leaf sheath is greater than that of the stem. (A, C, E) *Desmoncus orthacanthos*. (B, D, F) *D. polyacanthos*. Black symbols represent basal segments. A, B. Axial second moment of area, I (mm^4). C, D. Flexural stiffness, EI ($\text{N} \cdot \text{m}^2$). E, F. Structural Young's modulus, E_{st} (MN/m^2).

leaves for assuring mechanical attachment will also be linked to photosynthetic requirements. Further studies should, if possible, investigate these dynamics around crowns of climbing palms such as *D. orthacanthos*.

The developmental constraints linked to climbing in *D. polyacanthos* are quite different. The species does not reach the heights and lengths observed in *D. orthacanthos*. Although older leaves below the apex of mature climbing plants senesce and fragment, this smaller species does not have the same tendency to slip or ratchet downwards from its point of attachment. Furthermore, older axes do not entirely lose the outer leaf sheath, and old stages of axis do not form extensive loops and coils of cane-like stems seen in the larger, heavier *D. orthacanthos*.

Leaf sheaths of *D. orthacanthos* may fracture as result of excessive bending stress or falling from host plants (Fig. 13).

Local fractures of the leaf sheath strongly reduce EI thereby providing local flexibility. The compliancy of the surviving inner stem allows repositioning of axes but because the fractured leaf sheath is only broken locally, the rest of the axis remains intact and sufficiently rigid to retain an overall climbing position. This kind of mechanical response to traumatic mechanical stress has also been observed among calamoid rattans (Rowe et al., 2004). The mechanism was not observed in *D. polyacanthos* in which lighter axes often remain firmly attached to the surrounding vegetation by highly catchy cirri. In cases of severe disturbance, slender axes can bend relatively easily and reorientation of the growing apex produces a characteristic "S"-shaped axis if a growing apex detaches or emerges from an understory support (Fig. 2C).

Comparisons with dicotyledonous lianas—Mechanical architectures of *Desmoncus* differ markedly from most investi-

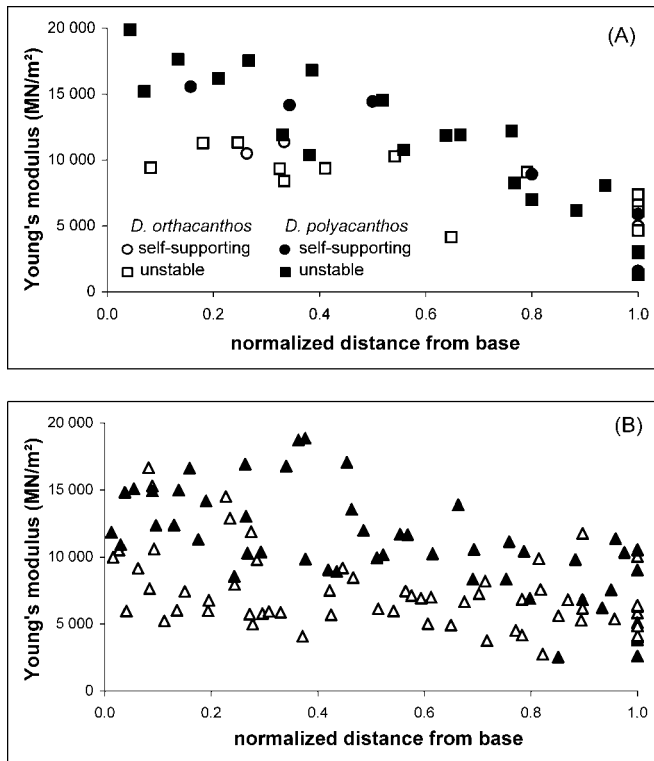


Fig. 10. Structural Young's modulus (E_{str}) of stems without leaf sheath plotted against normalized distance from the base for *Desmoncus orthacanthos* and *D. polyacanthos*. (A) Young self-supporting stems and unstable stems. (B) Old climbing stems.

gated dicotyledonous lianas. Well-known trends observed in dicotyledonous lianas consisting of a drop in E_{str} during development (Rowe and Speck, 1996, 1998, 2004; Speck and Rowe, 1999; Isnard et al., 2003a, b) are not observed. Lacking secondary growth, the potential for modifying mechanical properties of stems might be more constrained than in dicotyledonous lianas. Older climbing axes of *D. orthacanthos* had an increase in E_{str} at the very base in the part of the axis where the leaf sheath had been shed. A localized increase towards the base was also observed in older stages of *D. polyacanthos*. These patterns differ from most tested woody lianas, which have a more general decrease in E_{str} from the youngest apical parts of mature plants toward the base. They also differ from most self-supporting plants tested that show a progressive and continuous increase in structural Young's modulus toward the base (Speck, 1994; Speck and Rowe, 1999). A comparison of *Desmoncus* with old stages of a wide range of dicotyledonous lianas (Table 1) shows higher values of E_{str} in the climbing palms by a factor of 10–20. High values of E_{str} and relatively little overall change in material properties during ontogeny are, however, consistent with some kinds of woody dicotyledonous climbers referred to as semi-self-supporting growth forms (Rowe and Speck, 1998; Speck and Rowe, 1999). These often have relatively stiff and straight stems compared with twining or winding lianas and among tropical climbers include species of *Strychnos* and *Croton* (Rowe and Speck, 1998; Gallenmüller et al., 2000, 2001; Rowe et al., in press), which can show relatively high values of E_{str} and stiff material properties in older ontogenetic stages (Table 1). In *Desmoncus*, the outer leaf sheath provides stiffness during maturation of stem tissues

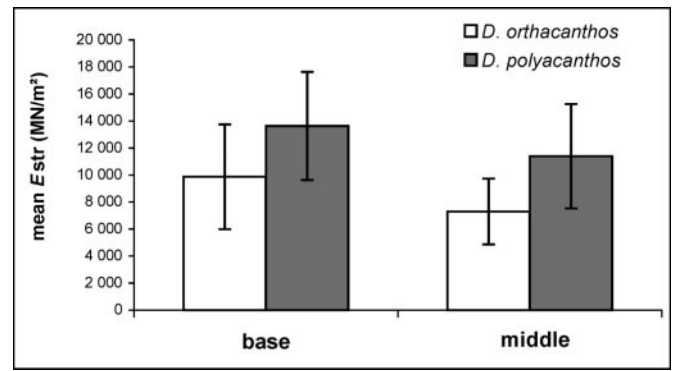


Fig. 11. Mean structural Young's modulus of stems without leaf sheath at the basal and median parts of the plant (± 1 SD) for *Desmoncus orthacanthos* and *D. polyacanthos*.

in youngest stages of growth and ensures a self-supporting orientation before the stem contributes much to overall stiffness. Furthermore, as suggested by Putz (1990) for Asian rattans, young stems and searchers of *Desmoncus* with thick outer leaf sheaths are much stiffer in terms of EI than most young woody vine leaders. This difference relying on geometry-enhanced stiffness allows climbing palms to span large gaps between host supports.

Absence of secondary growth and the climbing habit—

Anomalous cambial growth is widespread in dicotyledonous lianas, often increases stem flexibility in older parts of the stem (lowers E_{str}), and prevents or limits damage and breakage when

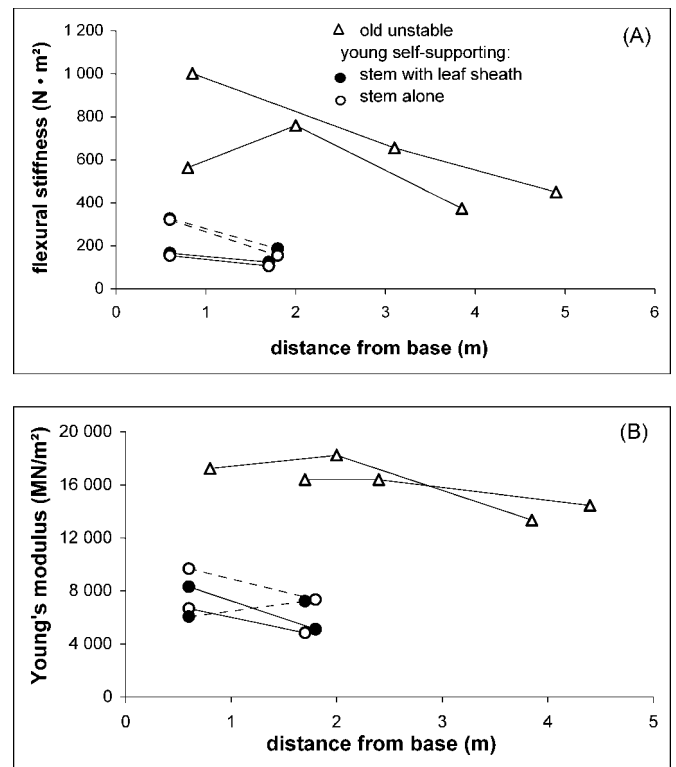


Fig. 12. Mechanical parameters plotted against distance from the base (m) for *Bactris major*. (A) Flexural stiffness, EI ($N \cdot m^2$). (B) Structural Young's modulus, E_{str} (MN/m^2).



Fig. 13. *Desmoncus orthacanthos* and local fracture of the leaf sheath exposing the more flexible inner stem following partial fall and exposure of the axis to high bending stress.

stems are twisted, coiled, or bent (Putz and Holbrook, 1991). Anomalous cambial development also promotes healing of injured stems (Dobbins and Fisher, 1986; Fisher and Ewers, 1989, 1991). The increase in E_{str} towards the base and lack of secondary growth in *Desmoncus* are not at all consistent with such strategies. Furthermore, climbing palms cannot replace damaged vascular tissue and consequently might be viewed as being highly vulnerable to mechanical damage (Tomlinson and Zimmermann, 2003). In *Desmoncus*, greater flexibility is obtained via a more passive mechanism of leaf sheath fracture, but nevertheless constitutes an effective response to potentially critical mechanical forces. Though quite different from dicotyledonous lianas, we suggest that the composite stem/leaf sheath structure characterizing *Desmoncus* and possibly other climbing palms might represent at least part of the adaptive mechanical control over stiffness and flexibility, which is so important for the climbing habit, particularly among larger-bodied species.

The ability to resprout from the stem after damage to the shoot allows many dicotyledonous lianas to survive mechanical damage (Caballé, 1977, 1980; Putz, 1984). Many climbing palms including *Desmoncus* are not able to produce reiterations or adventitious roots from the aboveground stem. *Desmoncus* does have additional characteristics that are probably adapted to the climbing habit. First, the ability to sprout from the rhizome (Putz, 1983) after damage and/or dieback of a ramet is an alternative way to replace rather than survive mechanical damage. Second, axes of *D. polyacanthos* are narrow and in spite of relatively high values of E_{str} , resistance to bending forces remains small by retaining a narrow diameter.

TABLE 1. Means of structural Young's modulus (MN/m^2) and standard deviations of old ontogenetic stages of different non-self-supporting dicotyledonous and two species of the climbing palm *Desmoncus*.

Species	Structural Young's modulus (MN/m^2) of old parts of the plant
<i>Doliocarpus</i> sp.	290 \pm 30
<i>Condylocarpon guianense</i>	310 \pm 50
<i>Bauhinia guianensis</i>	350 \pm 100
<i>Maripa scandens</i>	390 \pm 30
<i>Clematis maritima</i>	470 \pm 140
<i>Aristolochia macrophylla</i>	500 \pm 390
<i>Clematis vitalba</i>	560 \pm 90
<i>Croton pullei</i>	660 \pm 350
<i>Passiflora glandulifera</i>	630 \pm 130
<i>Fallopia aubertii</i>	730 \pm 150
<i>Croton nuntians</i>	849 \pm 210
<i>Strychnos</i> sp.	1750 \pm 40
<i>Desmoncus orthacanthos</i>	6880 \pm 2360
<i>Desmoncus polyacanthos</i>	8019 \pm 2546

Evolutionary context—Tree palms (*Welfia*, *Euterpe*, *Iriar-tea*; Rich, 1986, 1987) have mechanical architectures similar to the tested species of *Desmoncus* with an increase of EI and E_{str} toward the base. The comparison of *Desmoncus* and *Bactris* revealed little difference in stem stiffness and only marginally higher values of E_{str} in *Bactris*, although trends along stems are similar. The comparison based on mechanical properties is consistent with findings on the hydraulic architecture where the stem vascular system of *Desmoncus* resembles that of tree palms and the palm model based on *Rhapis excelsa*. Interestingly, this organization differs from the highly modified vascular architecture found in *Calamus* (Tomlinson and Zimmermann, 2003).

In terms of the mechanical and hydraulic organization observed in *Desmoncus* and possibly in general in the Arecoideae, differences between arborescent, semi-self-supporting, and climbing growth forms do not involve profound modifications of stem organization and material properties. This contrasts markedly to the situation in many dicotyledonous families in which trees, shrubs, and climbers can have drastically different patterns of developmental and mechanical properties, largely but not always mediated by variations in secondary growth.

Previous authors have noted the extraordinary morphological convergence of climbing forms in *Desmoncus* and the Calamoideae (Corner, 1966; Tomlinson and Fisher, 2000) as well as the great diversity of climbing species in Calamoideae (Uhl and Dransfield, 1987; Baker et al., 2000a, b). Beyond a broad similarity of height, size, and attachment in the two groups, it would be of great interest to know whether (1) the mechanical architecture involving a central stem, leaf sheath, and fracturing of the leaf sheath after extreme mechanical stress is similar for large bodied members of the Calamoideae and (2) whether smaller-bodied species show different architectures linked to habitat preferences as observed in *Desmoncus*.

Previous observers including Holtum (1955) noted the uniformity of growth pattern among monocotyledons that nevertheless gave rise to a wide variety of body sizes and growth forms. These observations led to the concept of establishment growth characterizing development in palms where the stem base thickens without internodal expansion and forms an obconical stem base (Tomlinson and Zimmermann, 1966). Development in *Desmoncus* does not pass through an extended

establishment phase, and internodes extend early after the second leaf opens (Putz, 1983). As suggested by Tomlinson (1979), habit evolution in palms could involve heterochronic modification of this developmental trajectory and retention of juvenile characteristics. In both species of *Desmoncus*, especially in *D. polyacanthos*, reduction of the establishment phase results in a slender stem. It is possible that a decrease in rate of stem thickening (the establishment phase) combined with an increase in internode elongation occurred in *Desmoncus* and possibly other climbing palms.

Recent investigations of dicotyledonous lianas have demonstrated that in some groups the transition from self-supporter to climber involved a wide array of hydraulic and mechanical novelties that strongly influenced and possibly constrained future growth form change and evolution in the group. In some families of dicotyledons such as the Aristolochiaceae, there is evidence that lianoid forms rarely reversed to “truly self-supporting forms” (Rowe and Speck, 2004). Such reversals observed in other groups can differ in their mechanical and geometrical characters compared with self-supporting species (Speck et al., 1997; Civeyrel and Rowe, 2001). Interestingly, in *Desmoncus* and possibly other climbing monocotyledons, the prevalent changes in development compared with self-supporting species appear to involve changes in stem size, geometry, and leaf sheath morphology rather than profound changes in the integral mechanical properties of the stem.

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