

Mechanical contribution of secondary phloem to postural control in trees: the bark side of the force

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Summary

- To grow straight, plants need a motor system that controls posture by generating forces to offset gravity. This motor function in trees was long thought to be only controlled by internal forces induced in wood. Here we provide evidence that bark is involved in the generation of mechanical stresses in several tree species.
- Saplings of nine tropical species were grown tilted and staked in a shadehouse and the change in curvature of the stem was measured after releasing from the pole and after removing the bark. This first experiment evidenced the contribution of bark in the up-righting movement of tree stems.
- Combined mechanical measurements of released strains on adult trees and microstructural observations in both transverse and longitudinal/tangential plane enabled us to identify the mechanism responsible for the development of asymmetric mechanical stress in the bark of stems of these species.
- This mechanism does not result from cell wall maturation like in wood, or from the direct action of turgor pressure like in unligified organs, but is the consequence of the interaction between wood radial pressure and a smartly organized trellis structure in the inner bark.

Key words: bark, Malvaceae, maturation stress, secondary phloem, tree biomechanics.

Introduction

A hundred years ago, D'Arcy Thompson (1917) published his renowned book *On Growth and Form*, pointing to the fundamental role of physics and mechanics in shaping living organisms. Nature has solved an infinite number of engineering problems and is a remarkable source of inspiration for materials science (Wegst *et al.*, 2015). The need for trees to grow straight vertically leads to optimised material and structural design. The vertical position is intrinsically unstable because gravity causes downward bending movement disturbing the direction of growth. To ensure vertical growth, trees need both a 'skeletal' system, which is achieved through the stiffness and strength of the trunk material (Niklas, 1992) and a 'motor' system (Mouliá *et al.*, 2006) to control plant posture by generating forces to offset the effect of gravity during growth (Alméras & Fournier, 2009). The motor function is driven by turgor pressure in unligified organs (Mouliá & Fournier, 2009) or results from cell wall maturation in wood (Clair *et al.*, 2011). The vertical posture of trees was long thought to be controlled only by internal forces in the wood during the formation of fibres (Scurfield, 1973; Fournier *et al.*, 2014). When the tree requires a strong reorientation, the composition

and organisation of the fibre walls can be strongly modified. In gymnosperms, cellulose microfibril angle increases greatly and lignin content increases in the cell wall to form compression wood (Timell, 1986); this wood is positioned on the lower side of the tilted stem and generates compression to push up the stem. In angiosperms microfibril angle decreases to zero and lignin content also decreases. In numerous species, the fibre cell wall is strongly modified into a peculiar gelatinous layer (Guedes *et al.*, 2017; Clair *et al.*, 2018). This wood, located on the upper side of the tilted axis, generates tensile stress and is termed 'tension wood'. It acts in the reorientation process by pulling the upper side of the stem. Tensile stress is generated in the gelatinous layer during maturation. Current description of the underlying mechanism is that swelling of the gelatinous polysaccharide matrix (Chang *et al.*, 2015) bends the cellulose network (Clair *et al.*, 2011; Alméras & Clair, 2016), putting cellulose microfibrils into tension. In numerous species, the gelatinous layer is no longer visible as it is later lignified, after generation of the tensile force (Roussel & Clair, 2015). In fewer species, especially in the Malvaceae family, gelatinous fibres are not present (whether lignified or not) and tension wood tissues are characterised by an increased amount of parenchyma cells and a reduced amount of fibres (Ghislain &

Clair, 2017). It is consequently doubtful that wood is the driving force of the posture control in these species.

Previous studies have suggested that, in a few species, bark may play a role in the posture control (Böhlmann, 1971; Fisher & Mueller, 1983; Kempe *et al.*, 2014; Zajaczkowska & Kozakiewicz, 2016). The aim of the present study was therefore to investigate the mechanical contribution of the bark to the up-righting movement in Malvaceae trees and to extend the study to several other botanical families to evaluate the contribution of the bark in a diversity of biomechanical designs.

Bark tissue is involved in multiple functions, including conduction of carbohydrates, protection against fire and biological aggression, storage of water and nutrients, respiration and photosynthesis (Paine *et al.*, 2010; Rosell *et al.*, 2014; Rosell, 2016). In many extinct species (such as *Lepidodendron*, *Tetraxylopteris schmidtii*), bark has also been shown to be the main contributor to stem stiffness (Speck & Rowe, 2003). This skeletal function has also been discussed in some studies on modern vascular plants (Niklas, 1999; Paine *et al.*, 2010; Kempe *et al.*, 2014; Rosell & Olson, 2014). But the motor function of the bark (as muscle) was usually disregarded in biomechanical and ecological studies, as wood was considered to be the main tissue with active mechanical functions. Only Böhlmann (1971), later followed by Fisher & Mueller (1983), suspected that bark was involved in tree reorientation. However, these studies did not provide mechanical evidence of bark contribution to up-righting nor a realistic mechanism for stress generation in bark.

Here, we provide evidence for the mechanical contribution of bark in the up-righting movement in trees. Combining mechanical measurements and microstructural observations of the wood and bark tissues, we identified the mechanism that enables the active generation of tensile forces in the bark of trees.

Materials and Methods

Plant material

The study was carried out on saplings of nine tropical species. *Cecropia palmata*, *Laetia procera*, *Pachira aquatica*, *Simarouba amara*, *Virola michelii* were collected as seeds or seedlings in the tropical rainforest in French Guiana in the vicinity of Kourou and Sinnamary and *Cordia alliodora* near Saül. *Tarrietia utilis* seedlings were collected in the plantation plot of the Paracou CIRAD Station and *Gossypium hirsutum* seedlings in a private garden in Kourou. *Theobroma cacao* saplings were provided by the CRB-PPG, CIRAD. These species were chosen as they represent a large diversity of tension wood types (Ghislain & Clair, 2017) and bark structures (Angyalossy *et al.*, 2016), with a specific focus on Malvaceae (*Pachira*, *Tarrietia*, *Gossypium*, *Theobroma*) as we first identified the bark mechanism in *Pachira*. Eight to 12 trees of each species were studied.

Plants were grown in a shadehouse in Kourou (French Guiana) under natural light with neutral shading nets and irrigated daily with drip irrigation. Saplings were grown for 3–10 months and acclimatised in new pots for 2 months. Their initial diameter before tilting ranged between 3 and 10 mm

(Supporting Information Table S1). They were artificially tilted and staked at an angle of 45° (Fig. 1a) to enable controlled gravitational stimulus that remained constant over time and in space (Coutand *et al.*, 2014). Saplings were released from the pole (Fig. 1b) and sampled after the stem diameter increased by at least one-third, to maximise the change in stem curvature (Alméras *et al.*, 2018).

In addition, experiments were performed on naturally tilted older trees sampled along the Kourou river (*Pachira aquatica*), near Sinnamary in the experimental forest of the ‘Piste de Saint-Elié’ (*Virola michelii*, *Virola surinamensis*, *Laetia*, *Goupia*), in the experimental forest of the agronomic campus in Kourou (*Simarouba amara*, *Cecropia palmata*) and in a plantation plot called ‘l’égyptienne’ near Roura (ONF) (*Tarrietia utilis*). Experiments were carried out on at least five trees per genus, using the same genus as in the seedling experiments. An additional species, *Goupia glabra*, was added because the surface of the bark showed a contrasted patterned on the two sides of tilted trees (Fig. S1). Tree diameters at breast height ranged between 6 and 47 cm (Table S2). Later in this paper only the genus name will be used instead of the full species name.

Stem curvature measurement

After being tilted for at least 3 months, the basal parts of the saplings were marked at nine points every 2.5 cm and trees were photographed with a black background. The release from the pole caused an instantaneous up-righting movement of the stem (Fig. 1b). A segment of *c.* 20 cm of the basal part of the stem (in the first 30 cm) was cut and the portion of the stem was placed horizontally on a black board to take a second photograph of the stem, free of self-load (Fig. 1c). The bark was then removed from a 5-cm section in the middle of the segment and a third photograph was taken in same conditions as the second (Fig. 1d). Saplings were cut in the morning in the shadehouse. To avoid drying, samples were brought to the laboratory in a plastic bag and debarking was done in < 1 min the same day. A photograph (4752 by 3168 pixels) was taken with a Canon EOS 500D camera at a distance of *c.* 1.5 m for whole plant images (*c.* 5 pixels mm⁻¹) and *c.* 0.6 m for segments (*c.* 10 pixels mm⁻¹). Changes in curvature were measured on the photographs using ImageJ software (Schneider *et al.*, 2012). The change in curvature (ΔC) due to spring back (ΔC_{sb}) when releasing the stem from the pole, and the change in curvature due to the removal of bark (ΔC_{bark}) were determined as the change in angle ($\Delta\alpha$) between the two straight lines connecting two marks on the left side and two marks on the right side, divided by the reference length (L): $\Delta C = \Delta\alpha / L = (\alpha_f - \alpha_i) / L$. (Fig. S2). Curvatures are given in degree per decimetre (° dm⁻¹), i.e. the change orientation angle of the apex compared with the basal part of a 10-cm segment. This unit give an easier representation, considering the size of the studied plants. A metrological study, performed on five samples with four repetitions per sample, evidenced repeatability on the measurement (mean of standard deviations) of $\pm 0.56^\circ \text{ dm}^{-1}$ for spring-back measurement and $\pm 0.17^\circ \text{ dm}^{-1}$ for debarking measurement.

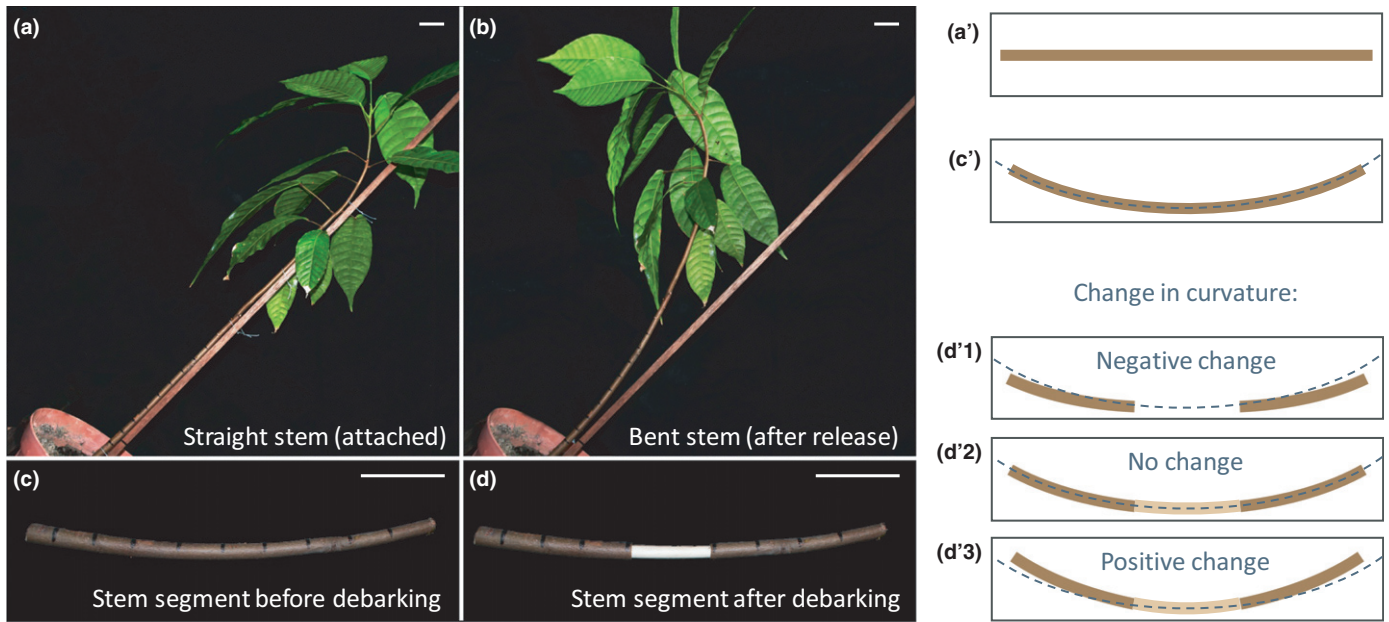


Fig. 1 Photographs and schematics of the bending of the stem during the experiment. Example of a sapling of *Theobroma cacao* before (a) and after (b) release from the pole. Photograph of the stem segment before (c) and after (d) debarking. Schematics of bending at each step: first, stem is straight (a') then in all trees, release from the pole led to positive change in curvature (c'). Later, when the bark was removed, curvature either decreased (d'1), remained stable (d'2) or increased (d'3). Bars, 5 cm.

Standardisation of stem curvature

The curvature is defined at the level of a segment as the change in angle per unit length. However, the change in curvature in response to stress induced in the stem tissues strongly depends on the diameter of the stem. To remove this size effect, we use a standardized curvature, corresponding to the change in curvature that would happen for a stem of a given diameter (arbitrarily set at 1 cm), all other parameters (stiffness of the tissues and relative thickness of the stressed layer) being assumed to be size independent. Based on biomechanical calculations (Alméras & Fournier, 2009), it can be shown that the curvature in this case is proportional to the inverse of the diameter, so that the standardized curvature is defined as: $\Delta C_{\text{stand}} = \Delta C \times D/D_1$ (in $^{\circ} \text{dm}^{-1}$), where D is the diameter of the stem segment in cm and D_1 a standard diameter arbitrarily fixed at 1 cm.

Measurement of released strains on mature trees

The state of mechanical stress of a structure can be probed using the released strain method. The principle of this method consists of measuring the strain that is released when a piece of material is isolated from surrounding material. This method is commonly used to probe the state of stress of wood in trees (Yoshida & Okuyama, 2002). To assess the mechanical state of wood and bark, released strains were measured on naturally tilted mature trees in both tangential and longitudinal directions using the method detailed in Clair *et al.* (2013). Strains were recorded using biaxial strain gauges $0^{\circ}/90^{\circ}$ stacked rosette (Kyowa KFG-5-120-D16-11L1M2S) connected to a data logger (P3 Vishay). The tangential strain was released by two longitudinal grooves

made on both sides with a sharp knife at a distance of 5 mm from the gauge. The longitudinal strain was then released by sawing tangentially at the same distance above and below the gauge.

Measurements were made both on bark and wood. For the measurements on bark, the external part of the bark (cork, see Fig. S3) was first peeled to ensure that measurements were made on phloem. Measurements on wood were made at a distance of at least 30 cm from the bark measurement. After removing the bark, the soft cambial cells were peeled before gluing the strain gauge.

Statistical analysis

In order to check the significance of the departure with a theoretical null mean of the changes in curvature as well as the wood and bark differential longitudinal strain, Student's t -tests were performed at a 5% significance level. Correlations between bark and wood longitudinal strain and between bark longitudinal and bark tangential strain were assessed by Pearson's correlation coefficients. These analyses were conducted at the species level using R statistical software (R Core Team, 2016).

Anatomical observations

In the seedling stems, cross-sections were cut in the vicinity of the debarked area. The cross-sections included the whole surface of the stem. In the naturally tilted trees, longitudinal/tangential sections were prepared on both the upper and lower sides of the bark. The greater thickness of adult trees enabled sectioning at three different distances from the cambium: near the cambium, in the middle of the phloem, and near the cork (Fig. S3).

Longitudinal sections 20–40 μm thick were cut on fresh samples with a sliding microtome and stained with safranin and astra blue. Observations were made with a bright field optical microscope (Olympus BX2, Japan).

Results

Bark may either facilitate or prevent the active bending of stems

After being tilted and fastened for at least 3 months, the saplings were released from the pole. This caused an instantaneous spring-back movement of the stem (Fig. 1) confirming the active reaction of all trees to recover verticality (Alméras *et al.*, 2018). The lowest changes in curvature were recorded for *Cordia* (mean: 3.1°dm^{-1}) and the higher changes in *Cecropia* (mean: $15.9^\circ \text{dm}^{-1}$) but most species remain in a common range between 5.5 and 8.5°dm^{-1} as mean value (Table 1).

Bark was then removed from segments of the stems, and the consecutive change in curvature was measured in photographs taken at the two stages (Fig. 1). When the bark of *Pachira*, *Theobroma*, *Gossypium* and *Tarrietia* trees (all belonging to Malvaceae family) was removed, stem curvature decreased by $3\text{--}7 \text{dm}^{-1}$ in average, i.e. in the same order of magnitude as the change in curvature during spring back, thereby demonstrating the major contribution of bark to bending forces in these species (Fig. 2). In *Cordia* trees, the higher contribution of bark compared with wood was also evidenced but at a lower extent (change in curvature during debarking is *c.* -1°dm^{-1}). In *Simarouba* and *Virola*, no significant change in curvature was observed after removal of the bark (details on statistics are given in Table S3), indicating that bark contributes to stem bending as efficiently as wood. Finally, in *Cecropia* and *Laetia* trees, the experiments show that bark partially impedes the bending action of wood.

Mechanical stress in the bark of adult trees

In a tropical forest, using naturally tilted trees, we measured the strain following the release of mechanical stress (Archer, 1986) in

Table 1 Mean value and standard deviation of change in standardized curvature (ΔC_{stand}) during spring back after stem release from the pole and after debarking ($^\circ \text{dm}^{-1}$)

ΔC_{stand} ($^\circ \text{dm}^{-1}$)	<i>n</i>	Spring back		Debarking	
		Mean	SD	Mean	SD
<i>Pachira</i>	12	8.3	3.3	-7.1	2.1
<i>Tarrietia</i>	10	7.7	3.7	-5.3	1.9
<i>Theobroma</i>	12	5.7	2.5	-3.7	1.9
<i>Gossypium</i>	11	6.2	2.6	-3.2	1.8
<i>Cordia</i>	9	3.1	2.3	-0.8	0.6
<i>Virola</i>	8	5	3.8	-0.4	0.5
<i>Simarouba</i>	10	6.8	2	0.2	0.6
<i>Laetia</i>	10	12.1	5	1	0.5
<i>Cecropia</i>	9	15.2	6.5	1.9	1.5

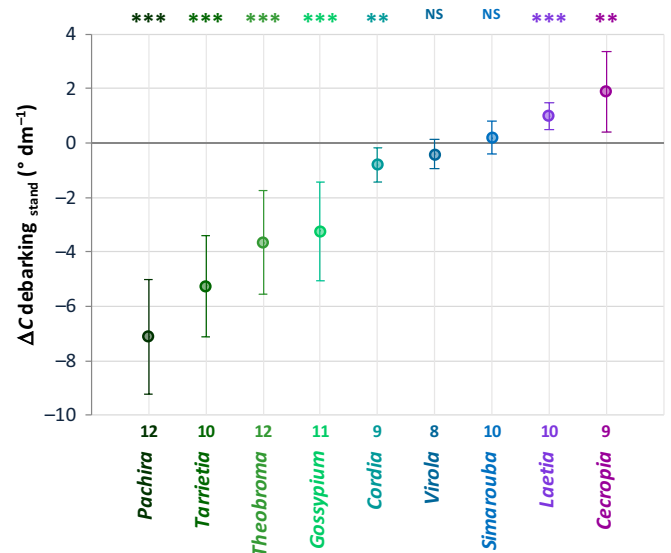


Fig. 2 Change in curvature (ΔC) during debarking in the nine species. A negative change shows that the bark contributed to bending the stem. A positive change in curvature after bark removal shows that the bark partially impeded the stem up-righting forces generated in wood. Absence of additional curvature during debarking shows that both wood and bark influence the bending of the stem in a similar way. Significance difference from zero (one sample *t*-test): **, $\alpha = 0.01$; ***, $\alpha = 0.001$; NS, not significant. Numbers indicates the number of trees investigated per species. Details on statistics are given in Supporting Information Table S3.

both bark and wood, on both the upper and lower sides of the stem. A positive released strain (swelling) indicates a compressive stress, whereas a negative released strain (shrinkage) indicates tensile stress. Results showed that all trees produce wood with longitudinal tensile stress on the upper side of the stem (Table S2). The up-righting efficiency of trees depends on the difference in tensile stress between the two sides causing an upward change in stem curvature (Alméras & Fournier, 2009). Measurements revealed that the mechanism of differential tensile stress in wood is shared by all the species we studied (Fig. 3a), but the differential longitudinal strains in wood were lower in species in which we had previously highlighted the active role played by bark.

Interpreting the strain released in the bark is less straightforward than interpreting the strain released in wood as it includes all the stresses supported by the bark during the entire life of the tree (see Notes S1). However, measurements indicated that the bark of most of *Pachira*, *Tarrietia*, *Virola*, *Simarouba* and *Cecropia* trees is under longitudinal tensile stress on both sides. In *Pachira* and *Tarrietia*, tensile stress was higher on the upper side than on the lower side (Table S2). The difference between the upper and lower sides is thus always negative (Fig. 3b) suggesting that the bark contributes to the up-righting process. In *Cecropia*, *Laetia* and *Goupia*, the positive difference between the upper and lower sides (Fig. 3b) indicates that bark partially counteracts the up-righting process (Table S2). In these species, bark appears to be passive (or not sufficiently active) and is subject to the upward bending of the stem driven by the action of wood, putting the bark under compression on the upper side and under tension on the lower side. The action of the wood on the bark is even visible

in some trees, where the surface of the bark is wrinkled on the upper side and smooth on the lower side (Fig. S1).

An active contribution of bark to the up-righting process was found in species in which the wood was less efficient in generating an upward movement. A passive contribution was found in species with efficient wood (Fig. 4a, Pearson correlation, $\rho = -0.77$, $P < 0.05$).

All barks exhibited high tensile tangential stress (Table S2) and the higher the tangential tensile stress, the higher the longitudinal tensile stress (Fig. 4b, Pearson correlation, $\rho = 0.78$, $P < 0.05$). Tangential stress results from the increasing diameter of the wood, which pushes the bark ring radially. As the increase in the perimeter is not fast enough, tension is induced in the tangential direction.

Contrasted organisation of the phloem fibres

To investigate the mechanism which enabled the bark to control tree posture, we prepared semi-thin sections of wood and bark. Cross-sections (Fig. 5 (1–3) and Fig. S4 (1–3)) show the bifacial cambium between the inner wood core and the outer secondary phloem. The pattern of the wood formed on the upper side of the stem, called tension wood, contrasts with that of the opposite wood. In *Cecropia*, *Goupia*, *Laetia* and

Simarouba, wood fibres have a typical gelatinous layer (Wardrop & Dadswell, 1948) with different degrees of lignification (Roussel & Clair, 2015). In species belonging to the Malvaceae family, and in *Cordia* and *Virola*, the tension wood is characterised by very low wood fibre content, with no visible gelatinous layer, and many radially elongated parenchyma cells. This typical pattern has been described in several Malvaceae species but also in Annonaceae (Ghislain & Clair, 2017). The bark side of the section also shows diverse organisation. In *Goupia* and *Laetia*, phloem is made up of apparently randomly organised bundles of phloem fibre in a matrix made of parenchyma encrusted with sclereids. In *Pachira* (and others Malvaceae), *Cordia* and *Virola*, phloem fibres are organised as ‘flames’ (including sieve elements) separated by enlarged parenchyma rays (Fig. 5-a2). This triangular organisation is a direct consequence of the building process. Phloem fibres are all produced by cell division in the cambium and the triangular shape originates from the original number of cambial cells, which increases with the increase in stem diameter (Fig. S5). In contrast, the organisation of the phloem parenchyma cells results from their long life, which allows late division and enlargement of the cells. This dilation phenomenon (Angyalossy *et al.*, 2016; Kotina *et al.*, 2017) makes it possible to compensate for the increasing perimeter.

Fig. 3 Differential longitudinal strain released on the upper and lower sides of the tilted stem (mean \pm SD). (a) In wood. The absence of positive values confirms that the differential stress in wood is a mechanism shared by all species. (b) In bark. Significance difference from zero (one-sample *t*-test): *, $\alpha = 0.05$; **, $\alpha = 0.01$; NS, not significant. Numbers indicates the number of trees investigated per species.

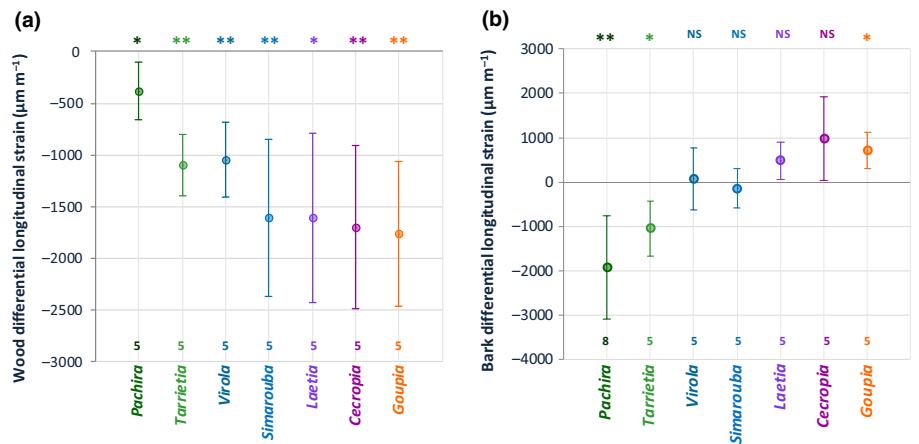
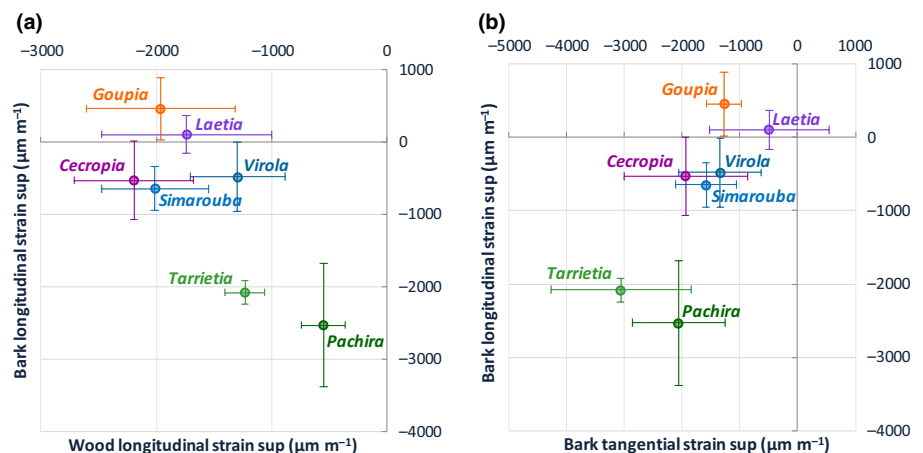


Fig. 4 Strains released in the wood and bark measured on the upper sides (sup) of the tilted stem. (a) In both wood and bark in the longitudinal direction. (b) In bark in both longitudinal and tangential directions (mean \pm SD).



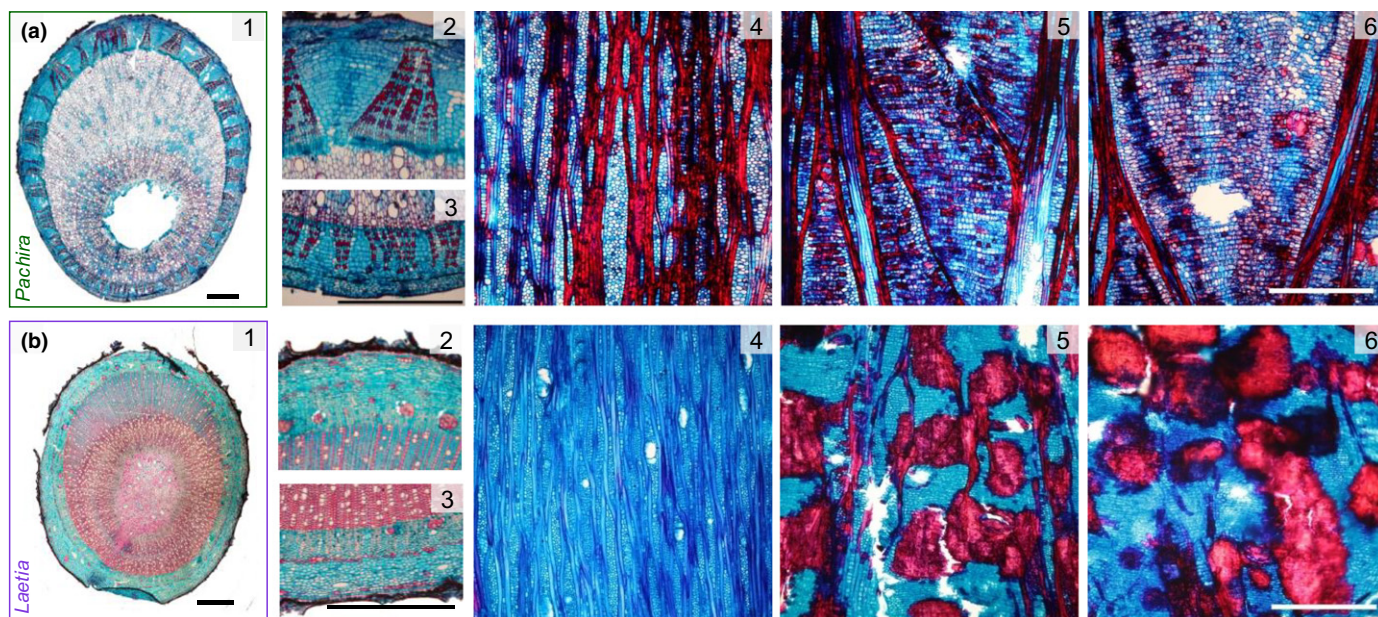


Fig. 5 Organisation of the tissues in wood and bark of (a) *Pachira aquatica* and (b) *Laetia procera*. 1, Full cross-section of a young stem. The top of the section corresponds to the upper side of the tilted stem, where tensile stress is generated to bend the stem upward. 2, Detail of the upper side of the stem, including wood (bottom) and bark (top), separated by the cambium. 3, Detail of the lower side of the tilted stem including bark (bottom) and wood (top). 4–6, Longitudinal sections of the phloem (inner bark) of a larger tree with thick bark at increasing distances from the cambium. Bars, 1 mm. The phloem fibre network is well organised in *Pachira* and nearly absent in *Laetia*. Conversely in *Laetia*, phloem shows numerous sclereids, which are absent in *Pachira*.

We also analysed longitudinal sections of inner bark at different distances from the cambium (Fig. 5 (4–6) and Fig. S4 (4–6)). In *Virola*, *Cordia* and all Malvaceae and to a lesser extent in *Simarouba* and *Cecropia*, longitudinal sections revealed an interconnected network of phloem fibres. In the vicinity of the cambium, the network fibres were separated by narrow bands of ray parenchyma cells (Fig. 5a4). Further away from the cambium, the network widens with the enlargement of the band of parenchyma between the phloem fibres (Fig. 5a6).

Discussion

Evidence that bark develops differential tensile forces

The spring-back curvature occurring when the stem is released from the pole is the consequence of asymmetric forces set during growth in tilted position. These forces may develop in wood and/or in bark. Measurements of change in curvature during debarking provide information on differential forces located in bark. To facilitate interpretation of these data, it is convenient to separate virtually the cylinder of wood from the hollow cylinder of bark. When these cylinders are released from the stake and virtually separated from each other, they may curve only as a consequence of the asymmetric forces present in each tissue when the stem was attached to the stake. The occurrence of an intrinsic curvature of a tissue reveals the presence of asymmetric forces located in it. The intrinsic curvature of wood can be directly observed after debarking. The intrinsic curvature of bark cannot be directly observed, but it can be partly deduced by comparing the intrinsic curvature of wood to the spring-back curvature of the stem. Indeed, the curvature of the stem as an assembly of

wood and bark is the average of the intrinsic curvature of each tissue (weighted by their contribution to bending stiffness). Therefore, the curvature of the stem can be larger than the curvature of wood only if the intrinsic curvature of bark is larger than that of wood. This case corresponds to the negative change in curvature during debarking observed in Malvaceae species (*Pachira*, *Tarrietia*, *Theobroma* and *Gossypium*) and *Cordia* (Fig. 2) and is an evidence of strongly asymmetric forces developed in the bark of these species during growth in the tilted position. A change in curvature during debarking close to zero (as for *Virola* and *Simarouba*, Fig. 2) means that the intrinsic curvature of bark is close to that of wood, also evidencing the occurrence of asymmetric forces in bark, although of less intensity. Finally, a positive change in curvature during debarking, as observed for *Laetia* and *Cecropia* (Fig. 2), reveals that the intrinsic curvature of bark was less than that of wood, and may be zero. It reveals either a low level of asymmetry or the absence of asymmetrical forces.

Complementary measurements of released strains on adult trees revealed that forces present in bark were, on average, strongly tensile for Malvaceae species, and slightly tensile or close to zero for other species (Fig. S6). Differential strains measured between the upper and lower sides of Malvaceae species confirmed that forces set in their bark during growth in tilted position were tensile on both sides, with larger magnitudes of tension on the upper side (Fig. 3b).

Looking for the origin of the force

Böhlmann (1971) was the first to suggest a mechanism by which tensile forces may be induced in bark of *Tilia cordata*, based on its specific anatomy. The swollen appearance of the phloem

parenchyma cells in this Malvaceae species led him to suggest that, during their division and enlargement, parenchyma cells may put tangential pressure on the phloem fibre bundles to move them apart, so that the trellis tends to shorten and produce longitudinal tensile stress. Such a mechanism based on the swelling of parenchyma cells in a rigid network at the millimetre scale represents an exciting analogy with the mechanism supposed to occur within the tension wood cell wall at the sub-micrometre scale (Almérás & Clair, 2016) (Fig. S7). However, such a mechanism would be expected to create compressive tangential stress in the bark, whereas a strong tensile tangential stress in these species was always measured (Fig. 4b and Table S2), especially on the upper side of the stem. The similarity of the mechanisms is therefore limited to the trellis organisation of the fibre network, which efficiently redirects transverse extension into longitudinal tension, but the driving force is different.

Wood radial growth as the driving force of bark tensile longitudinal stress

Tangential tensile stress measured in bark shows that the elongation in the tangential direction cannot result from internal swelling of inner bark parenchyma cells, which would then have generated compressive stress. As an alternative hypothesis, we suggest that the mechanism in these woody species is similar to the one proposed by Kempe *et al.* (2014) for the giant herb *Carica papaya*. The driving force would be the radial growth of wood, increasing the perimeter and therefore pulling the bark tangentially, consistent with the strong tangential tension measured in bark. In turn, this tangential strain would generate strong longitudinal tensile stress, thanks to the efficient redirection of stress induced by the trellis organisation of the bark (Figs 6, S5). Tangential growth of phloem parenchyma is therefore not used to produce compressive stress acting on the fibre bundle, but to reduce tangential stress in enlarged rays, which would otherwise rapidly cause their rupture.

The trellis structure of bark was found on both sides of the stem. The efficiency of the mechanism is therefore linked to the asymmetric production of wood (Fig. 6), as supported by the pronounced eccentric growth of species that rely on this mechanism (Fig. 5), rather than by only the asymmetrical differentiation of the bark itself. Therefore, this relies on the production of a specific type of ‘reaction wood’ rather than ‘reaction bark’. In Malvaceae representatives, *Cordia* and *Virola*, growth of ‘reaction wood’ in the tilted stem is achieved through the intense production of elongated parenchyma cells or thin-walled fibres on the upper side. As parenchyma cells have very thin cell walls, and therefore low density, this strategy makes it possible to respond to mechanical disturbance at low carbon cost. What is more, this soft material can be easily bent by the action of phloem, thereby increasing the overall efficiency of the mechanism.

When sister cells share the control of the force

By measuring the change in curvature during debarking, we demonstrated the efficiency of this mechanism and provide

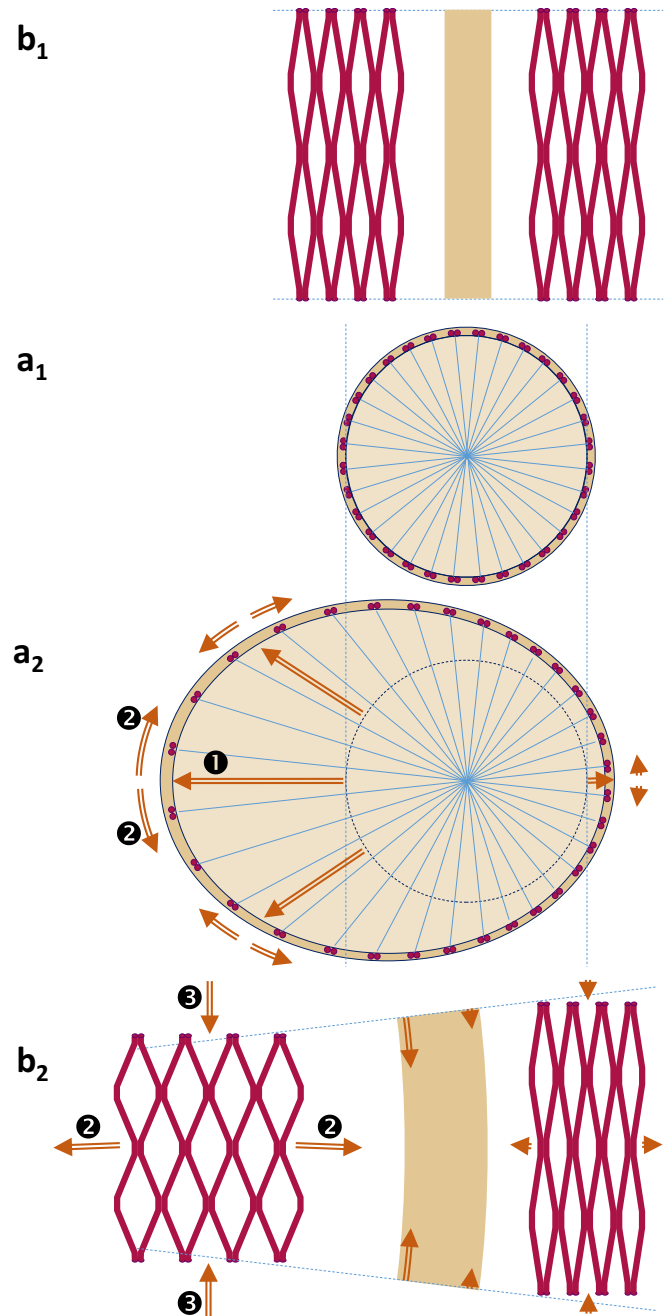


Fig. 6 Schematics of the change in curvature induced by the wood radial growth on one side of the stem. (a) Stem section before (a_1 at t_1) and after (a_2 at t_2) radial growth. (b) Phloem fibre trellis organisation at t_1 (b_1) and t_2 (b_2). Wood radial growth (1) leads to tangential extension of the bark (2) causing longitudinal shortening of the trellis (3). Differential growth on the two sides of the axis leads to differential shortening and therefore bending of the stem.

evidence for its use by different tree species in a combined action with wood, with a variable balance between the two mechanisms. It is generally considered that two kinds of motor systems are used by plants (Mouliá *et al.*, 2006): (i) turgor-based mechanisms, in which differential strains or growth in turgid tissues directly induce a bending movement in herbaceous stems, and

(ii) mechanisms based on stress accumulation, found in woody tissues. In this study, we showed that a third type of motor system should be considered, in which the irreversible growth of parenchymatous wood is coupled with a specific structure of the fibrous bark to induce a force. This mechanism could be widespread in vascular plants.

It is noteworthy that in species that do not rely on this mechanism, tissues produced by sister cells on the wood side and on the bark side are in conflict, evidencing that, in nature, design does not only respond to the best engineering solution to a given design problem but accounts for other vital functions. However, the species highlighted in this study showed that well designed structural organisation may lead sister cells to act in synergy to control forces.

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Author contributions

B.C. initiated the study. B.C., B.G., J.P., R.L., J.B. and T.A. helped design the experiments, B.C., B.G., J.P. and R.L. performed the experiments. All the authors discussed and interpreted the results. B.C. and T.A. wrote the paper. All co-authors discussed and modified the text and figures and gave their final approval for publication.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article:

Fig. S1 Bark of *Goupia glabra* after peeling of the external part (cork).

Fig. S2 Schematic representation of measurements of the change in curvature.

Fig. S3 Schematic representation of the position of the sections.

Fig. S4 Cell organisation in the wood and bark of *Tarrietia utilis*, *Theobroma cacao*, *Gossypium hirsutum*, *Cordia alliodora*, *Viola michelii*, *Simarouba amara*, *Cecropia palmata* and *Goupia glabra*.

Fig. S5 Schematics of the 3D organisation of tissues in a growing stem of *Pachira* (and other Malvaceae).

Fig. S6 Mean longitudinal released strains in naturally tilted trees.

Fig. S7 Analogy between the mechanisms generating tensile stress in trees at two different scales.

Table S1 Data relative to measurements made on saplings

Table S2 Measurements on the adult trees

Table S3 Statistical analysis of the change in curvature of saplings during spring back and during debarking measured on the nine species

Notes S1 Interpretation of released strains measured on bark.

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