

# Development and Growth Form of the Neotropical Liana *Croton nuntians*: The Effect of Light and Mode of Attachment on the Biomechanics of the Stem

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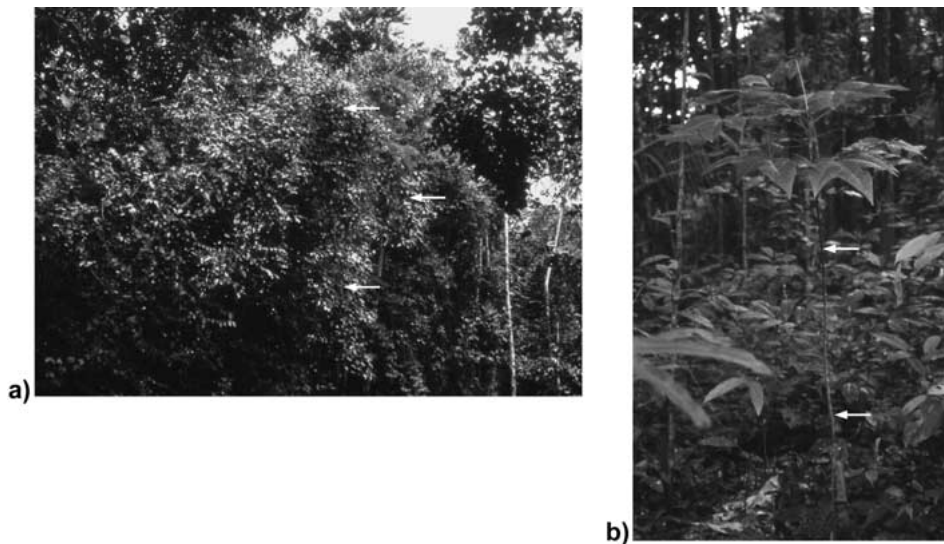
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## ABSTRACT

The neotropical liana *Croton nuntians* (Euphorbiaceae) can occur in a variety of different growth habits. Juvenile freestanding plants are mechanically stable without support and resemble morphologically young trees or shrubs, whereas adult plants are climbers. Ontogenetic variation of bending and torsion properties of different growth phases are analyzed by measurements of flexural stiffness, structural bending modulus, torsional stiffness and structural torsional modulus. Mechanical and anatomical data show two fundamentally different patterns for juvenile freestanding and adult climbing plants. In freestanding plants, mechanical properties and the contribution of cortex, wood, and pith to the stem cross-section vary only little during ontogeny as is typical for semi-self-supporting plants. In contrast, climbing plants become significantly more flexible during ontogeny, as is characteristic for lianas. This is accompanied by a transition to the formation of a less dense wood type

with large diameter vessels and an increasing contribution of flexible tissues (less dense wood and cortex) to the cross-sectional area and the axial second moment of area of the stems. Depending on the environmental conditions, freestanding plants can differ considerably in their appearance due to differences in branching system or stem taper. Therefore the influence of light quantity, measured as percentage of canopy opening, on the mechanical properties and the stem anatomy was tested. Freestanding plants grown with strong shade are significantly more stiff in bending compared with plants grown with a moderate light environment.

**Key words:** Bending mechanics; *Croton nuntians*; Flexural stiffness; Growth form; Liana; Mechanical properties; Semi-self-supporting; Structural torsional modulus; Structural bending modulus; Torsional stiffness



**Figure 1.** *Croton nuntians* in the freestanding and climbing growth phases. **a)** freestanding plant, height 1.50 m, **b)** climbing plant at a forest margin.

## INTRODUCTION

The anatomy and morphology of tropical lianas have been the object of scientific interest for more than a century (Darwin 1867; Haberlandt 1924; Schenck 1892, 1893, 1912; Troll 1937, 1939, 1943; Westermeier and Ambronn 1881). Many tropical lianas show “anomalous” secondary growth (for example, the formation of multiple cambium layers) (Bhambie 1972; Caballe 1993, 1998; Carlquist 1984; Darwin 1867; Fisher and Ewers 1989, 1992; Haberlandt 1924; Obaton 1960; Rowe and Speck 1996; Schenck 1892, 1893, 1912; Speck and others 1996a). During the last decades an increasing amount of information on the functional significance of the anatomical and morphological particularities shown by many lianas has become available. These studies concern (1) water transport in lianas (Ewers 1985; Ewers and Fisher 1991, 1995; Ewers and others 1991, 1997; Gartner 1991a; Gartner and others 1990; Tyree and Ewers 1996) and (2) mechanical properties (Fisher and Ewers 1989, 1991; Gallenmüller and others 2001; Gartner 1991b; Rowe and Speck 1996, 1998, 2002; Speck 1991a, 1991b, 1994, 1997; Speck and Rowe 1999a, 1999b, 2001a; Speck and others 1996a, 1996b, 1997).

Quantitative analyses of non-self-supporting lianas compared to self-supporting trees and shrubs have shown that different growth forms can be characterized by variations of mechanical properties during ontogeny (Gallenmüller and others 2001; Rowe and Speck 1996, 1998; Speck 1991a, 1991b, 1994, 1997; Speck and Rowe 1999a, 1999b, 2001a, 2001b; Speck and others 1996a, 1996b, 1997). According to these studies, a third intermediate

growth form can be distinguished known as semi-self-supporting plants, which are mechanically stable up to a certain size. After further growth, such plants lose their stability and “lean against” supporting structures. They finally get entangled in the surrounding vegetation via wide-angled branches and coarse leaves without the aid of specialized climbing structures (Gallenmüller and others 2001; Rowe and Speck 1998; Speck 1994, 1997; Speck and Rowe 1999a, 1999b, 2001a, 2001b; Speck and others 1996a, 1996b).

The variation of mechanical properties observed during the ontogeny of lianas is accompanied by a range of structural changes that can affect the overall stem structure, the tissue and cell structure, the ultrastructure of the cell walls or even the biochemical properties of the cell walls (Chabbert and others 1997; Hoffmann and others 2000a, 2000b, 2003; Speck and others 1996a, 1996b). Here we report on the biomechanics and stem anatomy of *Croton nuntians* (Euphorbiaceae). This is a woody climber of the lowland rainforest of French-Guyana. The species can occur in a variety of different growth habits. Adult climbing plants resemble typical lianas, but have no specialized climbing structures such as hooks, tendrils, twining stems or spines. A system of wide-angled branches with rough surfaces prevents the plants from slipping from their supports. The pronounced roughness of the leaves also appears to improve anchoring in the surrounding vegetation. Large climbing plants are typically found at forest margins, where they produce large trellises up to 20 m in height (Figure 1a). Furthermore, freestanding plants of *C. nuntians* are found, which have a fundamentally different appearance (Figure 1b). These freestanding plants



**Figure 2.** Sample area with the experimental *Croton nuntians* - plants in a forest margin area on the “piste de Counami”, French-Guyana.

are not in contact with the surrounding vegetation and maintain an upright position without a support. They are mechanically stable up to a height of approximately 7 m and smaller plants therefore resemble young trees of the understorey. Larger plants finally become unstable and lean on the surrounding vegetation, a feature known from semi-self-supporting plants (Gallenmüller and others 2001; Rowe and Speck 1998; Speck 1994, 1997; Speck and Rowe 1999a, 1999b, 2001a, 2001b; Speck and others 1996a, 1996b).

Freestanding and climbing plants of *C. nuntians* are clearly differentiated by different stem tapers and different growth rates (Gallenmüller unpublished data). The existence of juvenile freestanding growth phases has been described for many tropical liana species. They can constitute a large proportion of the understorey vegetation in tropical rain forests (Caballe 1980a, 1993, 1998; Coudurier 1992; Creemers 1973, 1974; Gallenmüller and others 2001; Kennard 1998; Putz 1983, 1984, 1990; Putz and Chai 1987; Putz and Holbrook 1991). In *C. nuntians* the freestanding plants are particularly conspicuous, as they reach much larger dimensions than so far described juvenile stages of other liana species. They occur abundantly in large gaps with high insolation and along the forest margins of forest tracks. Occasionally freestanding plants growing in shaded conditions can be found. Those grown under different light conditions differ strikingly in their habit due to differences in the branching system or stem taper. We have completed the analysis of overall biomechanical trends in different growth phases of *C. nuntians* by analyzing the influence of light conditions on the mechanical properties and stem anatomy in freestanding plants. We used hemispherical photographs to measure the light quantity as a practical field method in this first study on the influence of light conditions.

We tested different stem types separately, including main stems, branches and reiterative shoots. This procedure addresses the question of whether the branches that anchor plants in the surrounding vegetation once they have started to climb show mechanical adaptations as attachment structures. Reiterative shoots develop from adult climbing stems that have fallen to the ground and resemble juvenile stages in their morphology (compare Gallenmüller and others 2001).

## MATERIAL AND METHODS

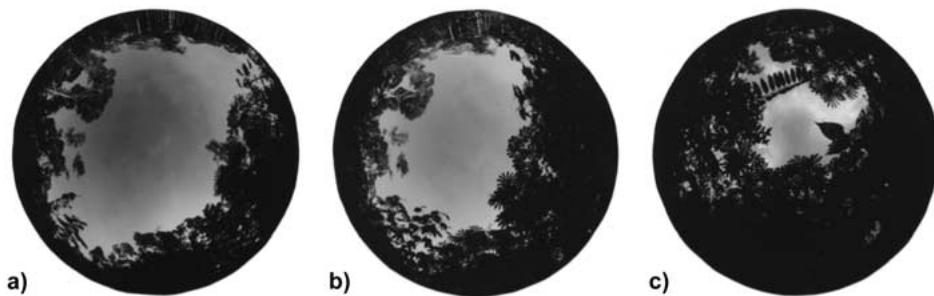
The field study was carried out in French-Guyana in the vicinity of the research camp ‘Counami’ (5°19’Nord, 53°13’W). Experimental plants grew at different distances from the forest margin. Plants close to the forest margin were provided with less sunlight during the day than plants growing more distant from it (Fig. 2). We refer to plants that maintain themselves upright without a support as “freestanding plants”. “Climbing plants”, on the contrary, are entangled in the surrounding vegetation and mechanically unstable without a support.

### Estimation of Light Availability

The light quantity was estimated with fisheye photographs taken 50 cm above the apical bud of each of 70 experimental plants. The fraction of open sky was calculated as the gap light index by using digital image analysis (Optimas) (Fig. 3).

### Biomechanics

After cutting, the stem samples were subjected to bending and torsion tests within 48 h. Bending properties were measured in conventional three-point and four-point bending tests with a steel frame bending apparatus. Stems longer than over 53 cm exceed the testable size range of the bending apparatus and were tested in two-point-bending. The bending force was applied by adding manually up to six weights and the maximum deflection was measured for each weight increment with a dissecting microscope mounted on the apparatus (compare Bodig and Jayne 1982; Vincent 1992; Speck 1991b). The applied weights range from 10 to 200 g according to the dimensions and properties of the tested stem segments. Whenever possible, 4-point-bending tests were carried out. To ensure that in two-point- and three-point-bending span-to-depth ratios (that is, the ratios of length to diameter



**Figure 3.** Example of hemispherical photographs taken 50 cm above the apical bud of three experimental plants growing at different distances from the forest margin. Gap light index = percentage of canopy opening: **a)** 48%, **b)** 31%, **c)** 12%.

of tested samples) were sufficient to avoid significant shear influence (Vincent 1992), two-point- and three-point-bending tests were carried out with increasing span-to-depth ratios until no further increase of the structural bending modulus was observed. This was done to determine the minimum span-to-depth ratio of testable segments. Lengths of tested stem segments range from 5 cm (that is, stems of seedlings) to 2 m (stem segments of large climbing lianas). Only straight stem segments with an approximately uniform diameter were chosen for the bending tests. Flexural stiffness and structural bending modulus were calculated from linear regression lines resulting from plots of bending force against the maximum deflection. Only linear regressions of force-deflection data with a correlation coefficient of 0.97 and above were accepted.

The structural bending modulus  $E_{str}$  is calculated by dividing the flexural stiffness  $EI$  by the axial second moment of area  $I_{ax}$  (Speck 1991b, 1994; Vincent 1992).  $I_{ax}$  is a geometrical parameter that takes into account the cross-sectional area and shape of an object, which is essential for the bending properties of this object. The axial second moment of area ( $I_{ax}$ ) was calculated by approximating the cross-sectional shape of the segments as an ellipse ( $I_{ax} = \pi/64 \cdot (a^3b)$ ,  $a$  = diameter in bending force direction,  $b$  = diameter perpendicular to bending force direction). The flexural stiffness ( $EI = E_{str} \times I_{ax}$ ) is dependent on the dimensions of a sample (described by  $I_{ax}$ ) and its material properties (described by the structural bending modulus). Originally the term "bending modulus" was defined as a property of a homogeneous material. Because plant stems are heterogeneous the terms *structural* bending modulus  $E_{str}$  and *structural* torsional modulus  $G_{str}$  are used (Rowe and Speck 1996; Speck and others 1996a). For more extensive treatment of the measurements and calculation of flexural stiffness and structural bending modulus we refer to Niklas (1992); Rowe and Speck (1996); Speck (1994); and Vincent (1992).

The torsion tests were carried out by applying a torque to the tested stem segments and measuring

the torque and the resulting angle with specially made spring-loaded cylinders (see Gallenmüller and others 2001). The torsional stiffness  $GI$  was calculated from linear regression lines resulting from plots of the resulting angle against the applied torque. The structural torsional modulus  $G_{str}$  was calculated by dividing the torsional stiffness  $GI$  ( $GI = G_{str} \times I_{pol}$ ) by  $I_{pol}$ , the polar moment of area ( $I_{pol} = \pi/32((a+b)/2)^4$ ). For more extensive treatment of the measurements and calculation of torsional stiffness and structural torsional modulus see Gallenmüller and others (2001).

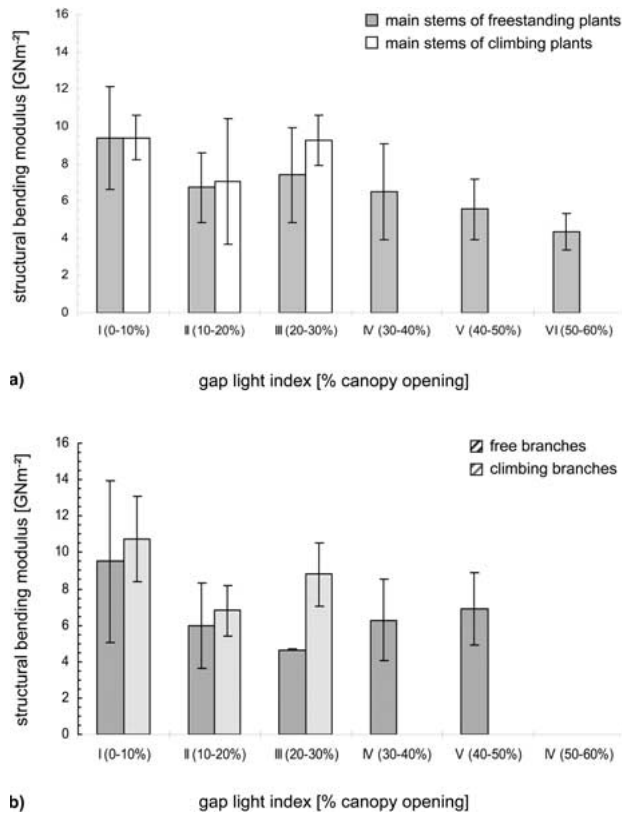
### Stem Anatomy

After the mechanical testing, middle parts of the studied stem segments were fixed in FPA (2% formaldehyde, 5% propionic acid, 45% ethanol, 48% distilled water). After removing the FPA by washing in water, thin sections of the entire stem were prepared and stained with 6% phloroglucinol in 95% ethanol, after irrigating in 18% hydrochloric acid. The contributions of cortex, wood and pith towards axial second moment of area were measured in cross-sections and calculated using digital image analysis (Optimas).

## RESULTS

### Influence of Light Quantity on Bending Properties

Data of structural bending modulus  $E_{str}$  reveal a significant influence of light quantity on the bending properties of *Croton nuntians* plants. In Figure 4  $E_{str}$  is plotted against the gap light index as mean values for different stem types. Values of the light gap index are classified with increasing light quantity in the classes I (0–10% canopy opening, lowest light availability), II (10–20%), III (20–30%), IV (30–40%), V (40–50%) and VI (50–60% canopy opening, highest light availability). Data are also grouped according to growth phase (freestanding or



**Figure 4.** Influence of light quantity on the structural bending modulus in stems of *Croton nuntians*. Mean values and standard deviations in different classes of light quantity (0-10% canopy opening = I, shade, 50-60% canopy opening = VI, highest light quantity). In freestanding plants  $E_{str}$  does not vary significantly during ontogeny (compare Figure 5). Therefore, within one class of the gap light index, data of the whole tested diameter range are pooled. In climbing plants, a modification of  $E_{str}$  is observed in bigger stems, therefore only data of stems with a diameter less than 15 mm ( $I_{ax} < 2.5 \cdot 10^{-9} \text{ m}^4$ , respectively, compare Figure 5) are included in this comparison, **a)** main stems of freestanding and climbing plants, **b)** free branches and climbing branches.

climbing plants) and the branch type (free branches or climbing branches).

Main stems of freestanding plants become significantly more flexible with increasing light quantity.  $E_{str}$  decreases over 50% from  $9.38 \pm 2.75 \text{ GNm}^{-2}$  in class I with the lowest light quantity to  $4.37 \pm 0.97 \text{ GNm}^{-2}$  in class VI with the highest light quantity (Fig. 4a). Differences are statistically significant if the mean value of class I is compared with the mean values of classes III, VI, V and VI (Table 1). In the main stems of climbing plants, variation of  $E_{str}$  with increasing light quantity is not significant in the tested range of 0-30% canopy opening. Values of  $E_{str}$  in main stems of climbing plants

averaged over the classes I to III amount to  $8.81 \pm 2.10 \text{ GNm}^{-2}$ . Within a single class of light quantity, values of  $E_{str}$  in freestanding and climbing plants do not differ significantly.

$E_{str}$  of branches is significantly influenced by the light quantity (Table 1). Figure 4b compares the values of free branches and climbing branches. Within classes I and II no significant difference between the two branch types is observed.  $E_{str}$  averaged over free branches and climbing branches decreased significantly from  $9.59 \pm 4.23 \text{ GNm}^{-2}$  in class I to  $6.21 \pm 2.10 \text{ GNm}^{-2}$  in class II. With further increasing light quantity, no further significant variation of  $E_{str}$  is observed in free or climbing branches. However, climbing branches in class III show a relatively high mean value of  $8.80 \pm 1.74 \text{ GNm}^{-2}$ , which is comparable to the value found for branches of shaded plants in class I.

## Variation of Mechanical Properties During Ontogeny

**Bending properties.** An analysis dependent on the actual age of stem samples is not possible, as *Croton nuntians* is a tropical plant, which does not form growth rings. Therefore the increase in diameter during secondary growth was chosen as a measure of ontogenetic development (expressed in terms of the axial second moment of area  $I_{ax}$  for the results of the bending experiments or in terms of the polar moment of area  $I_{pol}$  for torsion measurements).

According to the results of the analysis of the influence of the light quantity, data are pooled for stems grown in strong shade with a canopy opening of 0-10% and for stems grown in a more moderate light environment with a canopy opening from 10-50%. Data of plants grown with even higher insolation (gap light index 50-60%) are not included in the comparison because these plants show a strongly reduced growth, forming diminutive unbranched stems (Gallenmüller unpublished data).

Large climbing plants with a diameter greater than 15 mm (or an axial second moment of area  $> 2.5 \cdot 10^{-9} \text{ m}^4$ , respectively) are partially oriented horizontally, colonizing several host trees of the forest margin and therefore exposed to light conditions that vary along their stems. For these extensive climbing plants a measure of the gap light index with hemispherical photographs taken above the apical bud (as done for the freestanding plants and smaller climbing plants) is not applicable. However, at the relevant sites at a forest margin, a qualitative estimation of the light conditions suggests that light conditions are in the moderate range and plants are

**Table 1.** Results of ANOVA followed by Scheffé post-hoc Test comparing Structural Bending Modulus  $E_{str}$  of *Croton nuntians*-plants Grown with Different Light Conditions.

Gap light index [% canopy opening]	0-10	10-20	20-30	30-40	40-50
<b>main stems of freestanding plants</b>					
10-20	**				
20-30	-	-			
30-40	**	-	-		
40-50	***	-	-	-	
50-60	*	-	-	-	-
<b>main stems of climbing plants</b>					
10-20	-				
20-30	-	-			
<b>free branches</b>					
10-20	*				
20-30	-	-			
30-40	*	-	-		
40-50	*	-	-	-	
<b>climbing branches</b>					
10-20	*				
20-30	-	-			

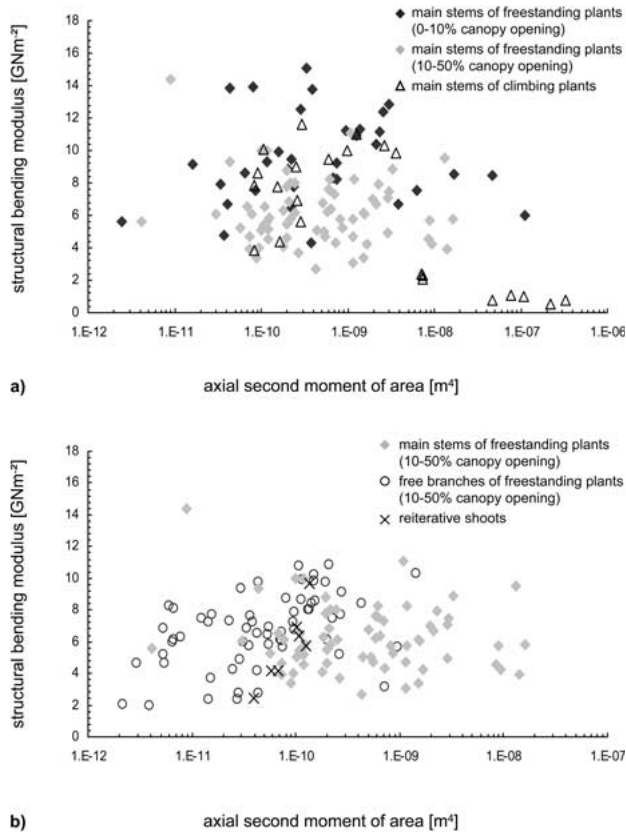
- no significant difference. \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

neither exposed to strong shade nor high insolation. This also holds true for the reiterative shoots considered below. In the analysis of the ontogenetic variation of bending properties in both freestanding and climbing plants, the comparison includes data of such extensive climbing plants for which no direct measurements of light quantity are available.

Freestanding plants grown in the shade (0–10% canopy opening) show significantly higher values of  $E_{str}$  compared to freestanding plants grown with a higher light quantity (10–50% canopy opening) (compare Fig. 4), but in both groups  $E_{str}$  scatters widely and shows neither an increase nor a decrease with increasing  $I_{ax}$  (Fig. 5a). In stems of shaded freestanding plants (canopy opening of 0–10%) the mean of  $E_{str}$  for the whole size range is  $9.38 \pm 2.76$   $\text{GNm}^{-2}$ . In main stems of freestanding plants grown with higher insolation (canopy opening 10–50%)  $E_{str}$  averages to  $6.39 \pm 2.14$   $\text{GNm}^{-2}$ . Superimposed on this pattern, main stems of climbing plants become significantly more flexible with increasing diameter. In younger stages of climbing plants, values of  $E_{str}$  are relatively high and comparable to those of freestanding plants (Fig. 5a, compare Fig. 4). In older stages values decrease by nearly 90% of the values found in younger stages. Table 2 gives the mean values of  $E_{str}$  for the different stem types in diameter classes. The statistical analysis is summarized in Table 3.

The bending properties of main stems, branches and reiterative shoots do not differ significantly (Fig. 5b). In branches, values tend to increase in the first ontogenetic stages ( $I_{ax} < 1.5 \cdot 10^{-11}$   $\text{m}^4$ ), but with further increase in  $I_{ax}$  no further clear pattern of  $E_{str}$  is observed. Values of reiterative shoots show an increase in  $E_{str}$  (Fig. 5b). In the size range in which data of all stem types are available ( $I_{ax}$  of  $4.0 \cdot 10^{-11}$  to  $1.5 \cdot 10^{-10}$   $\text{m}^4$ ), data vary widely for main stems, branches and reiterative shoots (Fig. 5b).

Values of flexural stiffness  $EI$ , which is calculated as the product of the structural bending modulus  $E_{str}$  and the axial second moment of area  $I_{ax}$ , are plotted against the axial second moment of area  $I_{ax}$  (Fig. 6). Two different patterns are found for freestanding and climbing plants. If increase of flexural stiffness was due only to secondary growth and the resulting increase of  $I_{ax}$  - with  $E_{str}$  remaining constant during ontogeny data would scatter along a straight line of  $EI$  with  $E_{str}$  of the youngest ontogenetic stages as slope. This is the case for freestanding plants, if plants grown with strong shade (0–10%) and with a more moderate light environment (canopy opening 10–50%) are analyzed separately. This pattern is consistent with the finding that in freestanding plants  $E_{str}$  does not vary significantly during ontogeny and can be considered as typical for semi-self-supporting plants (compare Gallenmüller and others 2000, 2001; Speck 1994;



**Figure 5.** Variation of the structural bending modulus  $E_{str}$  with increasing axial second moment of area  $I_{ax}$ . **a)** main stems of freestanding plants grown in strong shade and in moderate conditions of light quantity and main stems of climbing plants (compare Gallenmüller and others 2000), **b)** main stems of freestanding plants, free branches of freestanding plants and reiterative shoots.

Speck and Rowe 1999a). The flexural stiffness of plants grown in the shade (0–10% canopy opening) is higher than that of plants grown with higher light quantity (10–50% canopy opening). This means that plants with a certain stem diameter (that is, with similar  $I_{ax}$ ) and grown in the shade are stiffer in terms of  $EI$  than plants with a similar stem diameter but grown with a higher daily light quantity.

On the contrary for climbing plants in which a significant drop of  $E_{str}$  during ontogeny is observed, values of older ontogenetic stages (with higher values of  $I_{ax}$ ) are distinctly below the neutral line. This pattern has proved to be characteristic for lianas (Gallenmüller and others 2000, 2001; Speck 1991b, 1994; Speck and Rowe 1999a).

**Torsional properties.** Trends in resistance to torsion are similar to those observed for bending properties. Values of structural torsional modulus  $G_{str}$  of different stems are plotted against the polar second moment of area (Fig. 7). Freestanding plants

grown in moderate light (10–50% canopy opening) show a wide scatter with no significant variation during ontogeny in the tested size ranges (Fig. 7a). Two small stems ( $I_{ax} < 6.5 \cdot 10^{-11} \text{ m}^4$ ) of shaded freestanding plants (0–10% canopy opening) show similar values of  $G_{str}$  (Fig. 7a). However, in larger stems of shaded plants ( $I_{ax} > 6.5 \cdot 10^{-11} \text{ m}^4$ ) slightly higher values of  $G_{str}$  are suggested. Climbing plants show values comparable to those found in stems of freestanding shaded plants (Fig. 7a). A comparison of different stem types reveals no significant difference between the main stems and the branches, and a tendency for lower values in reiterative shoots (Fig. 7b).

## Stem Anatomy

Freestanding plants typically show cross sections of major tissues comparable with those of stems of trees or shrubs, in which cortex, wood and pith can be distinguished macroscopically. We include here as “cortex” all tissues positioned outside the cambium, including secondary phloem, remaining primary cortex, epidermis and periderm. Freestanding plants of *C. nuntians* form a dense wood type with narrow vessels (diameter  $< 0.1 \text{ mm}$ ) (Fig. 8a). All freestanding specimens studied have developed exclusively this dense wood type. Cross sections of adult climbing plants show a second, more peripheral less dense wood type with wider vessels (diameter up to  $0.2 \text{ mm}$ ) (Fig. 8b). A high proportion of tension wood is observed in the dense wood type of all tested specimens, whereas the less dense wood type with wide vessels shows no tension wood formation in any studied sample.

**Influence of light quantity on stem anatomy.** In freestanding plants, contributions of stem tissues towards cross-sectional area  $A$  and axial second moment of area  $I_{ax}$  vary slightly during the first growth stages up to a stem diameter of 10 mm, with a slight increase of the wood contribution and a concomitant decrease of contribution by cortex (Gallenmüller and others 2000). After a diameter of 10 mm, tissue contributions remain constant within a given stem. Therefore, in the analysis of the influence of light quantity, only data of stem samples with a diameter greater than 10 mm were taken into account. Stems of plants grown with a very high insolation (canopy opening  $> 50\%$ ) show reduced growth, resulting in diameters less than 10 mm. Therefore no comparable data are available for this range of light quantity.

In freestanding plants grown in different ranges of the gap light index, the contribution of the cortex

**Table 2.** Variation of the Structural Bending Modulus  $E_{str}$  during Ontogeny in Different Stem types

Diameter class [mm]	Structural bending modulus $E_{str}$ [GN m <sup>-2</sup> ]				
	0.0-5.0	5.1-10.0	10.1-15.0	15.1-20.0	> 20.0
Main stems of freestanding plants <sup>1</sup>	7.45 ± 1.72n = 7	10.21 ± 3.37n = 13	10.22 ± 1.37n = 7	9.85 ± 3.22n = 4	7.69 ± 1.43n = 3
Main stems of freestanding plants <sup>2</sup>	6.65 ± 2.23n = 26	6.02 ± 2.11n = 23	6.52 ± 2.14n = 20	7.35 ± 1.57n = 3	5.60 ± 2.29n = 5
Main stems of climbing plants	10.07n = 1	7.29 ± 2.43n = 9	10.20 ± 0.63n = 4	4.16 ± 3.79n = 4	0.84 ± 0.21n = 5
Free branches <sup>1</sup>	5.92 ± 2.31n = 31	7.44 ± 1.82n = 30	6.38 ± 3.64n = 3		
Reiterative shoots		5.64 ± 2.35n = 7			

<sup>1</sup>0-10% canopy opening, <sup>2</sup>10-50% canopy opening

Mean values and standard deviations in different diameter classes.

**Table 3.** Results of ANOVA followed by Scheffé, Post-hoc Test comparing Structural Bending Modulus  $E_{str}$  of *Croton nuntians*-plants in Different Diameter Classes

Diameter class [mm]	0.0-5.0	5.1-10.0	10.1-15.0	15.1-20.0
<b>Main stems of freestanding plants [0-10% canopy opening]</b>				
5.1-10.0	-			
10.1-15.0	-	-		
15.1-20.0	-	-	-	
>20.0	-	-	-	-
<b>Main stems of freestanding plants [10-50% canopy opening]</b>				
5.1-10.0	-			
10.1-15.0	-	-		
15.1-20.0	-	-	-	
>20.0	-	-	-	-
<b>Main stems of climbing plants</b>				
5.1-10.0				
10.1-15.0		-		
15.1-20.0		-	*	-
>20.0		**	***	-
<b>Free branches [10-50% canopy opening]</b>				
5.1-10.0	*			
10.1-15.0	-	-		

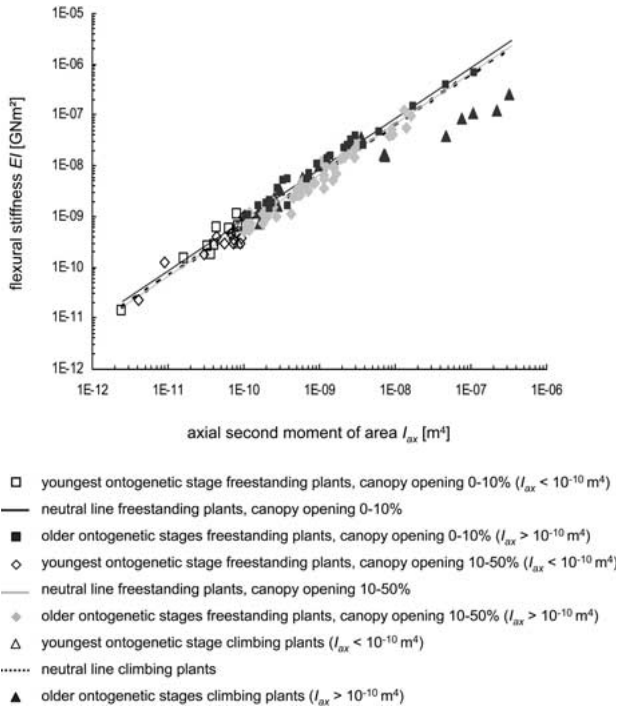
- no significant difference, \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

to cross-sectional area shows only a small variation with increasing light quantity (Fig. 9a). Lowest values are found for shaded plants grown with 0-10% canopy opening (mean value:  $17.2 \pm 5.0\%$ ) and highest values in plants grown with 40-50% canopy opening (mean value:  $21.0 \pm 3.2\%$ ). This difference is statistically significant. The contribution of the pith to  $A$  remains small and varies little around  $2.2 \pm 2.1\%$ . The variation in the contribu-

tion of wood to  $A$  mirrors that of the cortex (Fig. 9a).

Contributions of wood, cortex and pith to the axial second moment of area  $I_{ax}$  show the same tendencies as contributions to  $A$ . However, contributions of cortex to  $I_{ax}$  are higher than cortex contributions to  $A$  because of the peripheral position of the cortex. Consequently, the contributions of wood and pith are lower. The contribution of the cortex to





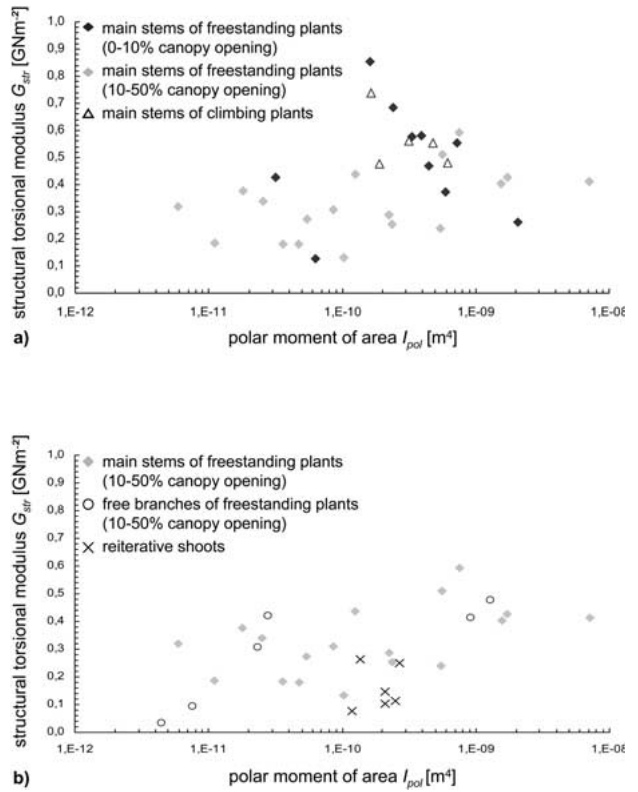
**Figure 6.** Double logarithmic plot of the flexural stiffness  $EI$  against the axial second moment of area  $I_{ax}$  of the main stems of freestanding and climbing *Croton nuntians* plants. The neutral lines are calculated with the mean structural bending modulus  $E_{str}$  of the youngest ontogenetic stages ( $I_{ax} < 10^{-10} \text{ m}^4$ ) as slope. Neutral line of freestanding plants grown in strong shade (0-10% canopy opening):  $EI = 8.68 \times I_{ax}$ , neutral line of freestanding plants grown with higher light quantity (10-50% canopy opening):  $EI = 6.60 \times I_{ax}$ , neutral line of climbing plants:  $EI = 6.76 \times I_{ax}$  (modified after Gallenmüller and others 2000).

$I_{ax}$  amounts to  $31.1 \pm 8.2\%$  in the range of 0-10% canopy opening, and to a significantly higher value of  $37.1 \pm 4.9\%$  in the range of 40-50% canopy opening. As in the contribution to  $A$ , the higher the contribution of cortex to  $I_{ax}$  the lower is the contribution of wood and vice versa. The contribution of pith to  $I_{ax}$  is very small and averages  $0.1 \pm 0.2\%$  over all tested ranges of light quantity (Fig. 9b).

The variation in contribution of the cortex to  $I_{ax}$  is small, but due to the low stiffness of the cortex and its peripheral position in the stem, the contribution of the cortex clearly influences the bending properties of the stems. In general, the higher the contribution of the cortex to  $I_{ax}$ , the lower the bending modulus (Fig. 10).

### Variation of Stem Anatomy During Ontogeny

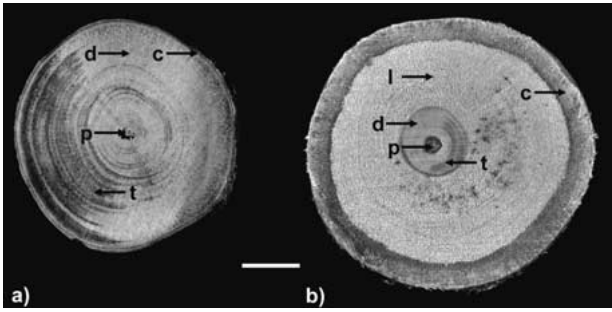
Because pronounced shade influences tissue distribution significantly, ontogenetic variations were



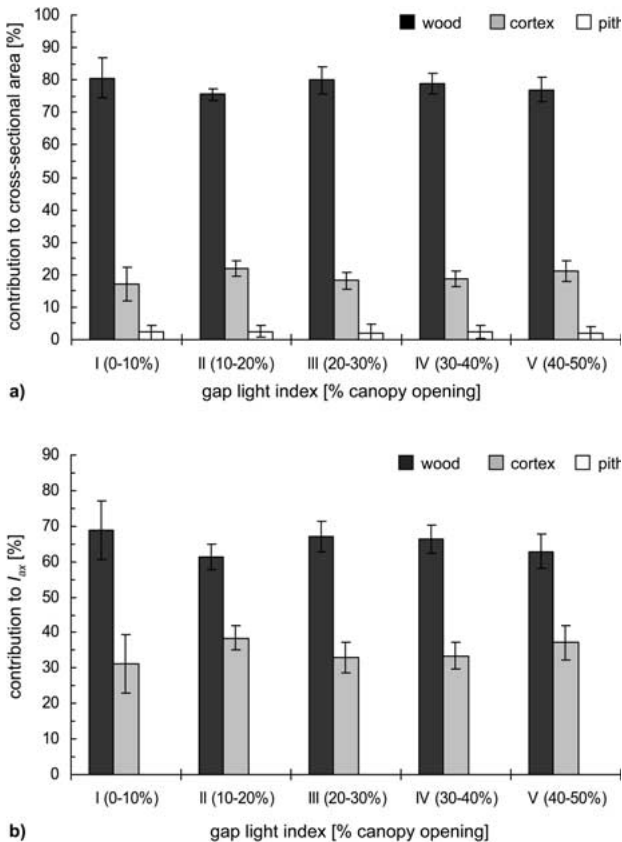
**Figure 7.** Variation of the structural torsional modulus  $G_{str}$  with increasing polar moment of area  $I_{pol}$ . **a)** Main stems of freestanding plants grown in strong shade and in moderate conditions of light quantity and main stems of climbing plants (compare Gallenmüller and others 2000), **b)** main stems of freestanding plants, free branches of freestanding plants and reiterative shoots.

compared only in stems grown in a moderate light environment of 10–50% canopy opening. In young stages of freestanding plants the contribution of the cortex to  $A$  and to  $I_{ax}$  decreases slightly and varies little with further increase in stem diameter; the contribution of wood slightly increases in the first ontogenetic stages but then also varies only little with ongoing secondary growth. In freestanding plants the contributions of wood to  $I_{ax}$  increases from  $57.2 \pm 5.5\%$  in small stems (diameter  $< 5 \text{ mm}$ ) to  $64.2 \pm 5.0\%$  in larger stems (diameter  $> 10 \text{ mm}$ ) (Fig. 11a). The contribution of the cortex to  $I_{ax}$  decreases consistently from  $39.9 \pm 4.0\%$  to  $35.7 \pm 5.0\%$  in the same diameter ranges (Fig. 11b). The contribution of the pith amounts to  $2.9 \pm 4.2\%$  in stems with diameters less than  $5 \text{ mm}$  and decreases in older stems with diameters greater than  $10 \text{ mm}$  to values below  $1\%$ .

Climbing plants show a drastic variation of the stem anatomy in older ontogenetic stages. Figure 11a shows the contributions of the different wood



**Figure 8.** Cross-sections of main stems of *Croton nuntians*-plants, stained with phloroglucinol / hydrochloric acid. **a)** Freestanding stem (diameter: 38 mm), **b)** climbing stem (diameter: 50 mm). p: pith, d: dense wood type with narrow vessels, t: tension wood, l: less dense wood type with wide vessels, c: cortex. The scale bar equals 10 mm.



**Figure 9.** Influence of light quantity on the distribution of wood, cortex and pith. All data are from main stems of freestanding *Croton nuntians*—plants with diameters greater than 10 mm. **a)** Contributions to the cross-sectional area  $A$ , **b)** contributions to the axial second moment of area  $I_{ax}$ .

types found in climbing plants separately. In small climbing plants, the contribution of the dense wood

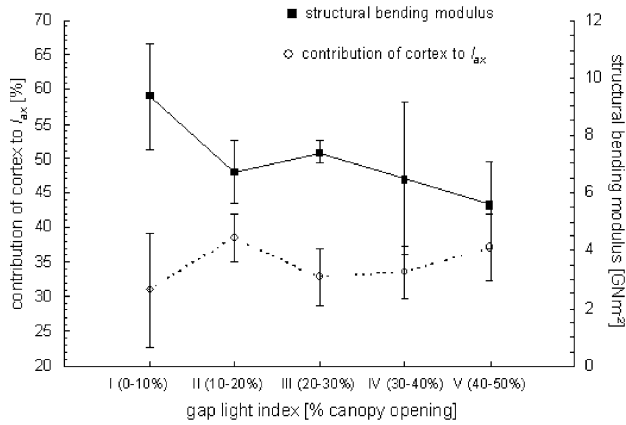
type is similar to values found in freestanding stems. In older ontogenetic stages of climbing plants, with diameters greater than 30 mm, when the production of the less dense wood type with large vessels has begun, the contribution of the dense wood type drops to  $2.8 \pm 2.3\%$ , whereas the contribution of the less dense wood type increases to  $46.0 \pm 6.3\%$  (Fig. 11a). A second striking variation concerns the amount of cortex: in climbing stems with diameters greater than 30 mm, activation of the cork cambium appears to take place and a significant increase in the contribution of the cortex to  $I_{ax}$  up to values over 50% is observed (Fig. 11b, compare Fig. 8b).

Comparison of the tissue distribution in different stem types of freestanding plants (main stems, branches and reiterative shoots) reveals no significant differences. In all tested diameter classes, tissue distribution of the branches and of the reiterative shoots is comparable to the values found for main stems (Fig. 12) and no significant differences were found.

## DISCUSSION

Mechanical trends during development reveal different patterns in freestanding and climbing plants of *Croton nuntians*. In terms of habit, freestanding plants may resemble young trees of the understory, with typically slender stems, but in terms of mechanical properties they are clearly differentiated from typical trees. The structural bending modulus varies little during ontogeny and consequently the flexural stiffness increases proportionally with increasing stem diameter. This pattern can be qualified as typical for semi-self-supporting plants (Speck 1994; Speck and Rowe 1999a, 1999b; Speck and others 1996a, 1996b). However, the variation of mechanical properties during ontogeny in self-supporting plants has so far been analyzed mainly in species of the temperate zones (which show a typical increase of the structural bending modulus during ontogeny) and few data for tropical trees are yet available. Initial measurements of the tree species *Croton matourensis* suggest that in some tropical tree species the bending properties may also remain approximately constant for a relatively long period of their ontogeny, although they are undoubtedly self-supporting trees (data unpublished).

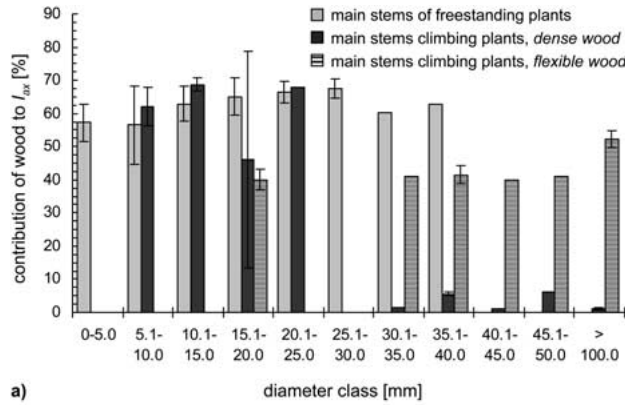
In comparison, data of individuals in the climbing growth phase show a completely different pattern. Stems of climbing plants become significantly more flexible during ontogeny, which is measured as a drastic drop of the structural bending modulus by up to 90% and a non-proportional increase of



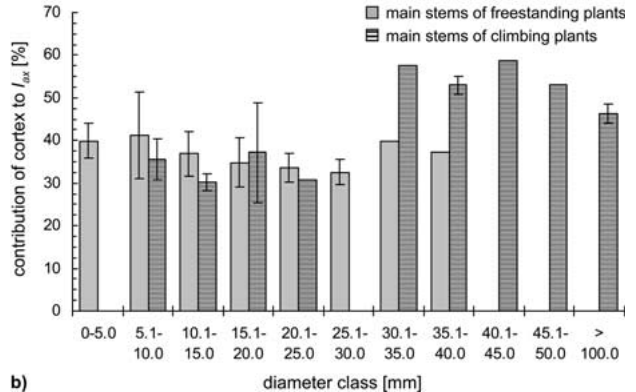
**Figure 10.** Influence of light quantity on bending properties (structural bending modulus) and tissue distribution (contribution of the cortex to axial second moment of area) in main stems of freestanding *Croton nuntians* plants with diameters greater than 10 mm. Mean values and standard deviations are in different ranges of light quantity.

flexural stiffness with increasing stem diameter. This pattern is characteristic for non-self-supporting lianas (Gallenmüller and others 2000, 2001; Rowe and Speck 1996, 1998; Speck 1991a, 1991b, 1994, 1997; Speck and Rowe 1999a, 1999b, 2001a, 2001b; Speck and others 1996a, 1996b, 1997). In summary, in climbing individuals of *C. nuntians* the mode of attachment via wide-angled rough branches and coarse leaves is typical for other semi-self-supporting plants (Darwin 1867; Schenck 1912; Speck 1994, 1997; Speck and Rowe 2001a, 2001b; Wilmanns 1983). Mechanical data, in contrast, approach those of typical lianas with specialized climbing structures, such as *Condylocarpon guianense*, *Bauhinia guianensis*, *Dolioscarpus* sp., *Maripa scandens*, *Passiflora glandulifera* and several *Aristolochia* species (Rowe and Speck 1996, 1998; Speck 1997; Speck and Rowe 1999a; Speck and others 1996a).

Different mechanical properties of freestanding and climbing plants of *Croton nuntians* can be regarded as advantageous for growth under different mechanical constraints. Freestanding plants, which are not in contact with a supporting structure, must have mechanically stable stems to withstand self-loading and other mechanical loads before attaching to suitable support. In contrast, for climbing plants it is advantageous to develop flexible stems in bending and torsion that can survive movement of host supports and other sources of stress without injury. This applies especially to liana stems that have slipped from their supports and may have to deform to coils and arcs on the ground. In many cases liana stems even survive the collapse of their host trees



**a)**

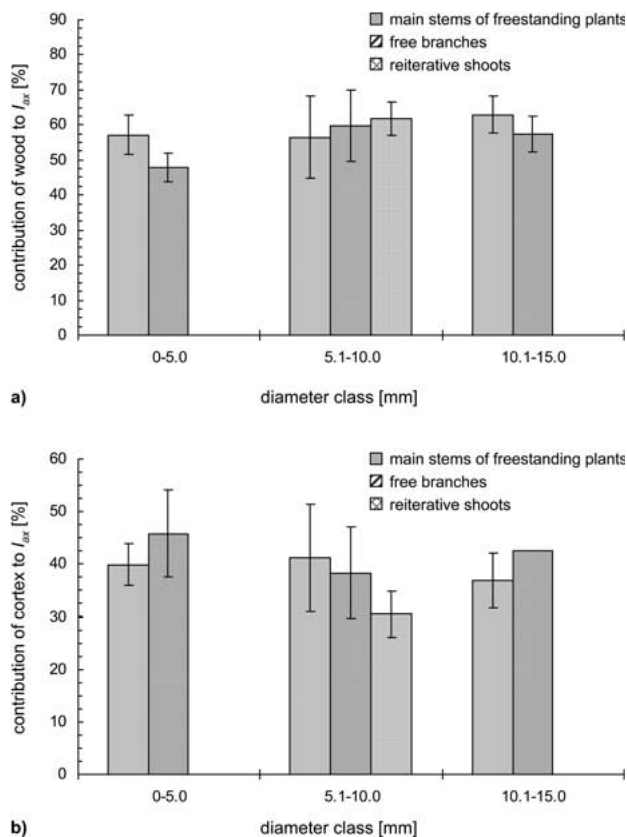


**b)**

**Figure 11.** Ontogenetic variation of the stem anatomy in *Croton nuntians*. All data are from main stems of freestanding and climbing plants grown with a canopy opening of 10-50%. Mean values and standard deviations in different diameter classes. All freestanding plants form exclusively a dense wood type. In adult climbing plants a transition to the formation of a second, less dense wood type occurs. Results obtained for the two wood types of climbing plants are presented separately. **a)** Contribution of wood to  $I_{ax}$ , **b)** contribution of cortex to  $I_{ax}$ .

relatively undamaged and high stem compliancy can afford at least a part of the mechanism behind this (Fisher and Ewers 1989; Gallenmüller and others 2001; Putz 1984; Speck 1994, 1997; Speck and Rowe 2001a; Speck and others 1996a, 1996b).

The ontogenetic variations of the mechanical properties are consistent with changes in the tissue distribution. In climbing plants an increase of the contribution of flexible tissues (the cortex and the less dense wood type with large diameter vessels) is observed. Concurrently the contribution of the dense wood type decreases. These structural changes may contribute largely to the observed variation of mechanical properties in adult climbing stems. The differences between the dense and less dense wood types reported here concern the diameter and number of vessels. It remains to be tested as to



**Figure 12.** Comparison of the tissue distribution in main stems, free branches and reiterative shoots of *Croton nuntians*. Mean values and standard deviations in different diameter classes. **a)** Contribution of wood to  $I_{ax}$ , **b)** contribution of cortex to  $I_{ax}$ .

whether the transition from the freestanding to the climbing growth phase is accompanied by further changes in other anatomical parameters of mechanical significance (for example, the thickness of fiber cell walls or the amount of wood parenchyma) (Gallenmüller unpublished data) or even variations of the cell wall ultrastructure or biochemistry (compare Hoffmann and others 2003).

Branches and reiterative shoots show no significant differences in mechanical properties, nor in stem anatomy, when compared with the main stems of freestanding plants. In this regard the branches cannot be considered as specialized climbing structures using the normal nomenclature. However, stiff wide-angled branches are important for anchoring the plant in the surrounding vegetation and therefore play a significant role in the climbing strategy of *C. nuntians*. Reiterative shoots have the function to renew the attachment in the canopy once a plant has fallen to the ground, or to bridge distances between support structures.

Therefore, in reiterative shoots, mechanical stability is as advantageous as in main stems of freestanding plants. The results obtained for reiterative shoots are consistent with the assumption that they show typical properties of juvenile stages (Bell 1994; Caballé 1993; Gallenmüller and others 2001; Hallé and others 1978; Putz and Holbrook 1991; Rowe and Speck 1998; Speck and Rowe 1999b).

So far the results of the mechanical and anatomical analysis of *Croton nuntians* are comparable with the results of a similar study of the neotropical liana *C. pullei*, which grows sympatically in the lowland rainforest of French-Guyana (Gallenmüller and others 2001). Both species 1) occur in freestanding and in climbing growth phases, 2) develop cylindrical stems with regular tissue distribution even in adult climbing plants, which distinguishes them from many tropical lianas displaying anomalous secondary growth in older stages, 3) become entangled in the surrounding vegetation via wide-angled branches and coarse leaves without specialized attachment structures, 4) show a mechanical trend during development typical of semi-self-supporting plants in freestanding plants and a trend typical of lianas in climbing plants. In summary, *C. nuntians* and *C. pullei* can both be described as climbing plants that behave like typical semi-self-supporting plants over large parts of their ontogeny, and develop into typical lianas only in the oldest ontogenetic stages.

Furthermore, in both species the transition from a dense wood type to a less dense wood type is observed exclusively in adult climbing plants. In *C. pullei*, it is concluded that the transition from one wood type to the other and the switch from the freestanding to the climbing growth phase is probably a reaction to an external stimulus (Gallenmüller and others 2001). However, the nature of this stimulus remains unclear. A regulation via the light conditions, especially the light quality and/or mechanical stimuli when the plants establish contact with suitable supports, are conceivable.

This uncertainty concerning the stimulus for a change in mechanical properties also holds true for *C. nuntians*. Large freestanding plants with large stem diameters are much more numerous in this species, but cross-sections of many climbing stems show that the transition to less dense wood can also occur at much smaller stem diameters in the development of the plant. This implies that the transition might take place simultaneously with the transition from the freestanding to the climbing growth phase. In studies of the stem anatomy of tropical lianas this assumption has been made by different authors (Caballé 1993; Gallenmüller and

others 2000, 2001; Rowe and Speck 1996; Speck and Rowe 1999a; Warburg 1883a, 1883b), but has not been verified so far. The first results of an investigation of the growth and the biomass distribution in *C. nuntians* suggests that the transitions between the different growth phases and the wood types occur at different developmental stages (Gallenmüller unpublished data).

Freestanding plants of *C. nuntians* reach larger dimensions than freestanding plants of *C. pullei*. Freestanding *C. nuntians* plants are mechanically stable up to a height of about 7 m and start to become unstable only beyond this limit, whereas freestanding *C. pullei* plants become unstable at a maximum height of 4 m. These findings may be related to the observation that the two species colonize different habitats. In the study area *C. pullei* is confined to low-lying creekside habitats where frequent gap formation is observed. *C. pullei* colonizes smaller gaps, but also remains established under the closed canopy (Gallenmüller and others 2001). In contrast, *C. nuntians* can be considered a pioneer species of larger gaps and forest margins (Gallenmüller and others 2000).

In their natural sites, freestanding plants of *C. pullei* display a homogeneous appearance, whereas freestanding *C. nuntians* plants occur in a variety of different habits (compare Gallenmüller and others 2000). This diversity can at least partly be attributed to the influence of environmental factors. Freestanding plants of *C. nuntians* grown under strong shading have a significantly higher structural bending modulus than freestanding plants grown under higher insolation, values show differences of over 50%. Differences in mechanical properties correlate with differences in stem tissue distribution. However, variation in stem anatomy observed for plants grown under different light conditions is only small. It is conceivable, that the light conditions affect the wood structure, and that differences in other parameters, for example, in thickness of fiber cell walls or vessel diameter, also play an important role. Furthermore, light conditions can also influence the growth rates, and thus modify geometrical factors such as stem taper, or the biomass distribution (for example, the weight of leaf biomass). These parameters influence the mechanical properties of a plant and have to be considered if predictions of mechanical stability of plants grown under different light conditions are to be made. This holds particularly for the taper of the stems. The lower the taper, the lower is the critical buckling length of a stem with a given basal diameter. In shaded freestanding plants of *C. nuntians* the structural bending modulus is consistently higher than in freestanding plants

grown in higher light, but this property is compensated for by differences in taper and in biomass distribution so that finally, the critical buckling lengths of shaded plants are no higher than those of plants grown with more light (Gallenmüller unpublished data).

The ability of a plant species to react to different environmental conditions with modifications in mechanical properties has consequences for the nature of its ecological niche. Here, a study with measurements of light quantity via hemispherical photographs gives a first estimation of the influence of light conditions, although other relevant factors such as the light quality are not considered. Previous studies have demonstrated that quantitative analyses of the mechanical properties can be used to explore exactly how different growth forms in plants vary during ontogeny and the underlying developmental features producing this variation (Rowe and Speck 1996, 1998; Speck 1991a, 1991b, 1994, 1997; Speck and Rowe 1999a, 1999b, 2001a, 2001b; Speck and others 1996a, 1996b, 1997). In these studies overall trends and development have been revealed, which illustrate how liana species differ and how they differ from other growth forms. This study shows that external environmental factors other than the tangible presence of supports can modify the mechanical properties of a given climbing plant species. The results reported here suggest that mechanical studies are not only a tool for understanding general tendencies in different plant species or systematic groups, but could also be used to better understand the ecology of a certain plant species when modifications of mechanical properties due to environmental factors are considered.

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