

RESEARCH PAPERS

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THE BIOMECHANICAL FORMATION OF TREES

Tree biomechanics and biomechanical tree stability are research problems that have been discussed in world literature for many years. The biomechanical profile formation in trees is an extremely complicated problem and has not been fully clarified to date. It is influenced by many factors, which determine tree growth, tree development, multifunctionality of organs, and anatomical elements in xylem. The phenomenon is further affected by the overlapping of functions and development of numerous interactions between all the systems found in living trees. This paper presents a synthetic description of selected research results, providing insight into the mechanical functioning of trees, from initial theories of mechanical tree formation to the influence of dynamic load on tree stability. Trees are a biological structure that shows high adaptability to external conditions. Thus, the response to a specific environmental stressor, including abiotic and biotic factors, should be considered. Analyses of the biomechanical system in plants need to be considered in a broader context than a selected single load. Due to the complexity of these phenomena and numerous interactions, we need more multidisciplinary research to explain biomechanical mechanism of tree development.

Keywords: tree biomechanics; tree stability; physiological system; mechanical system; Biomechanical model; tree formation; wind and trees

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Introduction

Problems connected with tree stability have been investigated for centuries. In the 17th century Galileo stated that every artificial or natural structure has a scaling boundary, which when exceeded makes its further normal functioning impossible. Studies referring to the structure (architecture) of trees were initiated as early as the 17th century by Euler and Greenhill [James et al. 2006]. Both scientists used statistical analyses to determine the maximal tree height, which when exceeded would result in the self-destruction of these trees [Spatz 2000].

Tree biomechanics were first described by Schwendener [1874], followed by Rasdorsky [1928]. Schwendener [1874] defined plant biomechanics in *The Mechanical Principles of the Anatomy of Monocotyledons* as an important direction of research [Niklas et al. 2006].

Contemporary knowledge on the mechanical formation of trees is incomplete due to the complexity of these phenomena and the overlapping effects of numerous endogenous and exogenous factors in the process of tree formation, which cannot be investigated within a single experimental design. Thus, tree biomechanics is an open field of science where theories and hypotheses have existed for many years now and must be continuously verified.

Theories and models of mechanical tree formation

There are two main directions of tree mechanics research, one connected with the concept proposed by Metzger and the other related to the theory presented by Jaccard [Pilat 1928]. Jaccard proposed a physiological theory founded on the architecture (mainly hydraulic architecture) of plants, which serve the conducting functions. According to Jaccard, the growth of woody plants in diameter and height are related to the hydraulic conductivity of the stem, which is limited primarily by its height and crown size. In turn, the latter is characterized by variable efficiency, which may affect changes in the relationship between its size and hydraulically conductive area [Jelonek et al. 2008]. In contrast, Metzger was a supporter of the mechanical theory, which assumes that in the growing tree resistance to the action of external forces is optimized thanks to the maintenance of an appropriate stem cross-section area and tree height [Jelonek 2013].

The theory proposed by Metzger stems from the concept of Schwendener, which first wanted to determine how ideas developed by engineering sciences might be applied in the understanding of functional anatomy and morphology of plants.

The aspect of the biomechanical stability of trees and the potential to estimate its damage and stems from the previously formulated hypotheses on the adaptation growth of trees, which is connected with the occurrence of growth stresses and plant response to the effect of mechanical stress [Metzger 1893;

Ylinen 1952; McMahon and Kronauer 1976; Wilson and Archer 1979; King 1986; Mattheck 1990, 1991; Niklas 1992].

Based on the knowledge available at that time, Ylinen [1952] provided a relatively accurate presentation of tree biomechanics. This was the first attempt at describing the biomechanical systems of trees and the relationships between the physiological and mechanical systems, which is called the theory of mechanical tree formation. Ylinen described several factors, *i.e.*, the tree crown area and form, bending strength of wood, variation in bending strength, modulus of elasticity of standing timber, weight of the stem and crown, and size of the root system.

With increased knowledge on tree formation, new models describe trees in terms of their mechanics. The first, simple biomechanical model of a tree, including the wood structure, was developed by Euler, followed by Greenhill [1881]. This model considered a tree as a gradually tapering pole made from a homogeneous material (fig. 1.) This model includes only three variables, *i.e.*, the length of the stem (x), its crosswise tilt (y), and weight (w) as shown in figure 1.

The next relatively simple model of a tree is a sum of two independent weights, *i.e.*, that of the aboveground part and that of the root system, connected with an elastic column (the stem). This model is a series of n logs, where branches forming the tree crown are clustered, as shown in figure 2 [Guitard and Castera 1995; James et al. 2006]. In turn, Baker [1995] presented a basic mechanical model of a tree as a system of two weights, *i.e.*, the weight of the crown together with the root system, which was connected with an elastic stem at a length equal to the distance from the ground surface to the center of gravity of the plant (fig. 2b). This mechanical model included as many as six variables. The considered parameters included the wind force, crown weight, inertia of the crown, as expressed by Eqs. 1, 2, and 3, respectively,

$$d^1 Y : dt^1 \quad (1)$$

$$EI \, d^2 y : dx^2 \quad (2)$$

$$H \, d^2 (dy : dx) : dt^2 \quad (3)$$

where Y denotes transverse displacement of the crown and the bending moment in the stem, E is the Young's

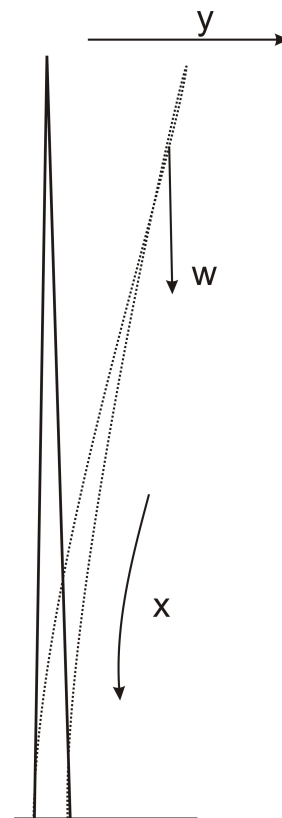


Fig. 1. Simple tree model from Greenhill [1881], where x is the length of the stem, y is the crosswise tilt, and w is the weight [re-drawn from the data of Spatz [2000]

modulus, I is the moment of inertia of the trunk/stem, EI is defined as stiffness of the trunk/stem, $dy:dx$ is the drag torque of the root system k and inertia of the root ball, and H is the moment of inertia of the root system mass.

Changes in the approach to tree biomechanics were introduced by Sanderson et al. [1999], who proposed a dynamic model composed of a conical trunk and a cylindrical crown (fig. 2c).

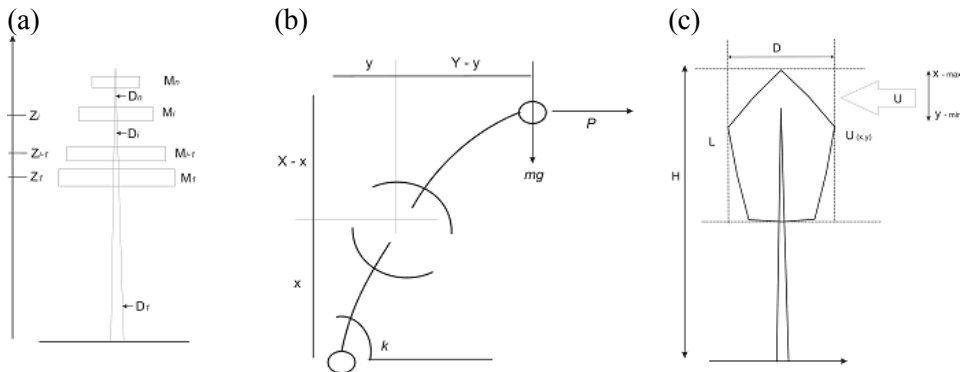


Fig. 2. Simplified tree mechanical models: (a) according to James et al. [2006] redrawn from the data after Guitard and Castera [1995], n – logs, i – number of elements, Z – height, M – weight, D – diameter, (b) mechanical tree model redrawn from the data of Baker [1995] P – changes in tree loading by the wind, mg – weight of crown, Y – instantaneous displacement of the crown mass, x – stem height, at which displacement by the y value is recorded, y – horizontal stem displacement, k – torque of the root ball mass, (c) geometric tree model redrawn from the data of Saunderson et al. [1999], $U(x,y)$ – load by a wind, H – tree height, L – crown length, D – crown diameter

Concepts referring to mechanical tree formation

Plant tissues are more complex than most engineering structures and as a result their mechanical properties are frequently difficult to definitely measure, interpret, or predict [Atkins and Mai 1985; Vincent 1990; Niklas 1992; Niklas 1999; Spatz et al. 1999; Plomion et al. 2001; Vogel 2003; Sanson 2006]. The natural variation of traits and properties of xylem is connected with the effect of genotypes, environmental factors, and anthropogenic factors [Wodzicki 2001]. According to Persson et al. [1995], genetic variability of trees determines their considerable potential, which as a result of the overlapping genetic factors and environmental conditions leads to the formation of phenotypes, frequently characterized by traits and properties, which aim is to enhance their resistance to stress (including mechanical stress).

The effect of genetic factors on the modification of xylem quality has been confirmed by Prescher and Ståhl [1986], Persson et al. [1995], Allona et al. [1998], Fujimoto et al. [2006], and Kumar et al. [2006]. In turn, environmental

effects like the climate, site, social class of tree position in the stand, and management operations are described by Persson et al. [1995], Kellomäki et al. [1999], Wiemann and Williamson [2002], Mäkinen and Isomäki [2004], Riesco Muñoz et al. [2008], Jelonek et al. [2009] and Tomczak et al. [2009].

The xylem, to a varying degree, is optimized during tree growth in terms of served functions and strategies facilitating tree survival. It is affected by the heterogeneity of the xylem, reflected in the complex chemical composition and species-specific anatomical structure, in turn determining physical and mechanical properties of wood [Barnett and Ironimidis 2003]. Even within one species, considerable differences may be observed in its tree traits and wood properties, *i.e.*, depending on the geographical location [Fabijanowski 1961], tree origin/provenances [Szaban et al. 2014], site conditions [Pazdrowski and Sława-Neyman 1996, 1997], and age or social class of the tree position in the stand [Pazdrowski and Sława-Neyman 1993; Fabisiak 2005].

A primary mechanism protecting a tree against stress resulting from dynamic loading is connected with the maintenance of an adequate stem stiffness. A key role is played here by the proportions between the height and stem diameter, and appropriate allocation of biomass [Kim 2000], which shows high variability and sensitivity on various factors [Poorter et al. 2015; Mensah et al. 2016]. Thus, the physiological system of a plant is closely related with biomechanical requirements consisting in the adequate distribution of weight at a proper scale of anatomical elements [Schniewind 1962]. All of these factors above provide insight into the importance of the functional and ecological complexity of biomechanical systems found in trees.

As reported by Spatz and Bruechert [2000], the growth of woody plants is to a considerable degree determined by certain limitations concerning photosynthesis and water transport. When physiological limitations are not exceeded, the size and shape of a tree are subjected to limitations imposed by the biomechanical system of the plant, which is the primary factor determining the architecture of self-supporting plants and their maximal size. This system is optimized so that at every stage of its life a tree is capable of transferring different physical loads, both static and dynamic. At the same time, structural requirements concerning its architecture and proportions between the tree size, properties, and functions of xylem increase with the progressing growth of woody plants [James et al. 2006].

The mechanical structure of a plant is important for its development and survival. The assimilating organ has to be distributed so that it may effectively compete for light. The assimilating organ is supported by the trunk and branches. The transport system has to be able to withstand the pressure of the column of liquid. The trunk and branches have to withstand static loading from the crown weight and dynamic loading, imposed by the wind. Adaptation changes affecting the structure of xylem may be attained at the expense of other functions, such as accumulation of carbon or propagation. At the same time, resistance to

mechanical stress guarantees survival in a particular abiotic environment [Givnish 1986]. Thus, plants have to create an "intelligent" system of mutual relations. As a consequence, the mechanical structure of a tree, starting from the cellular level up to the architecture of the whole plant, is the basis for its survival and is probably connected with a strong selective pressure.

Boundaries of structural resistance are reached when the maximum induced bending moment is greater than the breakdown torque. The volume of maximum structural loads depends on structural parameters (geometry of the cross-section) and properties of the material (the modulus of elasticity or critical compressive stresses leading to material failure when exceeded) [Spatz and Bruechert 2000]. As a consequence, tree biomechanics is rather difficult to describe, since we need to consider the complicated adaptation growth of trees as a response to mechanical stimuli. This phenomenon was confirmed qualitatively, but to date neither mechanical receptors nor the transduction chain signal have been identified [Telewski 1995; Wood 1995]. Thus, we are faced with the problem of the nature of the mechanical signal controlling secondary growth, which may be the adaptation growth of a plant. Metzger [1893] formulated a hypothesis of (uncertain) steady stresses. However, it is difficult to determine the effect of slight compressive stresses caused by the tree's weight on induction of signals for adaptation growth, particularly in view of large growth stresses [Gril et al. 1997]. Although the hypothesis proposed by Metzger [1893] intuitively seems to be correct, there are many questions to be answered. First, what is the structure of mechanoreceptors and where are they located? What mechanical signals are identified and how are they integrated in time? What is the transduction chain for the signal leading to adaptation growth of a tree? These questions have been proposed by Telewski and Pruyn [1998].

Another significant factor affecting the biomechanical system of plants is connected with relationships between environmental stress and mechanical properties. They may be specific and direct, guaranteeing plant survival, like the response of a tree to the action of strong wind by strengthening the structure of the xylem. Certain traits and adaptations may provide protection against many forms of stress. In both cases, the adaptation values referring to mechanical characteristics may vary between sites. Thus, it would be best to consider them in a broader context of the tree growth environment, and not only a specific stress.

Plants may also exhibit the above mentioned, considerable phenotypic plasticity of mechanical systems, consequently facilitating adaptation to the variable environment. However, it has not been clarified yet whether changes at the mechanical level have an adaptation background or whether they are a consequence of physiological changes caused by stress. Mechanical properties play a significant role in the plant survival strategy, the organization of the ecosystem and its functioning, such as trophic variation. Moreover, plants exhibit a considerable ability for phenotypic regulation of mechanical traits,

potentially facilitating phenotypic plasticity both in time and space [Read and Stokes 2006]. Although there are certain trends in biomechanical changes of woody plants along habitat gradients, it may be assumed that many variants of mechanical adaptations may occur in every habitat [Niklas 1997; Press 1999]. Some of these changes may be far from optimal due to limitations developed in the course of phylogenesis. Moreover, a variable stress caused by changes in the habitat during tree growth may contribute to the development of a variable mechanical profile of a plant within the same species [Niklas 1999]. Schenk and Jackson [2002] stated that biomechanical traits undergo dynamic changes within a species and change within the lifetime of a single specimen. As it was reported by those authors, it results mainly from the fact that plants need to develop different mechanical strategies, which simultaneously modifies their internal structure and external architecture.

Thus, biomechanical traits are highly characteristic of the environmental situation in which a given species is found and they exhibit a certain plasticity. However, some models may be observed throughout the plant kingdom. An example in this respect may be provided by the theory of allometry to explain the evolutionary change in plant size [Niklas 1994; West et al. 1999]. The latest models describing wood structure in trees suggest that in the course of evolution, plants developed a tapering structure of conducting elements, narrower at the circumference, which should minimize the cost of water transport from roots to leaves [West et al. 1999; McCulloh et al. 2003; Sperry et al. 2006]. However, these models do not consider multifunctionality of anatomical elements and their mechanical role in wood. Studies are being conducted on the evolution of xylem to provide insight into several compromises found in plants, depending on their hydraulic and mechanical requirements [Vogel 2003; Anfodillo et al. 2006]. Niklas and Spatz [2006] when considering the application of allometric theories in tree biomechanics stated that in the aspect of plant growth and survival none of the functions served by individual systems has any priority over others and their efficiencies have to be optimized in the overall energy balance.

Wood formation and functioning of trees subjected to dynamic loads

Wind has a significant effect on the development of forest ecosystems, and it is one of the factors determining the formation of trees, landscapes, and forest sites [Mitchell 2013]. It modifies characteristics of forest stands, significantly affects their composition and structure, and somewhat determines growth conditions [Ennos 1997; Jansons et al. 2014]. To a considerable extent, the susceptibility of trees and whole stands to wind damage depends on individual morphological traits of trees; in forest communities, it also depends on their structure. Many sources have described the effect of wind on forest ecosystems, including problems connected with the effect of wind on stem morphology and mechanics [England et al. 2000; Spatz and Bruechert 2000; Peltola 2006; Jelonek et al.

2013]. Dynamic loads may cause several reactions of trees, including physiological response, which at the stage of xylem formation leads to adaptation changes in its structure and properties [Wade and Hewson 1979].

Mechanical loads that effect the development, morphology, and structural traits of woody plants are the foundation for the concept of adaptation growth of trees, presented in the abovementioned publication by Schwendener [1874] and adapted to the requirements of forestry by Metzger [1893]. This concept was verified by Morgan and Cannell [1994], who stated that the development of tree formation (height, diameter) is dependent on stressors which a stem/trunk has to transmit, and it is optimized during the lifespan of the tree. Alm eras and Fournier [2009] stressed the role of gravity in the formation of xylem and tree formation. They introduced the concept of gravitropic correction, which is connected with long-term mechanical stability of trees. They stated that an increase in tree diameter (increment in diameter) equalizes disturbances caused by an increase in its structural load, while biomechanical limitations of trees are connected with an interaction between growth and gravity may be expressed as a function of basic morphological, anatomical characteristics, and wood properties. The above was formulated and included in the uniform theory of stress, stating that in the average range of mechanical loads stresses are distributed uniformly along the vertical axis of the stem, whereas under extreme distribution of stresses it will be non-uniform and will depend, among other things, on changes in the distribution of weight of the stem, the crown, and external loads [Mattheck 1991; Gardiner 1992; Wood 1995; Nyk anen et al. 1997; De Langre 2008].

Studies conducted on stability of trees and stands indicate that to a considerable degree it is dependent on the volume of external load and stand structure, in which a particularly important role is played by the species composition, tree height, and diameter at breast height, crown area, root depth and spread, stocking, and soil type [Coutts 1986; Kerzenmacher and Gardiner 1998; Peltola et al. 2000; Hale et al. 2004; Scott and Mitchell 2005; Peltola 2006; Jonsons et al. 2014]. James et al. [2006] stated that the stability of a single tree exposed to a dynamic load is influenced by its size, shape, and structure. Such understood stability is closely related with the process of growth, which to a considerable extent is determined by physiological limitations, particularly those connected with photosynthesis, water transport, and limitations of size and shape imposed by biomechanical systems [Spatz and Bruechert 2000]. For this reason, tree structure is designed to transmit increasing loads during tree growth. Optimization of growth that leads to the formation of trees, is connected to the static loads of trees, described above and resulting from the weight of the tree trunk and the crown, and dynamic loads, imposed by wind and causing the greatest mechanical stress in circumferential parts of the trunk [Mitchell 2013].

Along with the biometrics of trees changing in time (with age) and an increased risk of wind damage, the ultrastructure and properties of xylem are

naturally modified at all levels of its structure. As a result, the xylem in the trunk of a single tree is highly heterogeneous and exhibits variability both in the radial and axial planes of the trunk [Jelonek 2013]. In terms of mechanics, these changes may be a major determinant of wind resistance in trees.

Numerous studies have been conducted to provide insight into the behavior of trees under dynamic loading [Peltola and Kellomäki 1993; Peltola et al. 1993; England et al. 2000]. Moore and Maguire [2004, 2005] when analyzing the effect of crown size on wind-induced vibrations of trees stated that the vibration dampening effect is reduced with an increase in crown reduction and it is strongly connected with the ratio of DBH (tree diameter at breast height) to the squared height. Mayer [1987] presented an opinion that in order to reduce the risk of trees damage by wind, the effect of wind on tree sways needs to be reduced and the enhancement of their characteristic swaying frequency is required. In this case wind force takes lower values owing to the narrow energy transfer band. As it was reported by Milne [1991], dampening of tree sways is affected by the interference of branches of neighboring trees, aerodynamics of foliage, and vibration dampening by the trunk and the root system. In turn, Brüchert and Gardiner [2006] reported variation in tree formation and xylem properties depending on exposure of trees to wind. The frequency of tree swaying and dampening increases with an increase in the distance from the edge of the stand, where the tree exposure to wind is greatest. The most exposed trees, like those grown at stand edges, were generally characterized by lesser height and greater stem tapering in comparison to trees growing within the stand. These trees exhibit a greater stem rigidity at its base and its greater elasticity within the crown. In contrast, trees growing within the zone located away from the stand edge showed a greater trunk tapering, compensated by the increase in Young's modulus. Similar conclusions were reached in their studies on the effect of wind on biomechanics of Scots pine in Poland [Tomczak et al. 2014]. They observed morphological changes in trees depending on wind loading of trees in the stand. In the stand edge zone, exposed to the greatest wind loading, trees were on average over 10% lower and 3% thinner than trees growing within the stand. In contrast, their crowns were located relatively lower, which resulted in a lowering of the center of gravity and increased tree statics [Tomczak et al. 2014].

The effect of wind and snow on the functioning of forest ecosystems is considered to be important due to its economic consequences. Dependencies between the architecture of trees and their biomechanics have also been investigated in terms of the risk of wind or snow damage to trees [Baker 1995; Kellomäki and Peltola 1999; Peltola 2006]. Literature sources on the subject have devoted relatively much attention to problems connected with the prediction of stand damage caused by strong winds. Baker [1995] and Saunderson et al. [1999] proposed mathematical models, which describe the behavior of trees exposed to dynamic loading. Baker [1995] in his model stressed the importance of natural vibration frequency and wind velocity as the

basic parameter determining stability of woody plants. Studies on critical wind velocity in forecasting tree damage were conducted by England et al. [2000]. In turn, Peltola et al. [1997] presented a model of critical tree loading by the wind and snow pressure. Kerzenmacher and Gardiner [1998] developed a dynamic model of movement in spruce depending on wind velocity, while Valinger and Fridman [1997] described the probability of snow and wind damage in pine based on characteristics of trees. Cucchi and Bert [2003] considered the crown size and trunk diameter to be the most important traits of trees from the point of view of their stability. Those researchers observed lesser wind damage in stands, in which crown length and trunk circumferences are uniform. Damaged trees typically had thinner trunks, relatively shorter crowns, and higher slenderness to trees ratio, which did not suffer wind damage. Similar conclusions were drawn by Petty and Worrell [1981] when investigating the effect of slenderness on tree stability. In their opinion, the greatest stability is found in trees growing at lesser stocking, which are characterized by trunk tapering and a relatively low height.

Numerous studies have been conducted to provide insight into the behavior of trees under dynamic loading [Peltola and Kellomäki 1993; Peltola et al. 1993, England et al. 2000]. Mayer [1985] reported that tree stability under dynamic loading is influenced by three elements, the bending moment induced by the force of wind (Eqs. 4), the moment induced by the weight of the crown (Eqs. 5), and the moment induced by the weight of the trunk (Eqs. 6), where K_1 is the force of wind, K_2 is the weight of the crown, K_3 is the weight of the trunk, X is sway and h_k is the height of the crown center of gravity (fig. 3). In turn, Peltola and Kellomäki [1993] in the mechanical model estimating stability of pine (fig. 4), which form was expressed in the equation 7, included three variables in time, i.e. the force of wind ($F_1(z)$) and the coefficient resulting from gravity and aboveground biomass of a tree ($F_2(z)$) and horizontal sway of a tree ($x(z)$). In the presented model variable $F_1(z)$ was expressed in the equation 8, where: $U(z)$ is the velocity of wind, $A(z)$ is the forecasted area of the tree loaded by wind, C_p is the coefficient of sway and p is air density. In turn, variable $F_2(z)$ was determined based on the product (Eqs 9.), where $M(z)$ is the weight of the crown and the weight of the trunk, while g is the gravitational constant.

$$(MW=K_1*hk) \quad (4)$$

$$(MB=K_2*X) \quad (5)$$

$$(MS=K_3*X_1) \quad (6)$$

$$T(z)=F_1(z)*z+F_2*x(z), \quad (7)$$

$$0.5*C_d*p*A(z)*U(z)^2, \quad (8)$$

$$M(z)*g \quad (9)$$

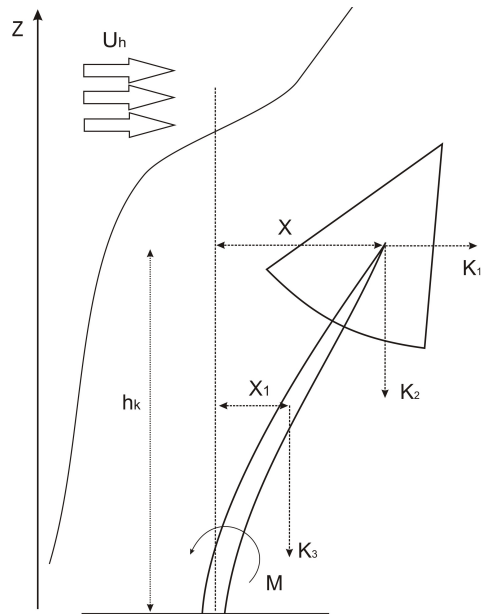


Fig. 3. The stability of trees in relation to dynamic loads caused by wind [redrawn from the data of Meyer 1985]

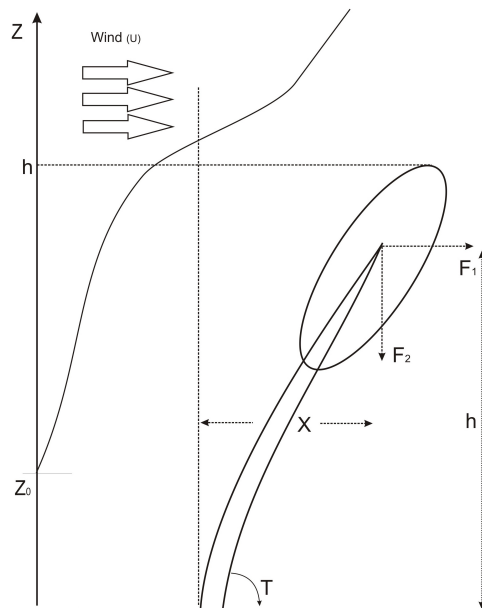


Fig. 4. Forces affecting a tree. F_1 wind, F_2 gravity, T total turning moment at the base of the stem [redrawn from the data of Peltola and Kellomäki 1993]

Tree biomechanics may be comprehensively understood because the complex analysis of many factors determine their mechanical stability. Fournier-Djimbi and Chanson [1999] presented general principles of mechanical analyses of trees. Those authors stressed that in studies on tree biomechanics we observed many overlapping factors, such as the complex tree geometry (in comparison to ordinary structures), heterogeneity of xylem at different levels, the effect of radial growth. These factors lead to the formation of atypical stresses and deformations resulting from internal physical and chemical phenomena occurring during xylem formation favouring development of primary stress, additionally overlapped with external loads.

Conclusions

1. As it was stated by Read and Stokes [2006], we are only beginning to discover the mechanical structure of plants. Despite significant broadening of our knowledge on the biomechanical functioning of plants, still numerous gaps need to be filled by science, particularly concerning interrelations between the physiological system of trees, their biomechanical system and energy balance of plants. At the same time we have to take into consideration the adaptation growth of plants, which is a response to specific environmental stress, including abiotic and biotic factors as well as nutrient deficits.
2. Depending on environmental factors adaptation growth may considerably vary even within a single species. In a poor habitat benefits resulting from tree resistance to mechanical loads may be greater than in environments with optimal growth conditions for a given species. For this reason analyses of the biomechanical system in plants need to be considered in a broader context than a selected single load. Moreover, woody plants exhibit considerable phenotypic plasticity, facilitating temporal and spatial modification of mechanical characteristics in relation to morphological traits.
3. Many earlier and contemporary studies conducted on wood structure, properties and mechanical functioning of trees have frequently neglected factors determining wood formation or have focused on variation limited to a narrow area. Due to the complexity of these phenomena and numerous interactions, tree biomechanics has not been fully clarified and requires further studies and verification of previously formulated hypotheses.

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