



Comparing structure and biomechanics of extant *Carica papaya* and *Ochroma pyramidale* stems allows re-evaluating the functional morphology of the fossil ‘seed fern’ *Lyginopteris oldhamia*

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ARTICLE INFO

Article history:

Received 31 March 2017

Received in revised form 20 July 2017

Accepted 21 July 2017

Available online 24 July 2017

Keywords:

Lyginopteris oldhamia

Carica papaya

Ochroma pyramidale

Cortex structure

Functional morphology

Growth form

ABSTRACT

This study aims at assessing the mechanical importance of the conspicuous sclerenchymatous ‘Dictyoxylon’ cortex of the extinct gymnosperm *Lyginopteris oldhamia* by comparing the latter to the extant angiosperms *Carica papaya* and *Ochroma pyramidale*, both possessing a cortex composed of mechanically relevant wedges of phloem fibres. Our studies show that the anatomical structure of the cortex in *L. oldhamia* is very similar to *C. papaya* and *O. pyramidale* and that comparable variations occur in the cortex of *L. oldhamia* as found in *C. papaya* and *O. pyramidale* when reorienting oblique stems or branches. This similarity in (adaptable) anatomical structures leads to the conclusion that the cortex of *L. oldhamia* was also able to readjust the orientation of stem and branches as a reaction to mechanical stress, shown for *C. papaya* and *O. pyramidale*. This finding supports the hypothesis that *L. oldhamia* stems might well have been self-supporting in (very) young ontogenetic stages and became semi-self-supporting or climbing in older ontogenetic stages.

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1. Introduction

Carica papaya and *Ochroma pyramidale* possess self-supporting erect stems of a height of up to 12 m (Sprecher, 1943) or 20 m (Fletcher, 1951), respectively, and occur in tropical and subtropical regions. Stem stiffness in trees of *C. papaya* and *O. pyramidale* is provided to a considerable part by the secondary phloem forming a lattice-like arrangement of partly sclerenchymatous fibres and resembles the similarly arranged outer ‘Dictyoxylon’ (= mesh) cortex in *Lyginopteris oldhamia*, an extinct species common in the Upper Carboniferous of Europe (300 Myr B.C.). Also the ‘Dictyoxylon’ cortex consists probably of sclerenchymatous fibres. These cortical structures are mechanically very important, as sclerenchyma fibres are responsible for mechanical stability necessary to withstand internal and external loads whereas the wood plays a limited mechanical role in these three genera. This is substantiated by the fact that *O. pyramidale* has one of the lowest wood densities (Chave et al., 2009) or that wood is completely lacking in the parenchymatous xylem of *C. papaya* (Sprecher, 1943). The

growth-form of *L. oldhamia* has been interpreted in various ways: self-supporting trees (Retallack and Dilcher, 1988), semi-self-supporting (leaning) plants (Zimmermann, 1959; Andrews, 1961; Mägdefrau, 1968; Speck et al., 1992; Stewart and Rothwell, 1993; Speck, 1994a, 1994b; Speck and Rowe, 1999; Rowe and Speck, 2004) or even lianoid climbers (Potonié, 1897–1899; Scott, 1923; Phillips, 1981; Galtier, 1986, 1988). Masselter et al. (2007) favoured a semi-self-supporting growth eventually becoming lianoid in relatively old ontogenetic stages after shedding the mechanically important sclerenchymatous outer ‘Dictyoxylon’ cortex. In *C. papaya*, the outer cortex with its phloem fibres is mechanically the most important structure contributing mainly to stem stiffness. Its morphology is strikingly similar to the ‘Dictyoxylon’ cortex in *L. oldhamia* (Fig. 1), raising the question whether this resemblance is just mere appearance or mirrored by a similar mechanical function that has evolved convergently. In *L. oldhamia*, the ‘Dictyoxylon’ cortex supports the stem in relatively young to middle-aged stages. In older stages, the increase in diameter of inner secondary tissues induces an extensive straining and ultimately disruption and loss of the cortex, resulting in a considerable drop of flexural stiffness (Masselter et al., 2007). In *C. papaya*, the structure of the phloem fibre mesh is also strained by secondary growth (Kempe et al., 2013, 2014). This straining is not only vital for realising a tree-like stem with increasing stem diameter but also for the realignment and reorientation of the stem after tilting (Kempe et al., 2013, 2014). Another extant plant that holds strikingly similar structures in the outer cortex is *O. pyramidale* (Fisher and

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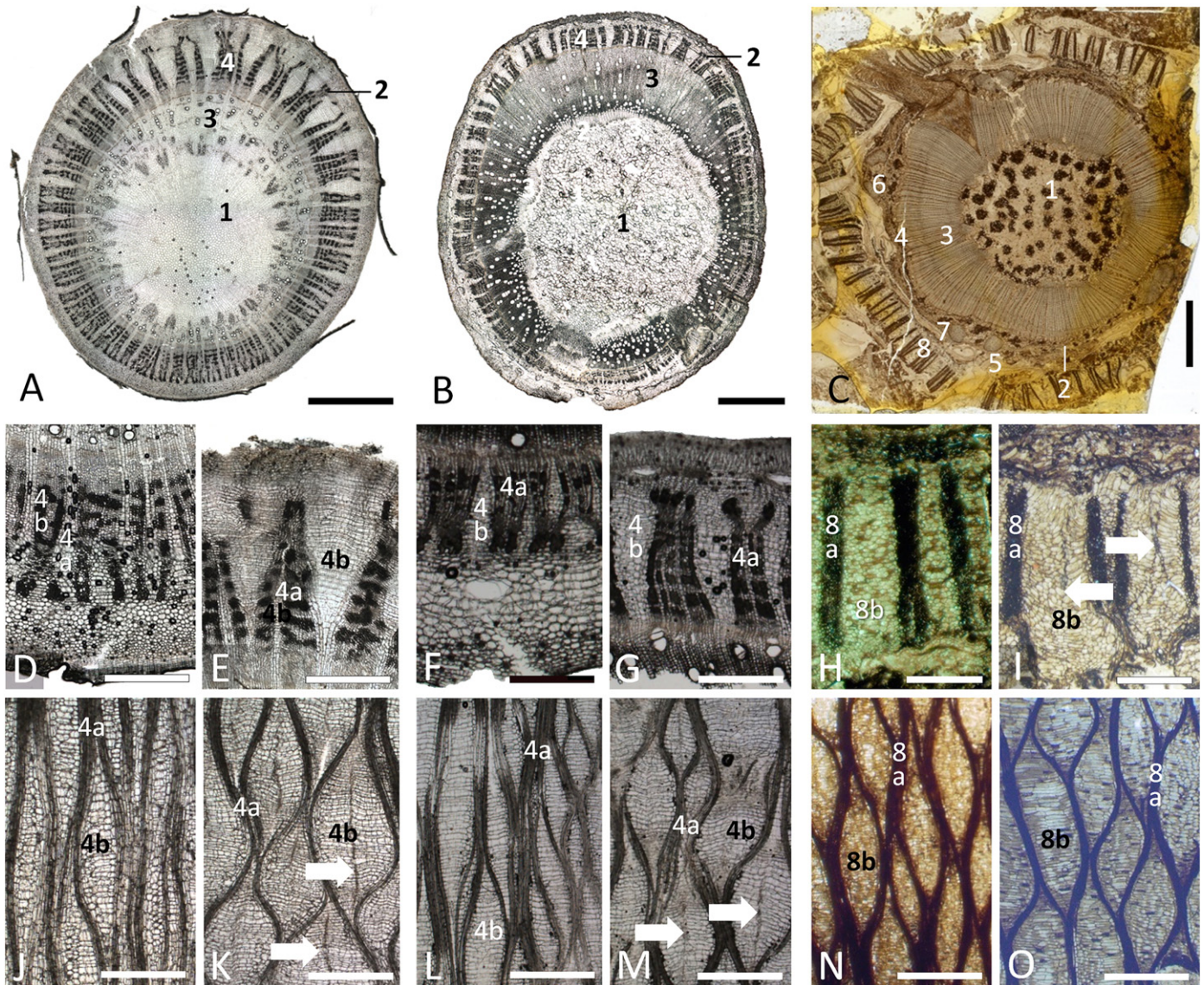


Fig. 1. Sections of branches of *Carica papaya* (A, D, E, J, K), *Ochroma pyramidale* (B, F, G, L, M) and *Lyginopteris oldhamia* (C, H, I, N, O). (A) Cross-section of *C. papaya* axis, note the strained phloem cortex on the adaxial side of the branch (upper part of the image), (B) cross-section of *O. pyramidale* axis, note the strained phloem cortex on the adaxial side of the branch (upper part of the image), (C) cross-section of *L. oldhamia* axis; (D, E) cross-sections of phloem cortex in *C. papaya*, (D) abaxial (unstrained) and (E) adaxial (strained) region of the cortex, (F, G) cross-sections of phloem cortex in *O. pyramidale*, (F) abaxial (unstrained) and (G) adaxial (strained) region of the cortex, (H, I) cross-sections of 'Dictyoxyylon' cortex in *L. oldhamia*, unstrained (H) and strained (I) cortex; (J, K) tangential sections of phloem cortex in *C. papaya*, (J) abaxial (unstrained) and (K) adaxial (strained) cortex, (L, M) tangential sections of phloem cortex in *O. pyramidale*, (L) abaxial (unstrained) and (M) adaxial (strained) cortex, (N, O), tangential sections of 'Dictyoxyylon' cortex in *L. oldhamia*, unstrained (N) and strained (O), respectively. (1) pith, (2) primary phloem, (3) secondary wood, (4) secondary phloem, (4a) phloem fibres, (4b) parenchymatous intercalations, (5) inner primary cortex, (6) leaf trace, (7) periderm, (8) outer primary 'Dictyoxyylon' cortex, (8a) sclerenchyma fibres, (8b) parenchymatous intercalations. Arrows indicate areas of cell proliferation. Scale bars: (A, B) = 2 mm, (C) = 5 mm, (D, E) = 0.5 mm, (F, G) = 0.2 mm, (H, I) = 1 mm, (J, K) = 0.5 mm, (L, M) = 0.2 mm, (N, O) = 2 mm.

Müller, 1983). This tree with soft wood is also supposed to reorient its stems by eccentric growth of the secondary xylem and differential straining of the secondary phloem fibres (Fisher and Müller, 1983). Most probably many (if not all) Malvaceae and related families exhibit such a structure in the phloem, which would explain the large number of fibre producing species in the family.

This leads to the intriguing question of whether the straining of the 'Dictyoxyylon' cortex could also have helped to stabilize and re-adjust the self-supporting orientation of the stem in *Lyginopteris oldhamia*. Consequently, the changes in morphology of *Carica papaya*, *Ochroma pyramidale* and *L. oldhamia* will be compared to answer that question, mainly relating to studies of the functional morphology and biomechanics of these plants by Fisher and Müller (1983), Masselter et al. (2006, 2007), Masselter and Speck (2014) as well as Kempe et al. (2013, 2014).

2. Material and methods

The specimens of *Carica papaya* and *Ochroma pyramidale* shown in Fig. 1 are side-branches of a fully mature plant originating from a commercial plant nursery and the Botanic Garden Osnabrück, respectively. Samples were cut from the curved region of the branch that is subjected to external stresses (mainly by gravity) and shows adaptive growth in order to reach/keep a vertical upward orientation. This allows for determining the changes in anatomy on both the adaxial and abaxial side of the bent branch. Thin sections for light-microscopy were prepared with a cryo-microtome (SLEE medical GmbH, Mev Cryostat) and studied unstained with an Olympus BX61 microscope prior to phloroglucinol staining in order to determine whether lignified tissues within the xylem and phloem of *C. papaya* and *O. pyramidale* are present or not.

The origin of *Lyginopteris oldhamia* specimens is described in detail in Masselter et al. (2006, 2007). These studies as well as those by Kempe et al. (2013, 2014) also provide the formulae and methodological approaches for the biomechanical tests in *Carica papaya* as well as for the ontogenetic and biomechanical reconstruction of *L. oldhamia*. Due to the very small number of tangential sections in the latter species, we analysed the straining of the 'Dictyoxylon' cortex preferentially in cross-sections.

3. Results

3.1. General anatomy

3.1.1. *Carica papaya*

The primary organisation of *Carica papaya* consists of a parenchymatous pith (Fig. 1A, 1) and primary phloem fibres (2). The secondary tissues originate from a cambium that produces a virtually unlignified secondary xylem (3) and partly lignified secondary phloem (4). Phloem fibres form a mesh structure (4a in Fig. 1D, E, J, K) and are tangentially separated by a phloem parenchyma (4b in Fig. 1D, E, J, K) in which regions with several cell divisions can be observed (Fig. 1K, arrows). The axes analysed in the present study have a diameter of approximately 8 mm.

3.1.2. *Ochroma pyramidale*

The primary organisation of *Ochroma pyramidale* consists of a parenchymatous pith (Fig. 1B, 1) and primary phloem fibres (2). The

secondary tissues are well developed and formed by a cambium that generates lignified secondary xylem (3) and lignified secondary phloem (4). Phloem fibres form a mesh structure (4a in Fig. 1F, G, L, M) and are tangentially separated by a phloem parenchyma (4b in Fig. 1F, G, L, M) in which regions with cell divisions can be observed (Fig. 1M, arrows). The diameter of the analysed axes is approximately 11 mm.

3.1.3. *Lyginopteris oldhamia*

The primary organisation of the stem shows a central parenchymatous pith (Fig. 1C, 1) and primary phloem (2) and a thick cylinder of secondary xylem (3) and secondary phloem (4). The inner primary cortex (5) consists of parenchymatous cells and includes leaf traces (6) and a periderm (7) (Fig. 2D), which forms the outermost tissue when old axes have shed the outer sclerenchymatous 'Dictyoxylon' cortex (8). This outer cortex is composed of more or less axially arranged sclerenchymatous strands (8a) with parenchymatous intercalations (8b) (Fig. 1H, I, N, O) with occasional cell divisions (Fig. 1I, O). The sclerenchymatous strands again form a mesh-like structure in tangential section (Fig. 1N, O). Diameters of mature axes range from 5 to 40 mm (Masselter et al., 2006, 2007).

3.2. Secondary tissues

Secondary tissues, i.e. secondary xylem and secondary phloem originate from a vascular cambium that is present in all three species producing a significant amount of markedly lignified xylem in *Ochroma pyramidale* and *Lyginopteris oldhamia*. In contrast, the secondary xylem

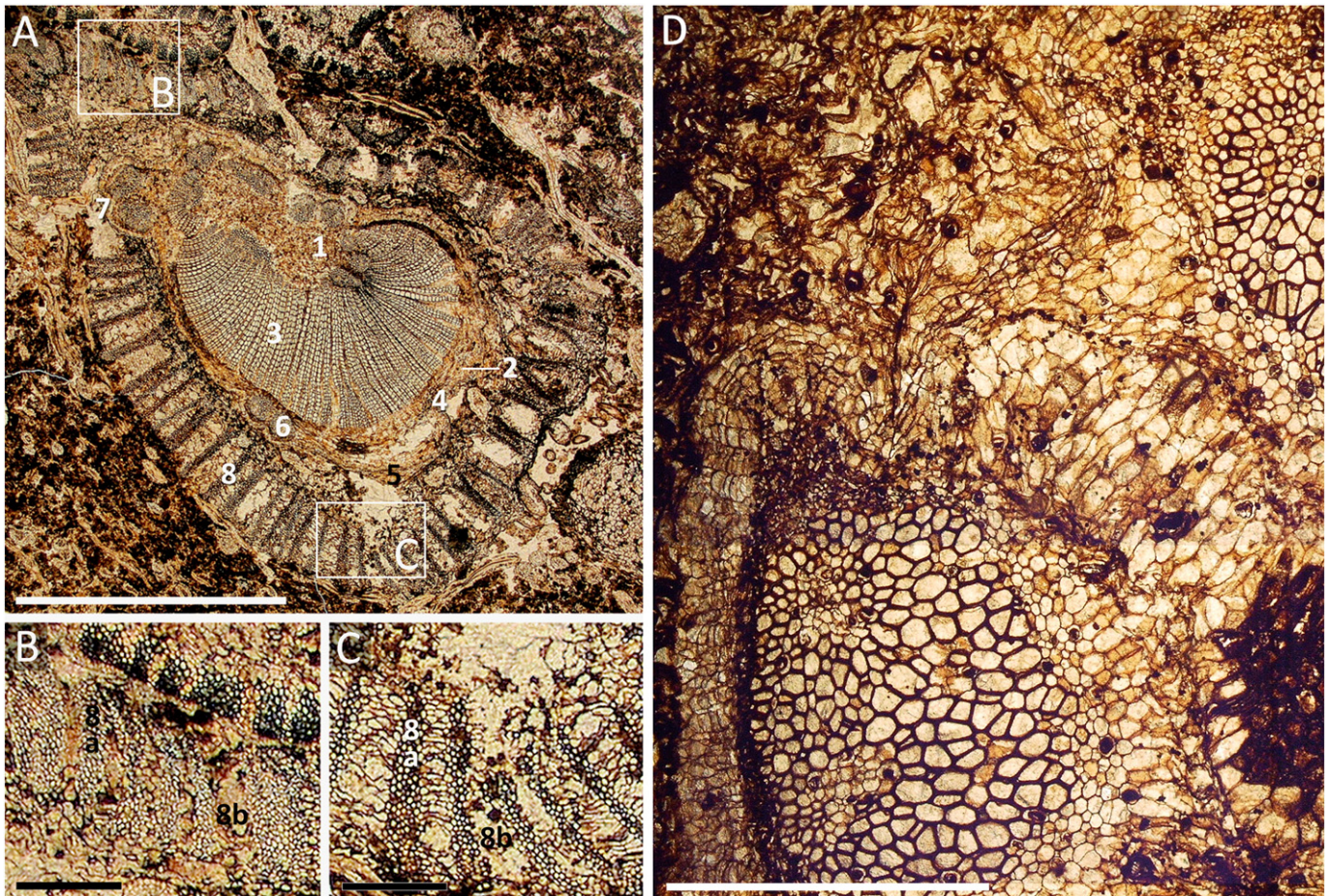


Fig. 2. (A) Cross-section of a *Lyginopteris oldhamia* axis, note the strained 'Dictyoxylon' cortex in the lower part of the image, (B, C) cross-sections of 'Dictyoxylon' cortex in *L. oldhamia*, unstrained (B) and strained (C), respectively, (D) detail of periderm running from the lower left towards the upper right and leaf traces taken from a close section parallel to (A). (1) pith, (2) primary phloem, (3) secondary wood, (4) secondary phloem, (5) inner primary cortex, (6) leaf trace, (7) periderm, (8) outer primary 'Dictyoxylon' cortex, (8a) sclerenchyma fibres, (8b) parenchymatous intercalations. Scale bars: (A) = 5 mm, (B, C) = 1 mm, (D) = 0.5 mm.

in *Carica papaya* is only poorly lignified. The amount of secondary phloem in *C. papaya* is higher compared to that of *O. pyramidale*. The gymnosperm *L. oldhamia* shows extensive formation of secondary xylem with lignified tracheids and only a moderate amount of secondary phloem. Low density wood, i.e. wood consisting of relatively few tracheids and a high number of parenchymatous wood rays is a common feature of *O. pyramidale* and *L. oldhamia*.

3.3. Changes in cortex during reorientation

3.3.1. *Carica papaya*

On the adaxial side of the reoriented tilted branch the parenchymatous tissue that fills the honeycomb-like mesh of phloem fibres shows regions with many cell divisions expanding the net of meshed phloem fibres tangentially (Fig. 1K).

3.3.2. *Ochroma pyramidale*

In *Ochroma pyramidale* as well, regions of cell divisions are visible in the parenchymatous tissue within the honeycomb-like mesh formed by the phloem fibres (Fig. 1M) that consequently expands in tangential direction on the adaxial side of the branch.

3.3.3. *Lyginopteris oldhamia*

The outer ‘Dictyoxylon’ cortex is progressively strained by the increased diameter of secondary vascular tissues. In young axes, the cells of the parenchymatous intercalations are isodiametric and most likely unstrained (Fig. 1H, N). In older ontogenetic stages, these cells are tangentially elongated indicating prior straining (Fig. 1I, O). This straining further increases with ongoing growth of secondary tissues. Additionally, cortex regions of extensive cell divisions in the parenchymatous intercalations exist (Masselter et al., 2006, 2007). Such regions also occur in axes in which other parts of the cortex are not strained (Fig. 2).

4. Discussion

The anatomy of the secondary phloem of *Carica papaya* and *Ochroma pyramidale* is very similar, as described by Fisher and Müller (1983). In both extant angiosperm species the fibre structure supports or is essential for the reorientation of tilted plants or branches (Fisher, 1980). Anatomical changes observed at the base of tilted stems during reorientation are identical to the anatomy of the base of lateral branches. Enlarging the circumference by radially directed growth of the secondary xylem – with more pronounced xylem formation on the adaxial side – causes the phloem mesh to expand in a tangential direction, inducing a contraction on the adaxial side and reorientation of the stem (Kempe et al., 2014) (Fig. 3). It can be stipulated that this mechanism also holds true for lateral branches as the same changes in anatomy, i.e., radially directed growth of the xylem and expansion of the phloem mesh, can be observed on the adaxial side of the studied branches (Fig. 1A, B, D–G, J–M). Cell division in the phloem parenchyma is expected to be a passive response to the extension of inner secondary tissues (xylem) to avoid rupture of the outer tissues.

The anatomy of the primary cortex of *Lyginopteris oldhamia* is very similar to *Carica papaya* and *Ochroma pyramidale*. However, due to the fossilized stage the mechanical relevance for stem support or reorientation by tangential straining of the cortex cannot be verified by mechanical tests. Therefore we like to address this problem on a theoretical basis by considering the two points suggested by Fisher and Müller (1983) for mechanical relevance of the cortex in *L. oldhamia*: (1) an interconnected mesh of fibres forming a skeleton must be developed as well as (2) these interconnections must be persistent, i.e. no slippage between fibre strands of the mesh in the attachment zones. This holds true for the ‘Dictyoxylon’ cortex in *L. oldhamia* until the cortex is finally shed in old ontogenetic stages. This, together with areas of cell division and elongation (Masselter et al., 2006, 2007) similar to those in *C. papaya* and *O. pyramidale* is a strong indication of a mechanically responsive tissue. This tissue allows for reorientation of stems and side branches due to tangential straining of fibre meshes in the cortex in *L. oldhamia*.

In order to determine if the structural similarity between the fibre meshwork (net) of the secondary phloem of *Carica papaya*, *Ochroma pyramidale* and the primary cortex of *Lyginopteris oldhamia* can have the same function, the structural Young’s modulus and the flexural stiffness of the three genera are compared below.

4.1. Structural Young’s modulus

The structural Young’s modulus generally increases in self-supporting plants with plant age (Speck, 1994a, 1994b; Speck and Rowe, 1999). Individuals of *Carica papaya* show values from of 1.0 ± 0.2 GPa for stems of a height of approximately 1.5 m and up to 2.5 GPa for mature stems (Kempe et al., 2013). These values are low compared to mature woody plants, since the bending modulus of “green” wood often is in the range of 10 GPa (Speck, 1994a, 1994b; Speck and Rowe, 1999; Kretschmann, 2010). The water content of axes of *C. papaya* exceeds 90% for secondary xylem while the secondary phloem contains approximately 90% (Kempe et al., 2013) and its maintenance is essential for the self-supporting habit of the plant (Kempe et al., 2013).

In young plants of *Ochroma pyramidale* with heights between 0.25 and 0.44 m, the structural Young’s modulus is found to be 0.2–0.3 GPa (Christensen-Dalsgaard and Ennos, 2012). Young’s modulus for specimens from mature wood with 12% wood moisture content is given with 3.4 GPa (Kretschmann, 2010). As the Young’s modulus for such dried specimens is generally 20 to 30% higher than that for fresh specimens (compare values in Kretschmann, 2010 as well as Christensen-Dalsgaard and Ennos, 2012), a value of approx. 2.4–2.7 GPa for mature fresh “green” wood of *O. pyramidale* can be assumed.

The structural Young’s modulus of *Lyginopteris oldhamia* was calculated to have a mean value of 3.1 ± 0.7 GPa in relatively large axes

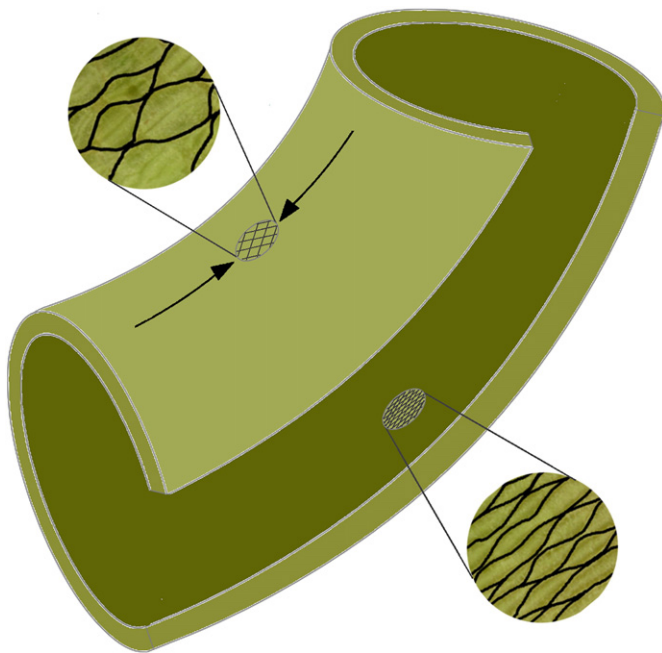


Fig. 3. Schematic illustration of the deformation of the adaxial (upper) side of the phloem fibre mesh in *Carica papaya* and associated shortening (arrows) of the mesh that leads to reorientation of the stem. The mesh has been cut away by approximately one quarter in order to show the abaxial (lower) side of the phloem mesh that remains unstrained.

with a mean comparable diameter of 27 ± 24.5 mm (Masselter et al., 2007). In summary, the structural Young's moduli of mature stems are similar for all three plants ranging from 2.4 to 3.1 GPa.

4.2. Flexural stiffness

In *Carica papaya*, the values range from approx. 0.1 Nm^2 for young axes less than one year old and a diameter of ca. 2 cm to approximately 5 Nm^2 for 2 year old axes and approx. $5000\text{--}50,000 \text{ Nm}^2$ for older axes with thick stems with a diameter up to 15 cm (Kempfe et al., 2013).

No values for the flexural stiffness of *Ochroma pyramidale* could be found in literature. Based on the data of Christensen-Dalsgaard and Ennos (2012) of 0.28 GPa for the Young's modulus of seedlings with a diameter of between 0.82 and 1.3 cm, a flexural stiffness of $0.08\text{--}0.5 \text{ Nm}^2$ can be calculated.

Mean values range from 0.1 Nm^2 for very young axes to 73.5 Nm^2 for the largest (menetogenetic) axes in *Lyginopteris oldhamia* (see Masselter et al., 2007). For (very) young axes, the values of flexural stiffness in *Carica papaya*, *Ochroma pyramidale* and *L. oldhamia* are comparable. For older stems the data base for a reliable comparison is scarce.

4.3. Growth form

Carica papaya and *Ochroma pyramidale* are able to form self-supporting stems and grow as small to medium sized trees (Sprecher, 1943; Fletcher, 1951). The flexural stiffness is similar compared to *Lyginopteris oldhamia* in very young ontogenetic phases with a steep increase by a raised second moment of area with increasing age in *C. papaya* (and most probably also in *O. pyramidale*), which is typical for self-supporting trees and shrubs (Speck et al., 1992; Speck, 1994a, 1994b; Speck and Rowe, 1999; Rowe and Speck, 2004). The increase of flexural stiffness in *L. oldhamia* is much slower with maximum values that are 68 to 680 times smaller compared to those measured for older axes in *C. papaya*. Based on these calculations and structural considerations, *L. oldhamia* was reconstructed as a semi-self-supporting plant that eventually becomes lianescent in old stages of growth after shedding the outer cortex (Masselter et al., 2007).

The results presented in this paper make it very probable that the outer primary cortex of *Lyginopteris oldhamia* is tangentially strained during increasing secondary growth, and the resulting shortening of the cortex may have resulted in an overall stiffening of the stem. Additionally if differential growth on two stem halves exists this may allow a reorientation of tilted axes also in this fossil species. Such a reaction of the cortex cannot be verified by serial sections along a bent stem in the fossils of *L. oldhamia* as the measurements are based on individual cross-sections from different specimens each representing only one specific developmental stage. However, as in curved specimens of *Carica papaya* (Fig. 1A) and *Ochroma pyramidale* (Fig. 1B), a distinct difference in different opposed parts of the outer regions can be seen in individual stem sections of *L. oldhamia* (Fig. 2). Therefore, it is conceivable that the regions with more isodiametric and putatively less strained cells correspond to the lower side of a bent stem (abaxial side in case of a branch) and the regions with elongated and therefore previously strained cells to the upper side of the stem (adaxial side in case of a branch).

In summary, the comparative analysis of stems of all three species support the idea that *Lyginopteris oldhamia* had self-supporting slender stems in very young developmental stages, i.e. thin axes, as the flexural stiffness is comparable to *Carica papaya* and *Ochroma pyramidale*, then entered a transitional (may be, however, long-lasting) semi-self-supporting stage, and finally became lianescent in relatively old developmental stages after the 'Dictyoxylon' cortex was shed. Thus, the young and thin axes of *L. oldhamia* should have been able to reorient tilted stems and branches by differential secondary growth and concomitant tangential straining of the fibre meshes in the 'Dictyoxylon' cortex, as it has been shown for *C. papaya* and *O. pyramidale*.

In contrast to *Lyginopteris oldhamia*, reorientation of woody fossil stems is most often accompanied by the occurrence of reaction wood as it is still present today. While the presence of fossil reaction wood is well proven for rather 'recent' eras of the Tertiary (Groover, 2016), as well as for the late Cretaceous and early to middle Jurassic (Blanchette et al., 1991; Chapman and Smellie, 1992; Wheeler and Lehman, 2005; Bodnar et al., 2013), evidence of reaction wood in earlier periods is often rather inconclusive (Schmid, 1967) but is also reported convincingly for *Cordaixylon* from the Pennsylvanian (Rowe and Speck, 2004; Taylor et al., 2009). These provide an interesting and approximately contemporaneous occurrence of righting mechanism in big pycnoxylic trees and the lighter cortex-dominated structures in the seed fern *L. oldhamia*.

It can be stipulated that these two reorientation systems for stems and branches, i.e. 1) the straining of the cortical mesh vs. 2) reaction wood that are still present today and have evolved independently were both present, albeit largely undetected, in fossil plants since the Carboniferous.

5. Conclusions

The cortical anatomy of the extant plants of *Carica papaya* and *Ochroma pyramidale* is very similar to the one described for the extinct seed fern *Lyginopteris oldhamia*. Ontogenetic (developmental) changes in the peripheral fibrous network play a major role for flexural stiffness and growth form also in terms of stem/branch reorientation. This is of special interest since the conspicuous 'Dictyoxylon' structure of *L. oldhamia* was generally considered not to exist anymore since the species is extinct. While this is undoubtedly true from an evolutionary perspective in the line of seed ferns and later relatives, we hypothesize that stems with a similar functional principle evolved several times independently during evolution, demonstrated by the secondary phloem of *C. papaya* and *O. pyramidale* representing only two examples of an unknown diversity of extant and fossil plants with similar functional traits. In light of the results of the present study, the ontogeny of *L. oldhamia* so far considered to be semi-self-supporting and later lianescent has now been completed and extended by adding a self-supporting early stage revealing a much more complex picture than previously expected including the ability to readjust the orientation of stems and branches by adaptive straining of the cortex. To the best knowledge of the authors, this is the earliest evidence of tissue adaptability based on differential growth of secondary tissues actively responding to inclination to re-align branches and stems. The present study again proves the importance of learning from functional morphology and biomechanics of extant plants for a better understanding of fossil plants even if the compared plants are not or only very distantly related.

Acknowledgements

We would like to acknowledge the staff of the Botanic Garden of Osnabrück for providing the specimen of *Ochroma pyramidale*. The authors thank Paul Kenrick and Lil Stevens from the Natural History Museum in London for providing the photograph for Fig. 2. We are grateful for the comments by the two anonymous reviewers which helped to improve the manuscript significantly. TM, SC and TS thank the German Research Foundation (DFG) for funding this study within the Collaborative Research Center TRR 141 'Biological Design and Integrative Structures – Analysis, Simulation and Implementation in Architecture' – Project A06.

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