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Vascular Cambium—Between the Hammer and the Anvil: A Tensile Stress Hypothesis on the Mechanism of Radial Growth of Broadleaved Trees

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Abstract: The vascular cambium is the main lateral meristem responsible for the secondary growth of trees. There are a number of explicit and implicit assumptions behind this statement which allow questions to be raised about the mechanism underlying the radial growth of trees. Based on the hypothesis of the diurnal strains of plant organs, it is anticipated that the process of radial growth can be understood as an adaptation to the cyclically changing mechanical stress in the radial direction generated by the phloem during the 24 h day cycle. This qualitative hypothesis treats cambium as a tissue subjected to nighttime stretching and daytime compression in the radial direction. The proposed osmo-mechanical hypothesis of the radial growth of vascular cambium links the daily change in water status and the considerable daily strains in the xylem and phloem with the radial net expansion of a tree trunk. We highlight transpiration as a major factor influencing the secondary growth of woody plants. Thus, we indirectly relate all the biotic (e.g., insect infestation, fungi infections, injuries, shadowing, intra- and interspecies competition, parasitism, symbiosis, etc.) and abiotic (e.g., humidity, water availability, wind, injuries, shadowing, day length in a vegetative season, altitude, temperature, insolation, etc.) processes influencing transpiration with radial growth. In the proposed hypothesis, we also infer that differences in the strains in phloem and xylem are the direct source of tensile stress, tensile stress relaxation, compressive stress, and compressive stress relaxation in the vascular cambium. This sequence appears to be crucial in understanding both the process of the radial growth of trees and the formation of differential wood patterns, within the same genotype as well as in different genotypes. It also provides arguments for the discussion on the mechanisms regulating processes in the vascular cambium. It points out the important role of the variable mechanical stresses in the radial, circumferential, and axial directions and their interference in the development of this lateral meristem. Thus, this hypothesis supports the concept of the epigenetic and systemic regulation of intrinsic wood patterns and tree forms by environmental factors. The hypothesis is focused exclusively on broadleaved trees and symplastic growth. This limitation of the scope is due to a concern for clarity. In this form, the hypothesis provides an alternative explanation for a pure process of radial growth and paves the way for a better interpretation of such phenomena as earlywood and latewood formation. At the same time, this approach to the vascular cambium provides answers to many questions related to the generation of the mechanical conditions necessary for the occurrence of intrusive growth between tangential cell walls; this is of fundamental importance for fusiform initials readjustment, vessel element and fibre formation, ring-porous wood formation, etc.



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1. The Aim of the Review

The aim of this review is to introduce a new hypothesis for the radial growth of trees based on the mechanism of diurnal strains in plant tissues.

2. Introduction

2.1. Radial Growth of Trees as an Epigenetic Process

It is increasingly recognised that complex and inherently flexible adaptive systems such as those of trees are subject to multilevel systemic regulation and integration. Therefore, an organism developing from identical genetic material may have completely different phenotypic characteristics depending on the environmental factors acting on it (e.g., dwarf trees growing under harsh environmental conditions may grow into full-sized trees in good or moderate environmental conditions). Little is known about the extracellular mediators of tissue formation. The question can therefore be posed in the following form: what constitutes the key element operating between genetic activity and organ shape formation? The most appropriate candidate seems to be one of the most fundamental forces giving shape to a cell, namely mechanical stress [1,2]. There is a growing body of evidence indicating that mechanical forces are fundamental to many aspects of plant development and its interaction with a constantly changing environment [3–13]. New research approaches postulate the coupling of applied mechanical forces to the cell surface with the cell nucleus—a mechanical signal transmitted through the cytoskeleton could lead to deformations in the 3D structure of the nucleus and alter genetic expression [14]. The structure of a tree and the interrelationships of its tissues generate a time-varying mechanical field of force, which has both integrative and morphogenetic functions [15]. In this context, the activity of the vascular cambium seems particularly interesting. Numerous morphogenetic processes are closely linked to the radial growth of cambium cells. The most important of these are: symplastic growth, periclinal divisions, intrusive growth, the formation of vessel elements and fibre growth, the formation of sieve tubes, ray dilatation on the phloem side, and the formation of juvenile wood, mature wood, earlywood, latewood, diffuse-porous wood, ring-porous wood, reaction wood, etc.

2.2. Adaptive Flexibility of Plant Cells and Plants to Mechanical Stress

In order to understand how tissue growth is regulated, we need to start by taking a closer look at the regulation of its constituent elements, i.e., individual cells. We can distinguish between two main types of cell deformation—elastic vs. plastic. In the case of plant cell growth, we usually have both. The plastic component of deformation (irreversible deformation) applies almost exclusively to the primary cell wall [16,17], and this usually concerns meristematic cells. The primary cell walls of plants consist of cellulose microfibrils embedded in a polysaccharide matrix, which is composed mainly of hemicelluloses and pectins [18,19]. The deformation of primary walls under the influence of an internal or external mechanical factor is a complex process involving not only cellulose microfibrils but also expansins, xyloglucans, and pectins [17]. The basic condition for cell growth is that the protoplast generates a sufficient amount of hydrostatic pressure [20]. This pressure acts on the primary cell wall. It is the main force responsible for its expansion [21,22].

The primary meristematic cell wall allows the development of different cell shapes. Therefore, the shape of a single meristematic cell surrounded by a primary cell wall will be largely determined by the mechanical factors of the internal and external environment, e.g., by hydrostatic pressure, the orientation of cellulose fibrils, and the contact of the wall with other objects or other cells [21,23]. It is therefore not an unexpected feature of the growing trees that, being composed of flexible and plastic elements, they are also highly adaptive to mechanical stresses at the level of the organism [9,15,24–26].

2.3. Why Is It Possible to Correctly Describe Radial Growth of the Vascular Cambium without Considering Intrusive Growth?

The vascular cambium is classified as a secondary meristem. The cells of the vascular cambium are arranged between the phloem and xylem to form a cylinder [27,28] (Figure 1).

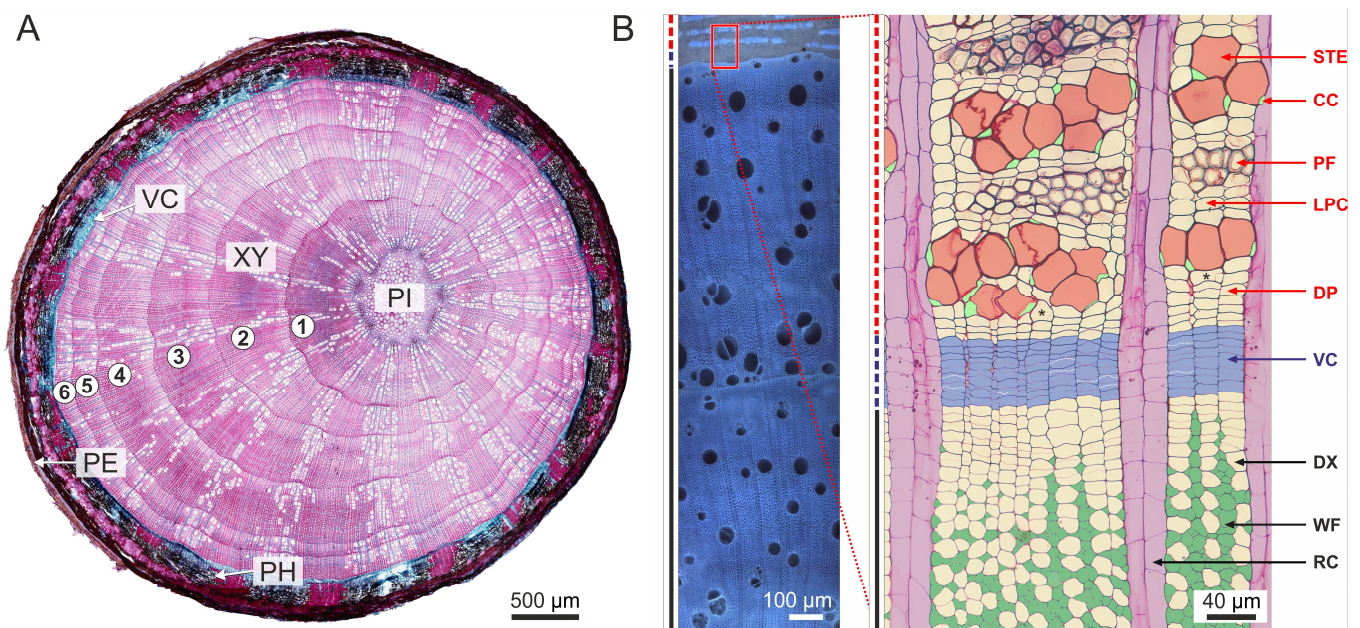


Figure 1. Transverse sections of stems of broadleaved tree species. **(A)** Six-year-old branch of *Carpinus betulus* L. Successive xylem increments are numbered 1–6. The sample was cut with core-microtome and examined using bright-field microscopy. Double staining was used (unlignified cells are stained blue by astra blue; lignified elements are stained red by safranin O). XY—xylem; PI—pith; PE—periderm; VC—vascular cambium (broad definition: cambial initials together with mother cells); PH—phloem. **(B)** Fragment of a branch (**left**) epi-fluorescence, FS01 filter, wavelength 365 nm, sample cut with razor blade) and a tree trunk (**right**) bright field, sample cut with Tesla ultramicrotome and stained with PAS and toluidine blue) of *Robinia pseudoacacia* L. Area containing tissues corresponding to tissues visible on the right side is marked with a red frame. Fusiform cambial cells are marked in blue (note that vascular cambium also includes ray initials and radial system mother cells). Radial system in a tree trunk is marked in purple. STE—sieve tube element; CC—companion cell; PF—phloem fibre; LPC—living parenchyma cell; DP—developing phloem cell; DX—developing xylem cell; WF—wood fibre tip (still growing); RC—ray cell.

Cambial cells grow in two distinct ways: symplastically and intrusively. The basic type of growth in the cambium is symplastic, i.e., coordinated cell growth within the enlarging tissue without the separation of adjacent cells walls [29,30]. Intrusive growth, on the other hand, concerns individual cells, and it results in changes in the contacts between cells [31–34]. For intrusive growth to occur, a tensile stress acting perpendicularly to the alignment of the middle lamella and separating neighbouring cells is necessary. As intrusive growth can only occur into a free space (microspace) [35,36] which can only be created by exceeding the threshold value of the tensile stress, the observation of such growth between tangential walls [34,37–39] indicates that the middle lamella is being stretched in the radial direction. At this point, the following question can be asked: is it possible to correctly characterise the radial growth of the vascular cambium without taking intrusive growth into account? More recent works on the functioning of this meristem have linked enlargement of the cambial cylinder exclusively to symplastic growth [28,34], whereas the rearrangement of cambial cells has been linked specifically to intrusive growth [28,39]. This allowed a fundamental redefinition of the role of intrusive growth in the radial expansion of the stem [27,28,34,37–43].

The details of the mechanism of intrusive growth differ in the case of the vessel elements and fibres; in both instances, the mechanism does not directly alter the circumference and intensity of the radial growth of the vascular cambium [32,33]. It is related to the relaxation of the internal mechanical stress generated by the maturing secondary xylem. Thus, it can be assumed that cellular events such as intrusive growth do not, in principle, affect the

intensity of the radial or circumferential growth of the vascular cambium. Therefore, the model of radial growth of the vascular cambium in its basic version would remain correct without taking intrusive growth into account.

2.4. Vascular Cambium and Pressure

The radial growth of the cells of the vascular cambium involves the growth of the radial walls and periclinal divisions of the cells. These cellular events precede the differentiation of the cambial cells and are directly responsible for the final size of the cells and their number in a radial row of a given annual increment. So far, it has been assumed that this growth is an intrinsic feature of the vascular cambium and that the external environment merely modifies this growth. This is well manifested in the functional definitions of the vascular cambium where secondary phloem and xylem tissues are produced through the activity of the vascular cambium [44]. The fusiform cells of the vascular cambium have a characteristic shape: they are axially elongated, radially flattened, and tangentially expanded. The shape of the cambial cells is far less dependent on hydrostatic pressure and hugely dependent on the pressure exerted on the vascular cambium by the phloem. Once the phloem is removed, the cells of the cambium divide transversely and produce callus. A restoration of the pressure acting on the cambium is needed to restore the characteristic fusiform shape [45]. It can therefore be said that the pressure exerted by the phloem has a regulatory and morpho-forming role in the vascular cambium [46–49]. These data were often treated as complementary and interpreted within a dynamically developing phytohormonal paradigm related to the regulation of development in the vascular cambium by auxins, cytokinins, gibberellins, jasmonic acid, and ethylene [50–53]. To date, no comprehensive hypothesis has emerged that integrates the physiological, anatomical, and biomechanical data on the development of the vascular cambium. However, this does not mean that such attempts have not been made. A very interesting general hypothesis (on the organismal level), which pointed out the function of mechanical factors in the regulation of tree growth, is the concept of the mechanical self-optimisation of trees [15,54,55].

In the osmo-mechanical hypothesis presented below, we will show that the vascular cambium can be regarded as a tissue that adapts to alternating mechanical and osmotic stressors [56]. These stressors are generated in a diurnal rhythm by the swelling and shrinking phloem in leafy trees. However, we will define a starting point and therefore look at the views on the radial growth of the vascular cambium.

2.5. What Do We Know about the Impact of Mechanical Stress on Radial Growth in Trees?

In the basic interpretations of the radial growth of trees, two fundamental processes appear from the outset: the radial growth and tangential growth of cambial cells, and two cellular events occur: periclinal divisions and anticlinal divisions. However, a problem soon arises when analysing anticlinal divisions because the most common type of anticlinal division is an oblique one. The occurrence of oblique anticlinal divisions leads to a shortening of the initial cells and, as a result, their growth to the so-called cell adjusted length [42]. This process is supposed to occur through an intrusive growth. The interpretation regarding the role of the intrusive growth of fusiform initials in reproducing their original length is combined with the following hypotheses:

1. Intrusive growth is involved in an increase in the circumference of the vascular cambium [29,47];
2. To maintain its structure, the cambium must be compressed in the radial direction [45];
3. To allow the growing cell end to intrude between adjacent cells, the middle lamellae between them must be stretched [47].

Furthermore, several additional observations can be added to the above points:

4. Under the influence of an axial tissue incision, the cambium deforms into an axially oriented lens, which indicates the existence of tensile stress in the circumferential direction (unpublished observations related to the collection of the vascular cambium samples in early spring);

5. Examination of collected secondary phloem, cambium, and secondary xylem fragments indicates that there is strong tensile stress in the circumferential direction in the vascular cambium [47];
6. The shape of the cambial cells in a cross-section (elongated tangentially and flattened radially) can be interpreted as resulting from compression in the radial direction and tension in the circumferential direction.

The abovementioned statements are part of an unstructured paradigm in which radial growth of the vascular cambium is assumed to result from the coordinated/symplastic growth of cambial cells (not changing contacts between neighbouring cells) in the radial and circumferential directions, which may be accompanied by periclinal and/or anticlinal divisions (Figure 2A). Auxin is indicated as the causative factor, whereas the changing pattern of mechanical stress (tensile stress in circumferential direction and compressive stress in radial direction) is indicated as a coordinating factor (Figure 2B). It is assumed that when the radial compressive stress in vascular cambium reaches a level that stops further radial expansion (its value becomes too high), then the tensile stress in the circumferential direction reaches a threshold value that leads to circumferential expansion. In this paradigm, the cambium is constantly compressed in the radial direction because it is pushed centrifugally by the growing and differentiating xylem, and it is constrained by the external tissues, namely phloem and periderm [47,49,57].

According to this interpretation, the circumferential growth of the phloem, which is centrifugally stressed by the xylem and the vascular cambium, relaxes the threshold tensile stress in the circumferential direction and thus reduces the radial compressive stress in the vascular cambium, allowing the continuation of the radial growth (Figure 2B) [58]. Simultaneously, auxin in this view is responsible for both the generation of mechanical stress (radial growth) and its relaxation (circumferential growth).

In this explanation, the occurrence of compressive and tensile stresses is attributed to the growth of the vascular cambium and the subsequent maturation of successive layers of xylem cells. With a very superficial approach to the issue of radial growth of the vascular cambium, it may appear that this paradigm proposes a logical and internally consistent cause-and-effect system. However, it actually leaves a great many processes and events unexplained, despite the fact that these are integrated into the phenomenon of the radial growth of the vascular cambium. Remaining within this paradigm, it is impossible to explain the process of cambial cell rearrangement, which is tightly coupled to the intrusive growth of the cambial initials between the tangential walls of neighbouring cells [27,28,34,37,38,41,42]. Among these phenomena are the formation of spiral and interlocked grains, the formation of vessel elements, and the xylem and phloem fibres. To explain these phenomena, it is necessary to identify the source of tensile stress occurring in the vascular cambium in a radial direction. Furthermore, within the framework of existing views on the radial growth of trees, it is difficult to explain the phenomenon of reaction wood formation and the associated variation in the rate of radial growth (asymmetric/eccentric growth). Finally, it does not allow a convincing explanation of phenomena such as the formation of juvenile and mature, early and late, diffuse-porous, and ring-porous wood structures.

All the abovementioned phenomena are strongly linked to the process of the radial growth of the vascular cambium, and their explanation must be based on a fundamental hypothesis concerning the mechanism of radial growth. The currently held views, according to the authors, do not provide such a basis.

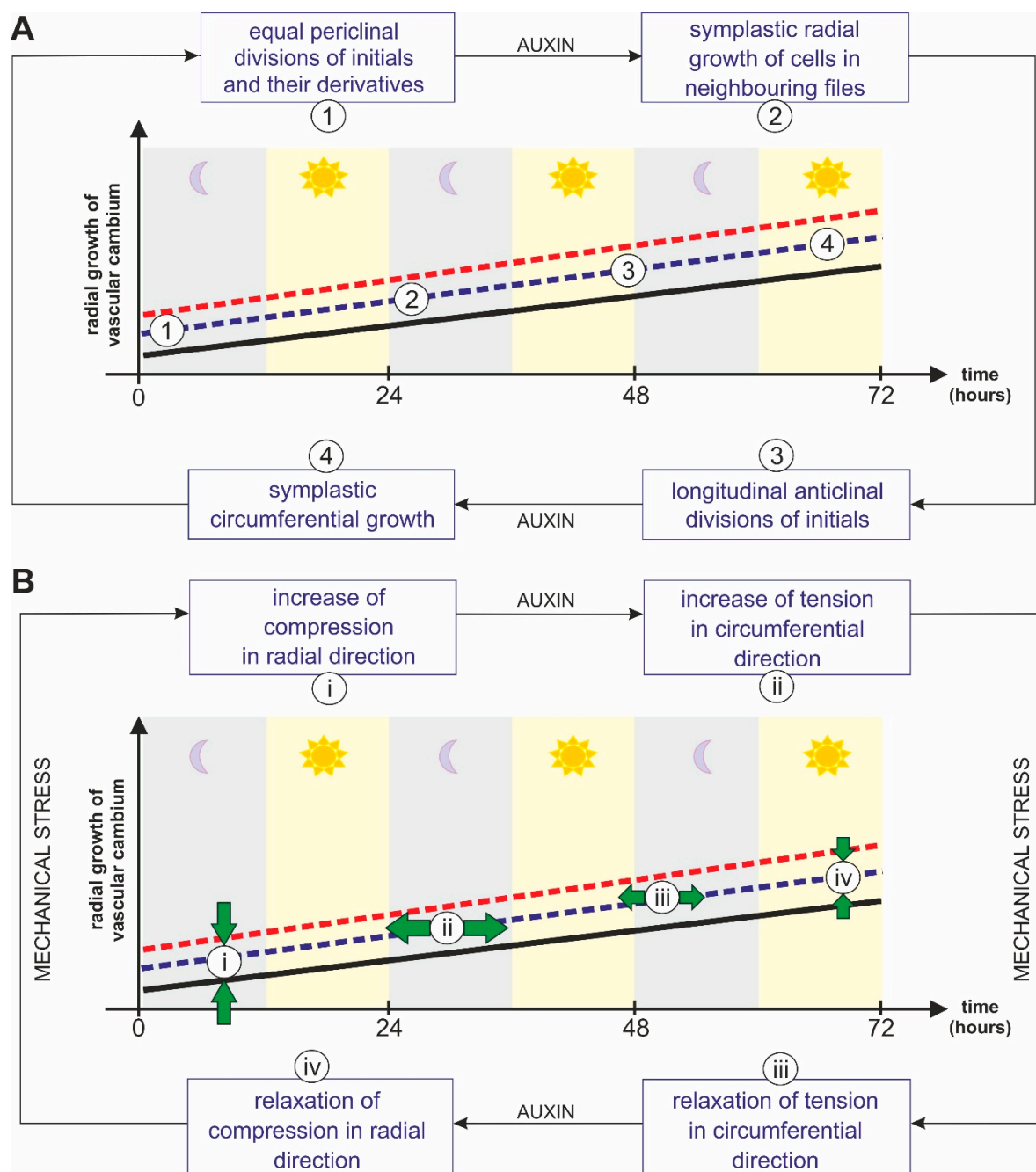


Figure 2. Scheme summarising the previous understanding of the mechanism of radial growth of the vascular cambium. **(A)** Basic cellular events involved in radial growth of the vascular cambium: (1) equal periclinal divisions; (2) radial growth; (3) longitudinal anticlinal divisions; (4) circumferential growth. **(B)** Mechanical stress involved in radial growth of the vascular cambium. Radial growth generates (i) compressive stress in the radial direction and is responsible for (ii) an increase in tensile stress in circumferential direction. The growth in circumferential direction (iii) reduces the tensile stress in circumferential direction and thus (iv) decreases the compression in radial direction below the inhibitory value of radial growth, allowing further radial growth of the cambial cells. Blue dashed line—vascular cambium. The radial growth of the phloem (red dashed line) and xylem (black line) is included. In this approach, the radial growth of the vascular cambium is induced by auxins and is not dependent on diurnal rhythms, which are marked as grey (night) and yellow (day) stripes. A period of 72 h was chosen based on the mathematical modelling concerning an average cambial initial in 1 m circumference cambial cylinder that deposited 3 mm thick annual ring—it was calculated that, on average, each initial cell divides periclinally approx. every third day [28].

2.6. Interaction of Auxin and Mechanical Stress in Regulation of Radial Cambium Growth

In the last few decades, much progress has been made in understanding the hormonal regulation of plant cell growth and the differentiation mechanisms (including cambial cells), as well as the molecular regulation of these processes, e.g., [59–65]. One of the most extensively studied plant hormones, associated with the loosening of the cell wall structure and cell wall expansion, is auxin [66–72]. When considering the role of auxin in cell growth as well as the formation of the vascular system, it should be noted that auxin accumulation occurs via polar transport and to some extent by diffusion [29,36,73–82]. Furthermore, it is known that PIN1 proteins (PIN proteins are one of the main types of transporters responsible for the directional transport of the hormone—auxin efflux carriers) show a polar distribution and face neighbouring cells following an auxin concentration gradient [74,76–78,80,81,83–88].

At the same time, there are many reports pointing to mechano-signalling as the basis of plant growth and the differentiation processes (discussed in: [48]). In this context, studies shedding light on the control of polar auxin transport by mechanical stress, e.g., [89–93] appear to be extremely important. Indeed, it has been found that the field of mechanical stress can regulate the site of auxin accumulation by controlling the distribution of PIN family proteins. These are transported to regions of the plasma membrane that are subjected to tensile stress [93]. Of course, the plasma membrane is connected to the cell wall, and the signal can be transmitted further to target cell organelles through signalling molecules or peptides [94–96]. However, at the intra- and inter-tissue level, mechanical stress is mainly transmitted through a continuum composed of cell walls [36,96,97]. It can therefore be assumed that (1) the occurrence of tensile stress (mechanical stress) contributes to the strain of the cell and leads to stress acting on the cell walls and middle lamellae of adjacent cells [36,96,98]. (2) Along with the cell wall, an adjacent section of the cell membrane is stretched [5,93,94,98,99]. (3) The cell receives information about the change in cell wall mechanical stress [12,96]. (4) Through the inhibition of endocytosis [89,90] and probably also the increase in exocytosis [93,100,101], a cell increases the amount of PIN1 proteins in the stretched region of the cell membrane [89,90,92] adjacent to the stretched section of the cell wall. PIN1 proteins, as auxin efflux transporters, are responsible for polar auxin transport [53,74,76–78,80,81,83–85,88,102–104]. (5) There is an effect of directing auxin towards a cell in which there is an increased auxin concentration [105–110]. (6) Auxin flows into a neighbouring cell, in which tensile stress has also occurred.

Interestingly, it has been found that not only PIN1 proteins but also cortical microtubules (CMTs) reorient in response to stress changes [91,92,111–113]. They align along (parallel to) the main direction of tensile stress. Subsequently, CesA (Cellulose Synthase A) proteins, moving along the microtubules, synthesise cellulose fibrils, simultaneously reinforcing the cell in the direction of their deposition [98,114–119]. It should be noted that cellulose fibrils have a very high tensile strength [36] and thus reinforce the cell in the direction of their deposition, i.e., according to the orientation of the CMTs [98,114]. It implies that the preferred direction of growth is perpendicular to the cortical microtubules and cellulose microfibrils [120–123]. When the cells enlarge, their growth occurs in a direction perpendicular to the deposited cellulose fibres, which, due to their high tensile strength, prevent cells from stretching in a direction parallel to their course. In view of this, anisotropic growth occurs, the direction of which, both in the cells of the apical meristem and in the vascular cambium, depends on the organisation of the cellulose skeleton of the cell wall, which may be largely implied by the cortical microtubule orientation, which in turn is related to the pattern of distribution of the mechanical stress [91,92,96,111,113,124] (Figure 3).

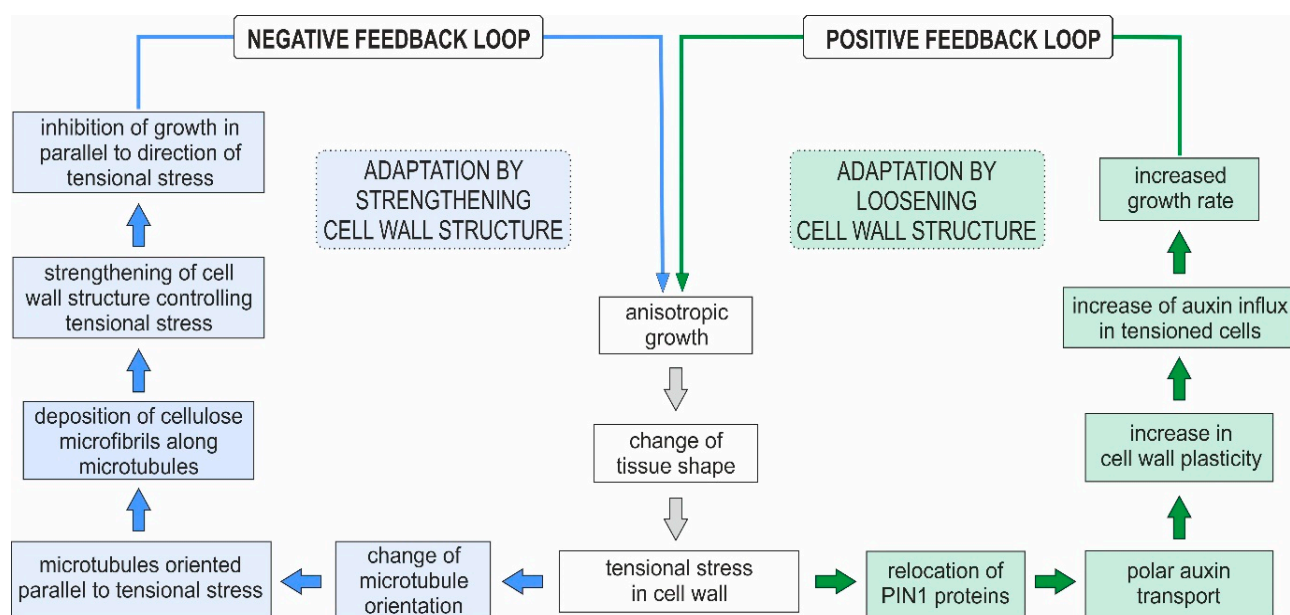


Figure 3. Proposed scheme showing positive and negative feedback loops that control plant cell growth (based on the literature cited in the main text). On the right is the green pathway associated with auxin action (polar auxin transport directed by PIN1 protein localisation). On the left (light blue), adaptation to mechanical stress leads to cell wall strengthening. Both feedback loops respond to a signal in the form of mechanical stress and control the growth of plant cells/tissues.

Two subsystems related to the control of cell growth can be distinguished, each having a feedback nature (Figure 3). The first is the auxin pathway, in which auxin enables cell volume to increase [73–78,80–83,85,125–127]. The second is growth control, which is dependent on the orientation of the cortical microtubules [91,92,98,111,113–117,119–123]. These are two different types of feedback. The auxin-mediated pathway is an example of a positive feedback, as the influx of auxin into the cell also increases its influx from neighbouring cells into the cell. On the other hand, the change in orientation of CMTs represents a negative feedback in terms of growth direction, as growth is inhibited in a direction parallel to the alignment of the cellulose microfibrils. These two subsystems are related to each other, and the element that binds them together is mechanical tension. The two couplings described—both the positive and the negative—affect the mechanical stress pattern and change the shape of the tissue.

Auxin can be regarded as a substance that relaxes cell wall tension and thus increases its plastic deformation potential (at the same temperature and hydrostatic pressure). It can also be referred to as the hormone responsible for relaxing mechanical stress at the cellular and tissue levels. It is noteworthy that the action of auxin can be substituted. For example, the application of expansins can lead to the same effect—in terms of initiating leaf morphogenesis—as the administration of auxin [128,129]; the application of pectin methylesterase (PME) can affect phyllotaxis, similarly to auxin [130]. Therefore, it can be concluded that auxin is a very important and necessary, though not superior, component of the complex growth mechanism, including radial growth. The hormone can be seen as an element embedded in various types of developmental–adaptive systems and the interrelationships between them, which are often of a feedback nature.

3. Biomechanics Takes the Stage

3.1. In Search of Tensile Stress between Secondary Phloem and Xylem

Our studies on the intrusive growth of the cambial initial cells [27,28,34,37–42,131–133], the intrusive growth of the vessel elements [31,32], and the growth of wood fibres [33,43], as well as the work on a model for the circumferential growth of the vascular cambium [27,28],

indicate that, in the cases mentioned, this growth requires the formation of spaces between the tangential walls of neighbouring cells. This means that the intrusive growth of fusiform initials, the formation of vessel elements, and the growth of wood fibres, all require tensile stress in the radial direction in order to occur. The view of the continuous compression of the cambium in the radial direction, derived from views on the mechanism of the radial growth of the cambium, makes it difficult or even impossible to explain the aforementioned processes involved in radial growth, i.e., the remodelling of the cambium cell arrangement, vessel element formation, and fibre growth. The question therefore arose as to how tensile stress can be generated in the radial direction. This article highlights two potential mechanisms that could be responsible for the generation of tensile stress in the radial direction in the vascular cambium:

1. The collapse of the previous year's sieve tubes in the phloem [47];
2. Diurnal strains (deformation produced by stress in a daily cycle) in the tissues [134].

As mentioned above, the collapse of sieve tubes in the phloem, as a mechanism for transient tensile stress in the radial direction, should be considered as an ad hoc hypothesis. As vessel elements grow intrusively between tangential walls of axial system cells, in both ring-porous and diffuse-porous trees [31] the spring collapse of sieve tubes cannot be considered as a universal mechanism generating tensile stress in the radial direction throughout the growing season. During an investigation of *Robinia pseudoacacia* xylogenesis, it was found that the phloem within the stem seemed to collapse much too early to explain the growth of the first broad vessel elements of earlywood [32,135]. Moreover, the collapse of phloem sieve tubes does not explain the formation of vessels in the summer and also in seasonless equatorial zone.

The osmo-mechanical hypothesis introduced in this article is based on the results obtained during research on the diurnal strains of tree trunks. This research indicated that living tissues shrink during the day when plants undergo transpiration and swell during the night when transpiration ceases [136,137]. Furthermore, the daily deformation of tissues composed mainly of living cells (e.g., phloem) is greater than that of tissues composed mainly of dead cells (e.g., xylem) [138]. Thus, we hypothesise that the tissue localised between the phloem and xylem (the vascular cambium) is cyclically stretched at night and compressed during the day. In addition, it should be noted that the more swollen the phloem (e.g., early spring in temperate climates) and the stiffer the secondary xylem (e.g., latewood), the greater the tension generated between the xylem and phloem. As the dial cycle is a universal phenomenon, a process of diurnal strain generation was indicated as the most likely mechanism responsible for the radial growth of woody plants.

3.2. Diurnal Strains of Plant Organs and Their Importance as a Source of Mechanical Force in Trees

The phenomenon of the diurnal strains of plant organs [136,138–144] has been described over the last hundred years. However, it has never been directly linked to the growth of the vascular cambium or considered in the context of an explanation for the mechanism of the secondary growth of trees. This does not mean that attempts have not been made to derive the magnitude of daily tree growth from such measurements [145–147]. Furthermore, an interesting study concerning the measurements of seven species with dendrometers has recently indicated the nocturnal radial growth of trees [148].

However, it is worth looking at the course of the whole process. During the day (Figure 4B), under the impact of the diurnal decrease in water potential on the tracheary elements of plants, there is a decrease in turgor in living cells, followed by a shrinkage of the cells and tissues. When the stomata close at night [149] and the water potential in the tracheary elements increases, the living cells re-hydrate, which causes the tissues and whole organs to swell (Figure 4A) [134]. The plant cells and tissues adapt to both stresses: the daytime osmotic stress and the nighttime mechanical stress.

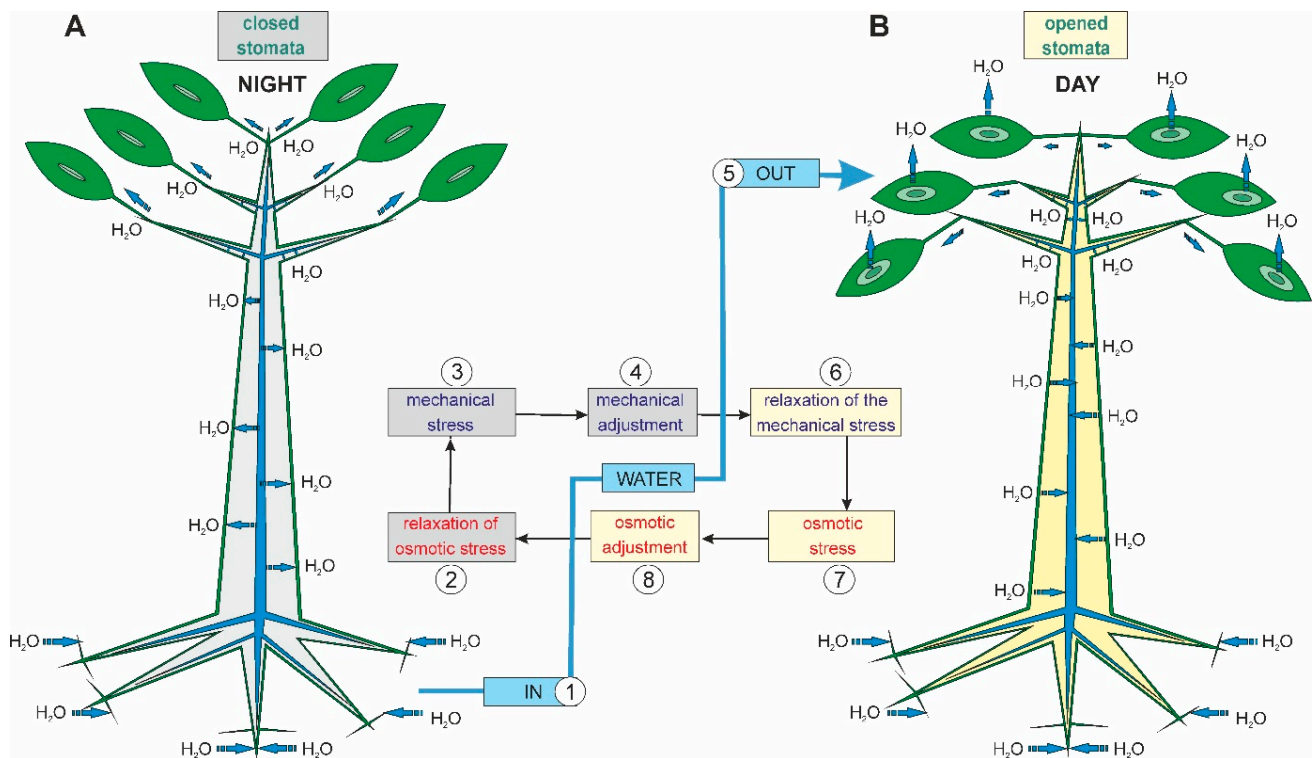


Figure 4. Proposed scheme showing the radial direction of water flow at night, when the stomata are closed (A), and during the day, when the stomata are opened (B). During the day (B), the sources of water used in transpiration are both the apoplast and symplast (mainly phloem) and the external environment (mainly soil). Transpiration (5), due to the lateral transport of water from the phloem to the xylem, leads to a relaxation of mechanical stress (6) and an increase in osmotic stress (7), which triggers a process of adaptation to osmotic stress (8). At night (A), after the stomata close, water taken up from the environment (1) is redirected to living cells, which have low water potential as a result of the daytime adaptation to water stress. Increase in tissue hydration results in the relaxation of osmotic stress (2) and the generation of mechanical stress (3). Elastic and plastic deformation of the cell walls of the phloem, the vascular cambium, and the xylem is an adaptive response to mechanical stress (4) generated during the night.

Living cells and tissues with a high proportion of living cells, including the parenchyma and phloem, are primarily subjected to these strains. In physiological studies, the diurnal strains of plant tissues are discussed in various contexts, but the contexts are mainly related to the diagnosis of the water status of the plant [144,150–152]; water transport [153–155]; transpiration rate [156]; wood morphogenesis [157,158]; sugar transport in the phloem [159,160]; embolism repair [161,162]; estimation of transpiration [156,163]; establishment of irrigation scheduling [164–166]; detection of the effects of pathogens on plant water status [167], etc.

4. Vascular Cambium as an Adaptive Tissue to Mechanical Stresses

4.1. Assumptions and Simplifications Used in the Osmo-Mechanical Hypothesis

As mentioned in the introduction, trees are among the most complex living systems and are subject to multi-level regulation. The hypothesis represents an element of the secondary growth mechanism of trees related to the radial expansion of the vascular cambium. This hypothesis focuses on describing the diurnal performance of the phloem, xylem, and vascular cambium in broadleaved trees, assuming an equinox in the full growing season. For the sake of simplicity, it can be assumed that this occurs in the equatorial zone and thus without any distinct seasonality. In this hypothesis, a description of the effect of the phloem–periderm interaction on phellogen was deliberately not included. It was considered

that this would overcomplicate the basic description of the growth of the vascular cambium. The osmo-mechanical hypothesis of the radial growth of the vascular cambium presented in this paper describes one of the many very complex processes involved in the secondary growth of trees. It is important to point out that the model presented in this article is as simple as possible, while maintaining its full factual correctness for the assumptions made. It therefore provides a starting point for explaining the radial growth-integrated processes and events of the vascular cambium, such as:

- The mechanism of xylem and phloem formation;
- The mechanism of early- and latewood formation;
- The mechanism of ring-porous and diffuse-porous wood formation;
- The mechanism of reaction wood formation;
- The mechanism of xylem/phloem differentiation responses to injuries;
- The mechanism of intrusive growth, including the growth of fibre tips, vessel elements, and cambial cell rearrangement.

The above cellular processes and events would require the inclusion of: the difference in the mechanism of phloem swelling between tree species that start radial growth before leaf development (ring-porous species) and those after leaf development (diffuse-porous species); the seasonal cycle; the explanation of the mechanism of formation of spaces between the tangential walls of neighbouring cells; and the explanation of the mechanism of summation and extinction of tensile and compressive stress acting in the radial direction, originating from various sources (diurnal cycle, wind, gravity, landslides, temperature, insect gradations, frost- and drought-induced embolism, wounding, etc.).

It should be emphasised that, in the simplified version presented, the hypothesis correctly describes the behaviour of a single radial row of fusiform cells of the vascular cambium during the diurnal cycle. It is assumed that individual cells grow sympastically and undergo equal periclinal divisions and longitudinal anticlinal divisions. The basis for this hypothesis is provided by studies on the diurnal relationships of the phloem (inner bark) and xylem [138,148,150,152,155,168,169]; the research on the mechanisms of cambial development [27,28,34,37–43]; and the works on the hormonal regulation of vascular cambium growth [53,58].

4.2. *Phloem as a Tensile and Compressive Stress Generator in the Vascular Cambium*

Between osmotic stress and mechanical stress, induced by diurnal and nocturnal water flux through the plant, time-varying patterns of mechanical stress emerge, which may have different developmental significance. The subject of this dial oscillation is primarily the phloem, the inner and outer parts of which behave oppositely during the day and night.

The whole process can be described as a cyclic generation and relaxation of tensile mechanical stress in the radial direction. The process can arbitrarily start with the opening of the stomata (1) at dawn (Figure 5) [170,171]. As a result of the loss of water, the xylem (2) and phloem (3) shrink. As the phloem shrinks to a much greater degree than the xylem [138,172], the vascular cambium, which after the night is stretched radially between the xylem and phloem (20), goes through successive phases of decreasing tensile stress values, first circumferentially (4), then radially (5), until the tensile stress relaxes in this direction (6). Further shrinkage of the phloem results in the compression of its inner part in the radial direction (7). Thus, the cambium (8) and then the xylem (9) is compressed in the radial direction. At the same time, the outer part of the phloem on the periderm side is stretched (10) in this direction. At night, the stomata close (11) [170,171]. The cessation of transpiration results in an increase in water potential in the tracheary system and the rehydration of the xylem. Its rehydration causes a slight swelling (12) [173], followed by a greater swelling of the phloem (13) [172,174]. The vascular cambium located between the xylem and phloem, which was under compression during the day (8), goes through the phase of a decrease in compressive stress value in the radial direction (14). Then an increase in the tension of the xylem in the radial and circumferential directions occurs (15), together with an increase in the tensile stress value of the vascular cambium in the circumferential

direction (16) until the relaxation of the radial compressive stress in vascular cambium (17). Further swelling of the phloem causes its inner part to be in tension in the radial direction (18) and the compression of its outer part on the side of the periderm (19). According to the hypothesis presented here, cambium stretching is generated in the radial direction between the inner part of the phloem and the outer part of the xylem (20).

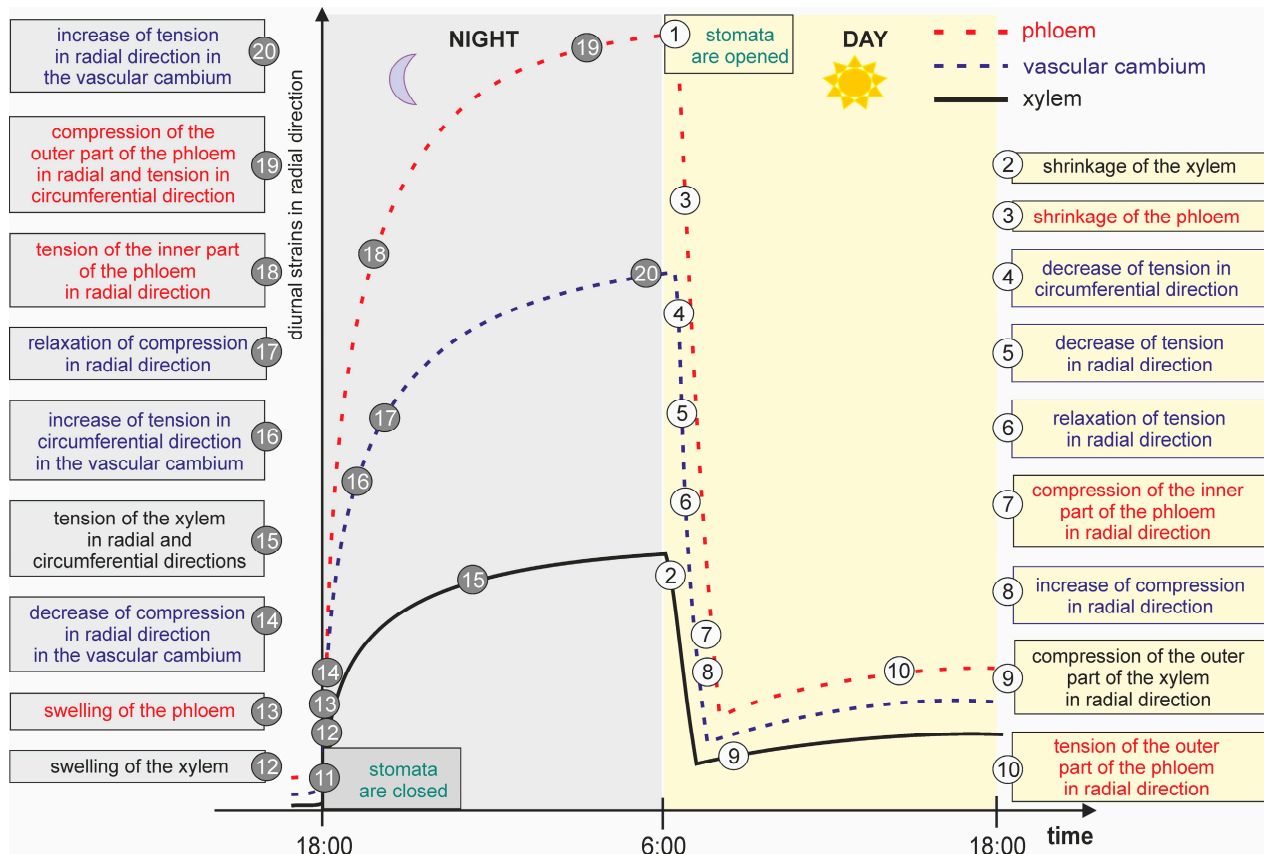


Figure 5. Generation of plant tissue strains in the tree trunk in the radial and circumferential directions due to the opening and closing of stomata in a diurnal rhythm. Tensile strains in the radial direction in the vascular cambium are generated by the swelling of the phloem at night, while compressive strains in the vascular cambium are caused by the shrinking of the phloem during the day (the scheme is an original development of the idea presented by Kojas and Rusin 2011 [134]).

5. The Osmo-Mechanical Hypothesis of Radial Growth of Trees

The osmo-mechanical hypothesis is built on the phenomenon of the diurnal strains of plant organs [134] and is schematically presented in Figures 5 and 6. According to this hypothesis, the radial growth of vascular cambium is an adaptation to diurnal cycles of mechanical stress. The hypothesis describes a mechanism for generating the tensile stress in a radial direction, which is necessary to explain the developmental phenomena occurring in the vascular cambium.

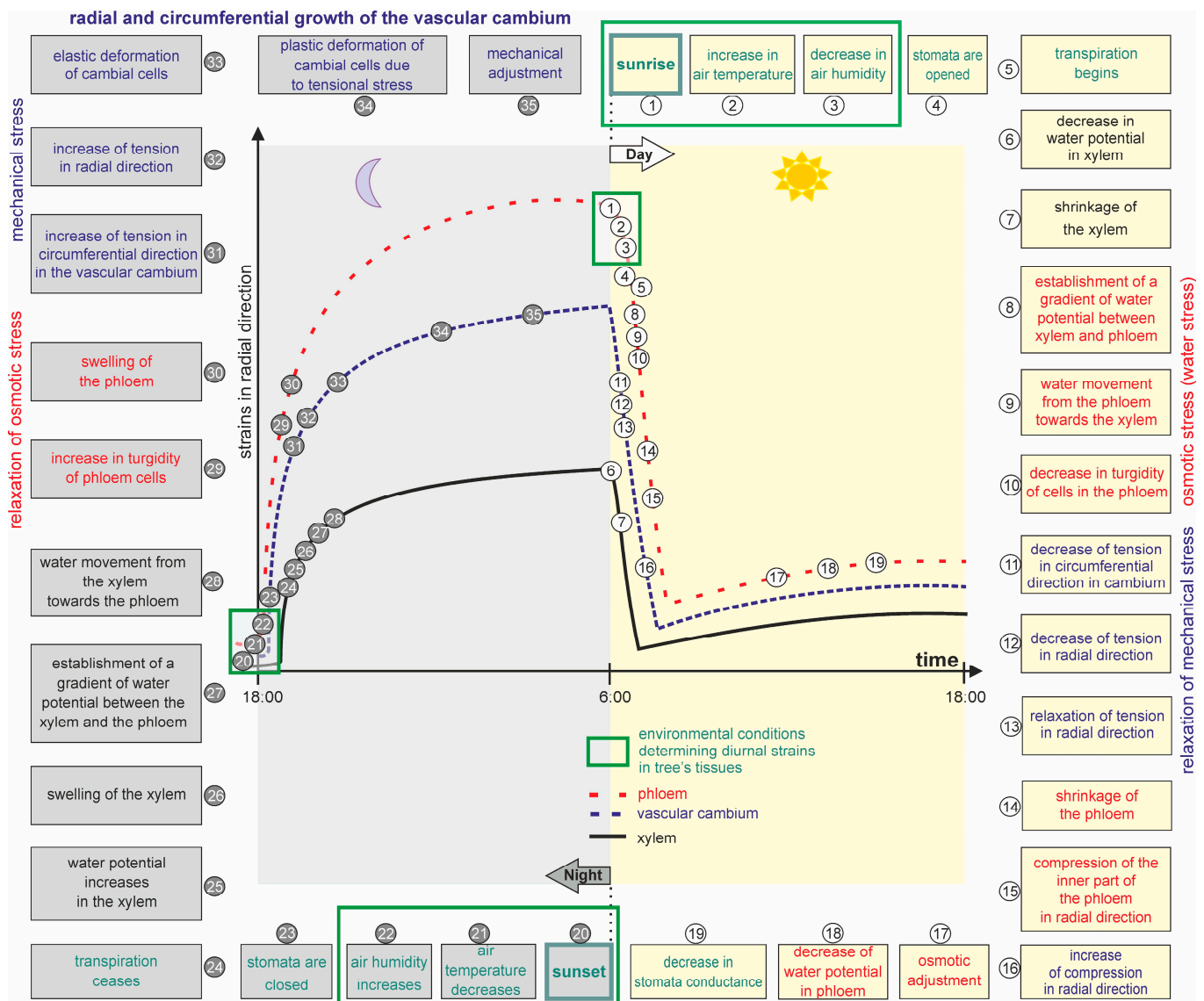


Figure 6. Osmo-mechanical hypothesis of radial growth of broadleaved trees. A single module (numbers 1–35) represents the mechanism of diurnal stress fluctuations in the tree trunk. Numbers 1 to 19 represent daytime processes and events, and numbers 20 to 35 describe nighttime processes and events. The description of the radial growth of trees under equinox conditions serves to simplify the message and thus, in the basic version of the hypothesis, allows us to abstract from the effects of day and night length changes during the growing season on a developmental process. For the sake of simplicity, it is also assumed that in the vascular cambium there are only longitudinal anticlinal divisions and equal periclinal divisions and that the growth is symplastic. See text for detailed description (the scheme is an original development of the idea presented by Kojš and Rusin 2011 [134]).

Although swelling and shrinkage of the phloem can be caused by both a change in its hydration and/or a change in the environmental temperature (e.g., early spring), the osmo-mechanical hypothesis assumes that the transverse flow of water through the vascular cambium is directly responsible for the mechanical stresses resulting from the diurnal swelling and shrinkage of the phloem [138,150,168]. As this phenomenon is cyclic in nature, the choice of starting point for its description appears to be irrelevant. It was arbitrarily assumed that the description would be started at dawn near the equator, when, after a twelve-hour night, a twelve-hour day begins (1; Figure 6). At that time, the sun's

rays reaching the earth cause the temperature to rise (2), resulting in a decrease in relative humidity (3) [175]. Under the influence of light, the stomata open up (4). Through the open stomata, the plants assimilate CO₂. At the same time, transpiration is triggered (5). It is transpiration, according to the hypothesis presented, that is the primary process responsible for daily osmotic stress and the activation of the adaptive response to it. This stress originates in the xylem, where the water potential falls due to transpiration (6) [176]. It is assumed that this creates a difference in water potential that allows the water column to be pulled upwards through the tracheary elements. This causes dehydration of the living and dead xylem cells and a slight shrinkage of the xylem (7) [138]. However, a process that is less discussed is the establishment of a water potential gradient between the xylem and phloem (8) [172,174,177]. The cells of the phloem after the night have a high turgor pressure and therefore a high water potential. This triggers a transverse/radial flow of water from the phloem to the xylem (9) [173,178,179]. It causes a decrease in turgor pressure (10) and thus a shrinkage of the phloem [138,180,181], which contributes to a decrease in the circumferential (11) and radial tensile stress of the vascular cambium (12). Initially, the tensile stress in the radial direction lowers its value. Then, as a result of further shrinkage, the radial tensile stress in the vascular cambium is relaxed (13) and, later during the day, phloem continues to shrink (14) and compression of the inner part of the phloem occurs (15) because the phloem shrinks more than the xylem [138,182]. In this way, the inner part of the phloem begins to compress the vascular cambium (16). This whole process is an adaptation to the decrease in water potential in the xylem and is directly caused by the decrease in turgor pressure in the phloem cells. In addition, osmotic adjustment mechanisms are activated in the living cells [183,184] (17). There is a further reduction in the water potential in the phloem (18) and a movement of water from the phloem to the xylem [172–174]. This process lasts until the xylem and phloem water potentials are equalized. Later, the living cells tend to overshoot this equilibrium [185]. It happens at the organismal level when the conductivity of the stomata is reduced (19) [171]. Thus, at the end of the day, the lateral flow of water from the xylem to the phloem may be observed [174,177,186,187]. The tree prepared for osmotic stress enters the second part of the day–night cycle (20). The environmental conditions change quite drastically, as the lack of sunlight causes a drop in temperature (21), an increase in relative humidity (22) and, in addition, the closure of the stomata (23) [188]. Under these conditions, transpiration decreases almost completely (24). This results in an increase in the water potential in the xylem (25), and it causes its slight swelling (26). However, this does not mean that water movement in the tree stops. As the water potential in the tracheary elements increases, a water potential gradient is established between the xylem and phloem (27) [177]. Water starts to move radially towards the phloem (28) [186,187]. This results in the increased hydration of phloem cells, an increase in turgor pressure (29) [172] and a strong swelling of the phloem (30) [138]. It is this swelling of the phloem, which is ca. threefold greater than the swelling of the xylem [138], which is responsible for the increase in the circumferential (31) and radial (32) tensile stress of the vascular cambium. This initially causes elastic deformation of the cambial cells (33), and if this stress exceeds the threshold for plastic deformation, the cambium cells will grow in a synchronised manner in the radial and circumferential directions (34) (see: [17]). This process can be described as an adaptation of the vascular cambium, and more broadly of the tree trunk, to the diurnal change in the mechanical stress generated by the phloem (35). As the hydration of the living xylem and phloem cells increases and the turgor pressure rises, they become increasingly sensitised to the effects of osmotic stress occurring during the next phase of the diurnal cycle, the daytime.

The oscillation between diurnal osmotic stress and nocturnal mechanical stress causes the vascular cambium to be alternately compressed and stretched in a radial direction. If the tension acting on the vascular cambium exceeds a threshold value, the cambial cells are plastically deformed, i.e., they grow. However, if the value is too low, the deformation will only be temporary and elastic [17]. With a new day, the whole cycle starts again.

As the tensile and compressive forces acting in different parts of the trunk may differ, this will result in different daily growth rates. The factors that can vary the radial growth pattern are all those that interfere with the effects of the diurnal cycle. These may include the unilateral insolation of the trunk [135]; the tree trunk inclination [189]; crown loads; landslides [190]; earthquakes; and wind blowing in a strongly dominant direction [191], but also internal stress patterns related to the growth stresses [157] that interfere with diurnal mechanical stresses. This hypothesis can, however, be used to describe the functioning of smaller radial sectors, such as those enclosed between two phloem rays.

Selected Predictions of the Osmo-Mechanical Hypothesis, or Why Do Trees Grow at Night?

This hypothesis has a fairly fundamental implication in the interpretation of the phenomena associated with the radial growth of trees. Namely, it implies that trees grow at night. However, it is important to highlight that this hypothesis was developed for broadleaved trees. Although it may turn out to be a general hypothesis, it should be remembered that broadleaved trees and coniferous trees are convergent systems and evolutionarily they are not directly related. The evolutionary pathways of gymnosperm and angiosperm trees are separated by tens of millions of years. Conifers evolved extensively under dry and hot climatic conditions from the Late Permian (Loping ca. 250 million years ago) to the Late Triassic (Karnian ca. 234 to 232 million years ago). That was a time of global environmental change and probably significant volcanism. During that time, conifers emerged and diversified significantly on land [192]. Broadleaved trees evolved under tropical climate conditions in the Upper Cretaceous (ca. 100–66 million years ago) [193]. Taking this into account, we are very cautious about concluding that there is a common secondary growth mechanism for broadleaved and coniferous trees. However, we do not exclude this possibility. Although the mechanism of diurnal strains in broadleaved and coniferous trees is similar, many developmental processes in the vascular cambium are different. This applies to the mechanism of reaction wood formation, the absence of vessels and fibres in coniferous trees, or the different mechanisms of wound regeneration, etc. Despite these remarks, on the basis of the hypothesis presented, it can be concluded that broadleaved trees grow at night. This implies that the main part of the cambium deformation, both the elastic and the plastic, occurs at night under the influence of radial tensile stress generated by the phloem (Figure 6). In this view, the cambium, as an adaptive tissue, would be ‘forced’ by the swelling phloem to expand in a radial direction and proportionally in the circumferential direction. The cambium does not, strictly speaking, grow; rather, it is ‘grown’ by the phloem. Thus, the proposed concept shifts the understanding of the radial growth of trees from ‘cambiocentric’ to ‘phloemocentric’. Going further, it can be argued that the cambium is the phloem’s way of relaxing the subcritical mechanical stress that arises between the xylem and phloem, i.e., between tissues with vastly different biomechanical properties. Finally, the most far-reaching interpretation is that the existence of cambium itself, and the process of the radial growth of the vascular cambium, are a side effect of the adaptation of the phloem to the cyclic mechanical stress generated by the swelling and shrinking phloem (this statement does not deny the existence of the cambium, it can be perceived as a proposal to change the status of the cambium, to expand its understanding, and its functional connection to the surrounding tissues).

This hypothesis, when extended by the change in the length of day and night and by seasonal changes, also predicts that the greatest tensile stress will arise between the stiffest xylem and the most strongly swelling phloem. In a temperate climate zone, the stiffest xylem is deposited in late summer/autumn (latewood), while the phloem swells most strongly in spring. When the tensile stress in the radial direction has its seasonal maximum values, the largest parenchyma cells should be deposited in broadleaved trees and the largest vessel elements should form. Within the framework of this hypothesis, it is also possible to understand why, as the vegetative season progresses, the tensile stress in the radial direction is reduced. Thus, the lumina of the parenchymatous cells, fibres, and

vessel elements are reduced, forming latewood or drought dependent intra-seasonal wood density fluctuations.

Further predictions of the hypothesis can be read from Figure 7, which is a transformation of Figure 6 into a hysteresis loop (hysteresis—a phenomenon exhibited by certain physical systems whose properties depend on their preceding history; for more information about hysteresis, see [194]). This scheme allows a closer look at the relationship of the elastic and plastic components of the diurnal strains and indicates that not every deformation of cambium in the radial direction will be transformed into radial growth. Indeed, if the value of the tensile stress generated by the phloem in the radial direction does not reach a threshold value, then such a deformation will only be of an elastic nature (Figure 8). This provides a better explanation of the relationship between various environmental factors, such as temperature, humidity, pressure, day length, and the patterns of daily and annual cambial growth. Thus, it is possible to link the factors affecting transpiration efficiency and transpiration length to the radial swelling and shrinkage of the phloem, as well as the force with which the vascular cambium is stretched in a radial direction, and in turn to radial growth.

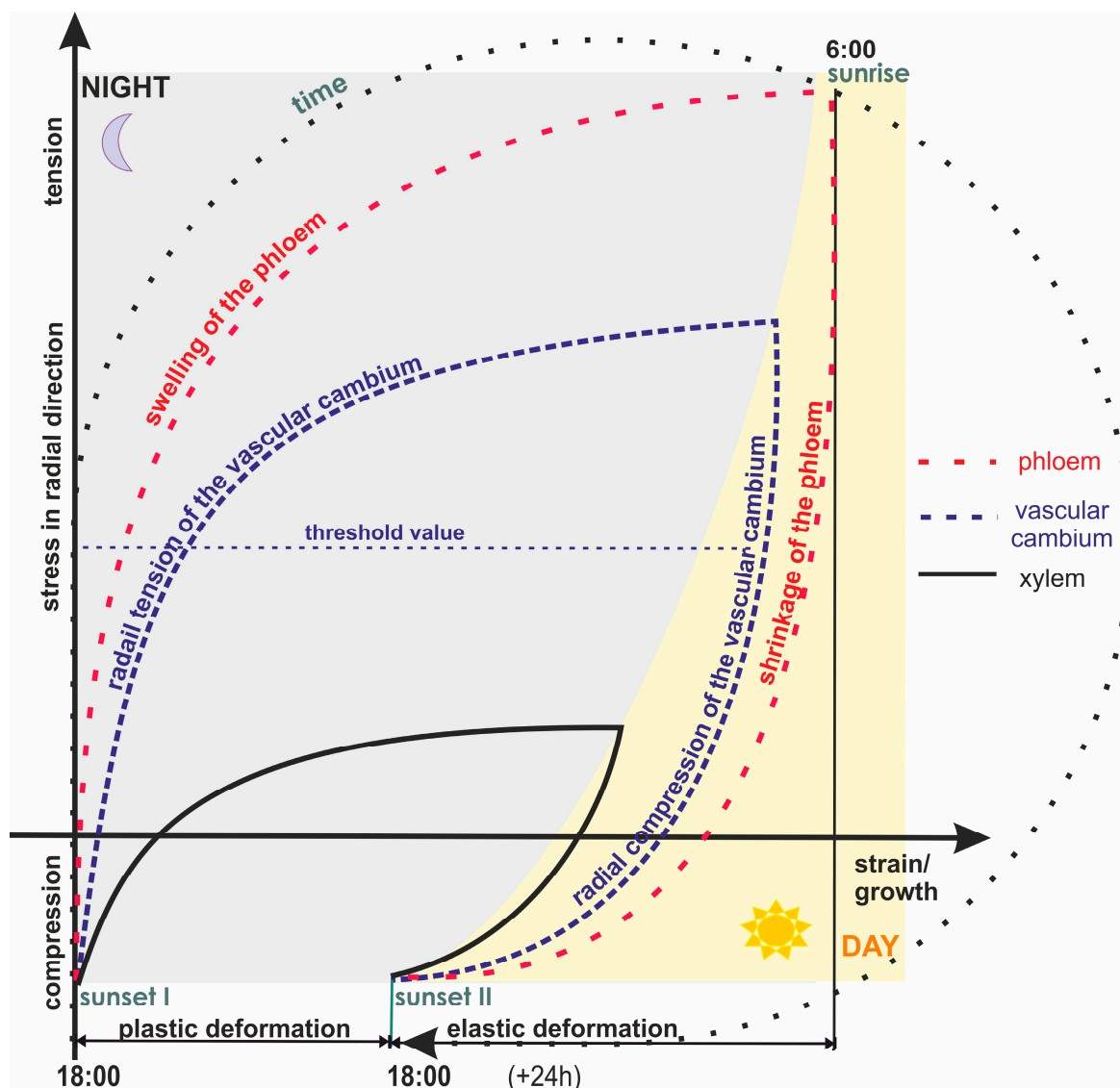


Figure 7. Hysteresis loop with plastic and elastic components illustrating the diurnal deformation of xylem and phloem. The elastic strain is due to the tensile stress of the vascular cambium below the threshold value while the plastic strain is due to the stress above the threshold value.

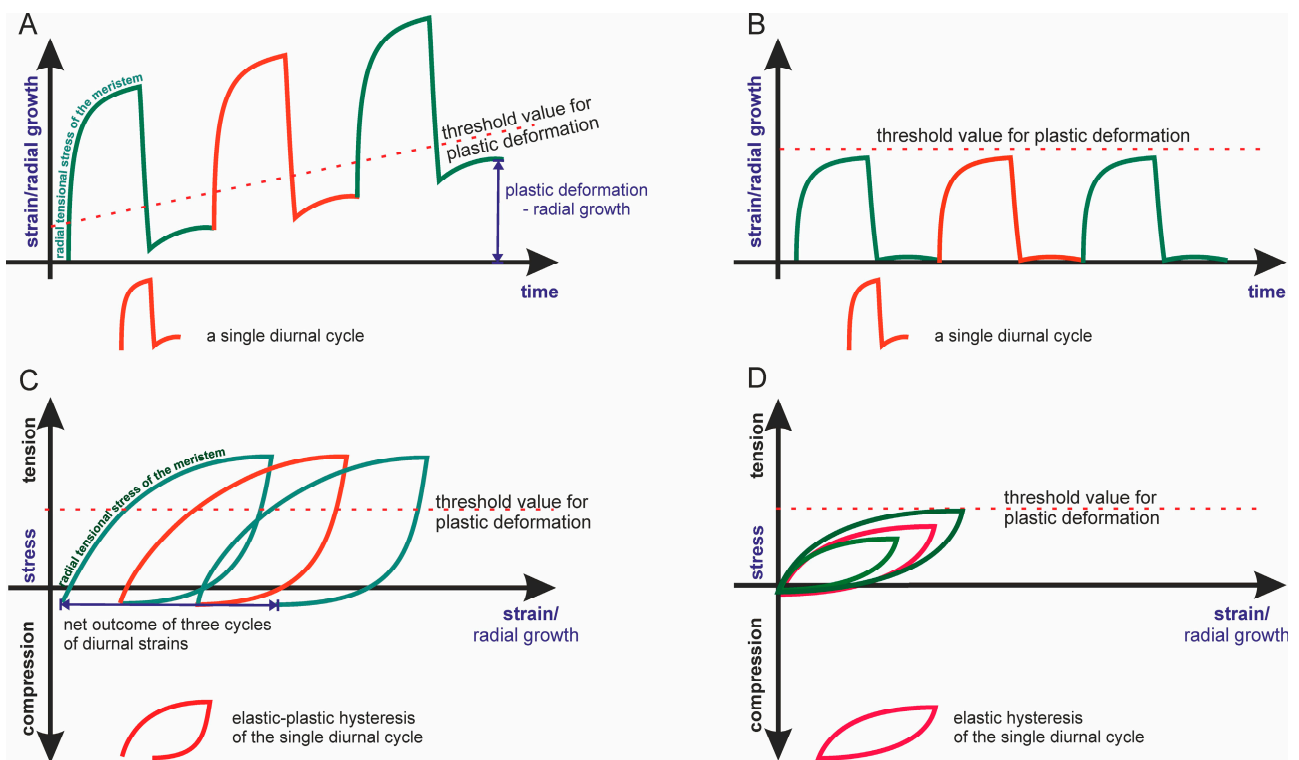


Figure 8. Proposed scheme of diurnal strains of the vascular cambium: elastic–plastic (A,C) and elastic (B,D). Deformation of the cambium due to a force exceeding threshold value is partially irreversible (A), while below threshold value it is fully reversible (B). Elastic–plastic deformation can be visualised using a hysteresis loop, which illustrates how the tissue deforms under tensile stress during successive loading cycles (C). In contrast, for deformations below threshold value, a deformation will be purely elastic (B) and can be visualised using multiple elastic hysteresis loops, which have no plastic component (D). In this case, we will not observe radial growth of the tree. The scheme is made on the basis of general information concerning deformation of elastic–plastic materials, such as the cell wall. Such materials under loading and relaxation cycles undergoes deformation, which has a hysteresis form on the graph (see: Burgert 2006 [195]). Its analysis indicates the potential for such a deformation of the meristematic (elastoplastic) tissue under the influence of the diurnal cycle (compare: Song and Muliana 2019 [194]). The scheme is an original development of the idea of elastoplastic deformation of the vascular cambium under cyclic radial strains and their relaxation by the phloem in a diurnal cycle presented in Figures 6 and 7.

In extreme cases, despite tens or even hundreds of diurnal strain cycles, there may not even be the slightest annual growth because all the diurnal strain cycles will not exceed the threshold value (Figure 8D). Although this may seem counterintuitive, in this case the cambium plays the role of an adaptive tissue. In reality, the pattern of these cycles is diverse, resulting in unique patterns of annual tree increments. Thus, the proposed hypothesis could provide a valuable interpretative tool to precisely link external environmental conditions with the intra-seasonal patterns of the annual increments of trees.

In order to point out the relevant difference between the previous views (Figure 9A) and the osmo-mechanical hypothesis (Figure 9B) of radial growth in trees, it is important to note that the two approaches do not differ as to the expected effect of vascular cambium growth. The main difference is that in the former approach, the predicted internal mechanical conditions in the vascular cambium oscillated around certain values. As the main source of this mechanical stress, the radial growth of the vascular cambium and xylem increment was indicated. Thus, the radial growth in this view is an immanent property of the cambium which can be modified by an internal and/or external environment.

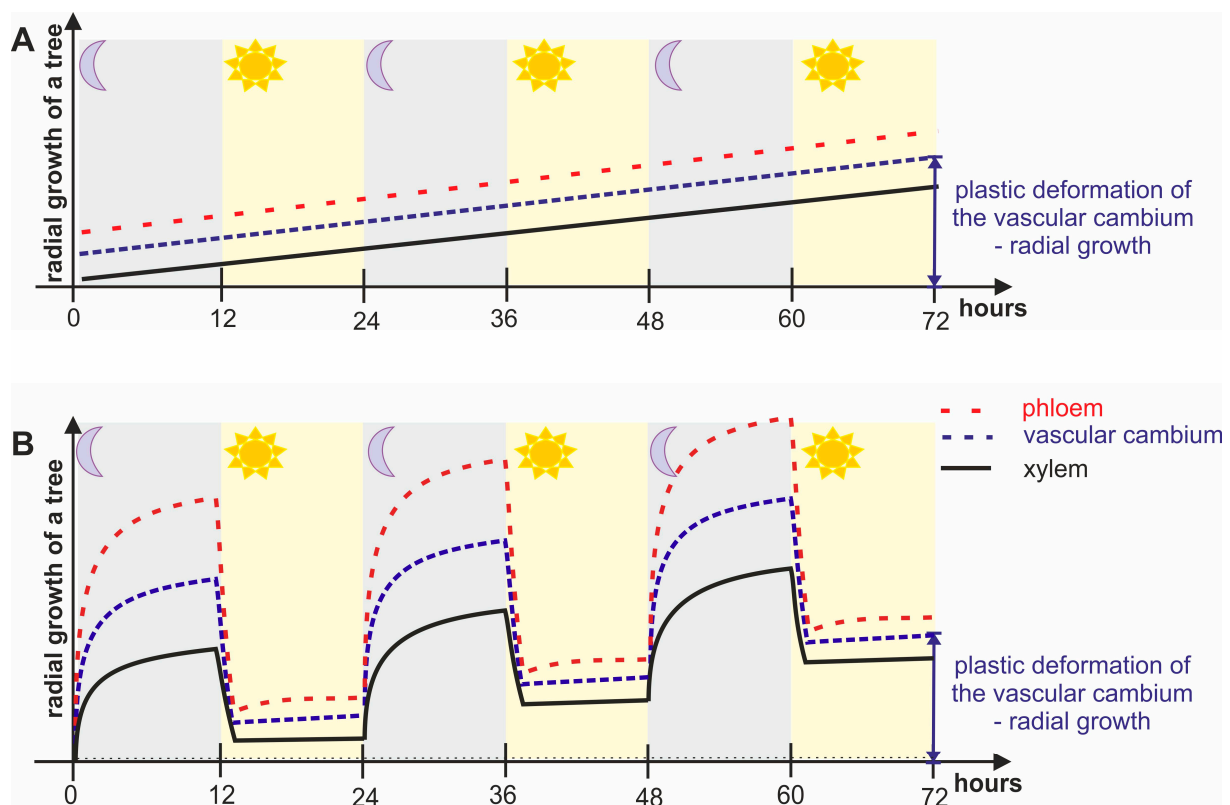


Figure 9. Comparison of two models of radial growth of the vascular cambium. (A) A synthesis of previous views of radial growth in trees, in which radial growth is independent of the dial cycle. (B) Radial growth of the vascular cambium according to the osmo-mechanical hypothesis, which strongly links radial growth to the water status of phloem. In both cases, the predicted outcome of radial growth is the same, but the mechanisms by which it is achieved are different.

In the osmo-mechanical hypothesis, on the other hand, there is a distinct dial cycle that pulls the vascular cambium out of equilibrium and forces it to adapt to external stressors. This reveals the source of both the tensile and compressive stresses acting on the vascular cambium in the radial direction. In this way, the hypothesis is able to explain all the events and processes occurring in the cambium for which the tensile stress acting on the tangential middle lamellae (necessary for intrusive growth) was postulated to occur. Such a possibility, as indicated earlier, is not provided by the previous views on the radial growth of the vascular cambium or, to put it more broadly, the secondary growth of trees. At the same time, this new hypothesis provides an explanation for phenomena that require compressive stress for their occurrence, as it points to a mechanism for the formation of this type of stress as well.

In this context, it is worth highlighting the need for anatomical and developmental studies related to the phenomenon of the radial growth of trees, not only in seasonal cycles, but also in diurnal cycles. In retrospect, it can be said that the rhythm of the laboratory work of tree developmental anatomists (those studying the vascular cambium) determined both the results obtained and their interpretation. It is no particular secret that almost all samples for tree anatomical studies are collected during the day, which reflects the work cycle in the laboratories. If we analyse Figure 9A,B from this perspective, it becomes clear that both hypotheses assume a similar developmental state of the cambium during laboratory work hours. As, on the other hand, the majority of us must have a reason (a theory, a hypothesis) that would justify undertaking such research at night, the previous views on radial growth certainly did not provide such a reason. For us, the rationale for undertaking night work on developmental processes in the cambium was the search for the radial tensile stress in the vascular cambium that was necessary to explain the mechanism of intrusive growth.

However, as it appears, a significant part of the developmental phenomena in the vascular cambium and in the xylem cell differentiation zone occurs at night. It is therefore hoped that the proposed hypothesis will become a starting point for more detailed studies that will allow a more comprehensive explanation of the phenomenon of the radial growth of the vascular cambium and, more broadly, of secondary growth in trees.

6. Research Prospects

The radial growth of trees in the osmo-mechanical hypothesis has been closely linked to external environmental conditions through the length of a day and night in the growing season, temperature, humidity, and transpiration. It can be stated that the growth response is an adaptation of a tree to change in the environmental parameters based upon its genetic potential. Pointing to this relationship and to the mechanism of alternating mechanical stress, which is associated with radial stretching at night and radial compression during the day, may open up new fields of interdisciplinary research comprising biomechanics, developmental wood anatomy, diurnal tree physiology, diurnal tree omics, etc. This hypothesis also makes it possible to reinterpret numerous findings related to the influence of environmental conditions on the development of the vascular cambium. This, in turn, allows the creation of interpretative tools for forestry and environmental, dendroecological, dendroclimatological, and dendrogeomorphological studies, as well as those related to the anatomy, physiology, and developmental biomechanics of trees. The hypothesis proposed in this work also allows for a more accurate design of molecular biology studies because it predicts/indicates which cellular events and processes dominate in a specific part of the day/night within a seasonal cycle.

7. Conclusions

The osmo-mechanical hypothesis:

- Assumes phloem swelling as a source of cyclic stresses that stretch the cambium in the radial direction enabling radial growth;
- Indicates that broadleaved trees grow when the phloem is swollen (mainly at night, when the stomata are closed and transpiration is suppressed);
- Relates climatic phenomena through transpiration, humidity, and temperature to the radial growth of the cambium by influencing the level of mechanical stress;
- Provides a starting point for explanation of the mechanism of the secondary phloem and xylem formation (including earlywood and latewood, reaction wood, ring- and diffuse-porous wood structure formation).

The osmo-mechanical hypothesis allows for an explanation of the phenomena accompanying the radial growth of the vascular cambium, as it points to a mechanism of radial tensile stress acting on the middle lamellae located between the tangential walls of neighbouring cells. The vascular cambium should be studied not only in seasonal cycles, but also in diurnal cycles.

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