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OPINION PAPER **Open Access**

Beyond the perception of wind only as a meteorological hazard: importance of mechanobiology for biomass allocation, forest ecology and management

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Abstract

Key message Although global changes are expected to intensify the impact of wind as a hazard, recent studies have emphasized the critical role wind plays in tree growth and development. Wind-induced swaying generates strains that the tree perceives, triggering a process known as thigmomorphogenesis. This process alters the tree's growth patterns and wood properties to enhance its mechanical stability. Thus, wind functions not only as a hazard but also as a growth factor, enabling the tree to acclimate to wind loads and reduce its mechanical risk.

Despite the significant role of thigmomorphogenesis in tree growth and carbon allocation, this process remains largely overlooked in forest ecology and management models. We strongly advocate for the integration of wind-induced strain sensing, the primary driver of thigmomorphogenesis, alongside established environmental factors in tree and forest growth models, as well as in instrumented forest stands aimed at studying the effects of environmental factors on tree growth. This crucial step is essential for a comprehensive understanding of forest growth dynamics and for informed decision-making in forest management.

Keywords Thigmomorphogenesis, Tree growth modeling, Wind risk, Biomass allocation, Forest management

1 Introduction

Despite the recent increase in drought and fire-induced tree mortality, wind storms are still responsible for over 40% of the wood biomass loss in European forests (Forzieri et al. 2021) thus largely impacting the wood production industry (Bastit et al. 2024), but also forest ecology (Ennos 1997). This trend is predicted to increase in the context of global change due to both direct and indirect effects (Seidl et al. 2014a; Forzieri et al. 2021). Considerable efforts have been made to understand the impacts of storm in forests at different scales (Gardiner 2021). Specific interest was given to detrimental effect of storms on the forest carbon storage capacity (Lindroth et al. 2009; Seidl et al. 2014a; Reyer et al. 2017). The need to improve tools predicting the risk of forest losses in the context of occurring global changes is therefore of high interest. Forest scientists are also very concerned about the effect of stand thinning increasing the risk of windthrow during strong wind episodes (Valinger and Fridman 2011; Albrecht et al. 2012; Wallentin and Nilsson 2014). Indeed, thinning is a major operation

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in silviculture, and it is now often advised to mitigate drought stress in forest trees by reducing leaf area index and consequently evapotranspiration (Sohn et al. 2016). Besides this risk approach for wood yield and carbon storage in productive forests, ecologists have been also concerned with wind resistance in more complex forests, searching for relevant functional traits (Fournier et al. 2013). They often considered wood density as a proxy for wood mechanical strength and finally resistance of trees to strong winds (Chave et al. 2009), attempting to relate its significance with the pressure of the community disturbances due to wind storms and their effects on tree lifespan.

However, wind does not have only detrimental effect over forests; it also acts as an important environmental signal controlling tree growth (Ennos 1997; Gardiner et al. 2016, 2019), through thigmomorphogenesis (Boyer 1967; Jaffe 1973). In this process, wind-induced mechanical strains in the living tissues are sensed and this sensing controls the activity of plant meristems (Moulia et al. 2015). This drives a preferential carbon allocation to the stem and root radial growth instead of primary growth and affects the stem taper, slenderness, and shape (stouter trees). The importance of thigmomorphogenesis has been clearly demonstrated on artificially bent saplings in a greenhouse (Moulia et al. 2015; Niez et al. 2019) and more recently on bigger trees in real forest condition (Meng et al. 2006; Bonnesoeur et al. 2016; Nicoll et al. 2019; Dongmo Keumo Jiazet et al. 2022a; Defossez et al. 2022) and surprised by its magnitude. Nevertheless, wind-induced strains remain neglected in most experimental studies addressing tree growth, and wind as a growth factor is absent from recent developments of forest growth models, wind risk modeling tools, or broader ecological analyses.

In this opinion paper, we argue that it is now time to include thigmomorphogenesis and wind-induced strain sensing in all these studies, side by side with other environmental factors. This requires an interdisciplinary effort bringing together biomechanists, forest-growth modelers, and experimentalists in forest management and ecology. This opinion paper aims to provide a rationale and common background to foster. To do so, we first review some basics of biomechanics, thereby establishing a framework to analyze the interplay between tree morphology (and growth), wood properties, wind loading, and tree resistance against wind. Then, we highlight recent advances in mechanobiology, the field that studies how cells produce, sense, and respond to mechanical forces, with a focus on the importance of thigmomorphogenesis in forest conditions. We show the high magnitude of its effects and its ubiquity. We then discuss the relevant traits for assessing tree biomechanical performance and their acclimation. We then emphasize the importance of thigmomorphogenesis in tree growth responses to disturbance. Finally, we discuss recent advances and gaps in forest growth and wind risk models and the importance of considering thigmomorphogenesis in these approaches.

1.1 A primer to the biomechanics of wind impact on trees

In the following, we briefly introduce basic concepts used in the mechanical analysis of the impact of wind on trees (a more complete introduction and more details can be found in James et al. 2018; Moore et al. 2018). Indeed, it is a prerequisite for understanding the following. Besides, we believe that the lack of background in biomechanics partly explains why the effects of wind on tree growth have been neglected so far. Let us consider a simplified representation of a tree as a mast firmly anchored in the soil, subjected to the drag of the wind on its foliage (referred to as a cantilever beam in mechanics).

The drag force F_{wind} on the whole crown foliage comes as:

$$F_{wind}(t) = \frac{1}{2}\rho_{air}A_w p_{t\_w} u(t)^2 \tag{1}$$

where ρ_{air} is the density of air, A_w is the streamlined projected area of the tree (crown and stem), u is the wind speed, and t is time. We designed as p_{t_w} the set of parameters that are not easily measurable and therefore often fixed as constant or unity, i.e., the drag coefficient c_d and the shape factor F_w representing the interaction between the wind and crown profiles. Note that the mechanical effect of the wind factor depends on the square of the wind velocity (so that a change from 60 to 80 km/h leads to almost 80% increase in wind drag), but it depends also on the actual tree size and shape. In general, a multiplicative "gust factor" is also included to account for the fact that wind speed peaks during wind gusts; however, we can neglect this for the purposes of this primer.

The wind-induced drag force bends the tree. However, this bending effect involves a mechanical amplification through a lever arm effect. This is modeled by computing the bending moment from wind loads at a given height z in the tree trunk as follows (Fournier et al. 2013; Fig. 1):

$$M_{wind(z,t)} = F_{wind(t)}(H_w - z) = \frac{1}{2}\rho_{air}A_w p_{t\_w}(H_w - z)u(t)^2 \tag{2}$$

where $M_{wind(z,t)}$ is the bending moment from the drag forces applied at the height of the center of the wind drag pressure H_w, z is the position of a given cross section along the stem, and $(H_w - z)$ is the lever arm at the height z (assuming that the trunk stays almost vertical). This formulation is relevant for isolated trees but has also

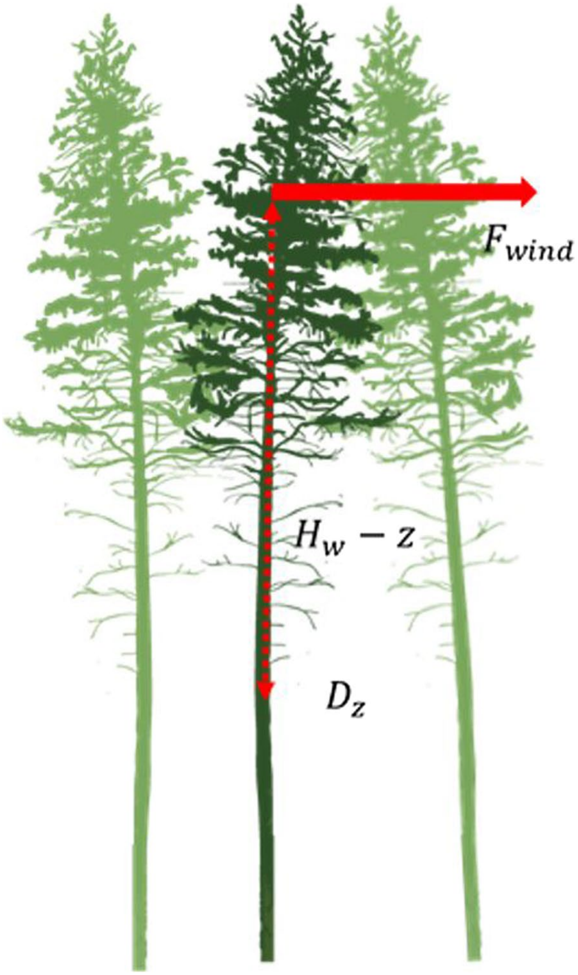

Fig. 1 Representation of the tree of a given diameter D_Z under the drag force F_{wind} where $H_W - z$ is the lever arm at a given height z in the tree

been validated for forest trees and included in wind risk management tools (Gardiner et al. 2008).

Because of this amplification, the bending load increases from the tip to the base of the stem, and varies among trees according to their height. Note that no other ecological factor has its action amplified by the structure of the tree itself (for light, amplification could come from "lense effects" but they are negligible in tree*light interaction at tree and forest scales).

The bending of a beam-like tree (but also branches or roots) involves local stretching or shortening of tissues (living and dead) called strains. Based on the beam theory that describes structures submitted to small deformations, the maximum values of strain are reached at the periphery of the organ and are related to the bending moment and stress as follows:

$$\varepsilon_z = \frac{M_{wind(z)}}{2EI_z} D_z = \frac{16 c_d \rho_{air} A_w F_w (H_w - z) u^2}{\pi E {D_z}^3} \tag{3}$$

and relation between strain and strength is governed by Hooke's law:

$$\varepsilon_z = \frac{\sigma_z}{E} \tag{4}$$

where ε_z is the bending strain, σ_z is the bending strength, E is the modulus of elasticity for the tissue (its elastic stiffness), I_z is the tree cross-section moment inertia (for a circular cross-section with a diameter D, $I = \frac{\pi D^4}{64}$), and D_z the tree diameter at a given tree height. Equation 3 shows that the relation between the strain generated during the wind sways at tree surface and wind speed is strongly modulated by tree size and shape, material stiffness, and tree exposure to wind. Thereby, if we consider for example a couple of trees, one suppressed and one dominant submitted to the same wind speed above the canopy, the strain perceived by each of them will differ.

The proposed framework considers only static loads, without consideration of effects of neighbor trees or roots which is the most common approach. Complete and detailed models of the tree-wind interaction in forest stands exist (Dupont 2016; Yang et al. 2020) and have been used to model wind damage propagation in forests (Dupont et al. 2015). Considering root anchorage, it is in general modeled through allometric relationship between the measured anchorage during pulling tests and the stem biomass or volume proxies (Peltola et al. 2000; Lundstrom et al. 2007). When the level of strain, stress, or tilt angle generated during a wind event exceeds a limit value (wood strain/strength at breakage or anchorage critical tilt angle), the tree breaks or is uprooted. The limit values are used in the wind risk assessment tools for computation of maximum wind speed a given tree is able to withstand without mechanical failure during wind events. However, the wind-induced strain is daily perceived by the cambium, providing the tree with a cue on its current exposure and vulnerability to wind. This triggers a thigmomorphogenetic syndrome that constantly changes these limit values, as well as most of the geometric and mechanical variables involved in Eq. 3 (and in its equivalent for root anchorage).

1.2 Highlighting the ecological importance of thigmomorphogenesis in forest conditions

It is well known that mechanobiology controls cellular functions of eukaryotic organisms through three sequential processes: mechanosensing, mechanotransduction, and mechanoresponses (Vogel and Sheetz 2006). In land plants, these processes have been described at both cellular and whole plant level (Coutand 2010; Moulia et al. 2011). At plant level, the syndrome of response that is driven by the sensing of external, non-damaging, mechanical stimulations has been called thigmomorphogenesis since the seminal works of Jaffe (1973) and Boyer (1967). In trees, thigmomorphogenesis has been studied for decades, but mostly in juvenile shoots growing in a greenhouse and submitted to artificial mechanical stimulation. It was found to strongly influence both apical and cambial activities and therefore growth of stems and roots. After a mechanical stimulation, apical growth of stem decreased while radial growth of stem and roots increased resulting in more stunted and better anchored individuals (Telewski and Jaffe 1986; Pruyn et al. 2000; Coutand et al. 2008; Roignant et al. 2018; Niez et al. 2020).

Real forest conditions, mechanobiology and thigmomorphogenesis interact with all other functional processes directly linked to resource availability (water use, irradiance interception…). Several field works have disentangled the sensing of mechanical signals and associated thigmomorphogenetic responses from other functional processes. Their results have revealed the huge role of thigmomorphogenesis in driving the growth of trees in forests: Meng et al. (2006) found an increase of 40% of height growth and a decrease of 25% of basal area at 1.3 m after reducing natural bending of 50–55 years old *Pinus contorta* in 4 different sites in Alberta, Canada. Further, more insightful experiments have then been implemented in forests under even aged silviculture in three species (*Picea sitchensis*, *P. pinaster*, and *Fagus sylvatica*). In these experiments, half of the trees were guyed in order to remove mechanical stimulation. The growth of these trees was then compared to similar free-standing and free-swaying trees. The guyed trees serve as a control for the effects of all environmental factors except for wind-induced strains and allow isolation of the thigmomorphogenetic effect from other factors. The relative importance of thigmomorphogenetic component is computed as a ratio between the difference in growth increments of free to sway and guyed trees and the growth increment in guyed trees. In these field experiments, thigmomorphogenesis increased radial growth of stems by 33 to 131% as summarized in Table 1 (Moore et al. 2014; Dongmo Keumo Jiazet et al. 2022a; Defossez et al. 2022). Thus, wind-induced thigmomorphogenesis is a key driver of wood formation and carbon allocation to secondary growth. In addition, it also significantly influenced the distribution of biomass along the tree height, modifying tree taper (Dongmo Keumo Jiazet et al. 2022a, Fig. 2). While trees free to sway allocated more biomass to the lower part of the stem, biomass allocation in guyed trees was reduced in the basal part of the stem and increased higher in the stem when compared to pretreatment growth. These results clearly question the commonly admitted theories about hydraulic conditioning of allometric laws for secondary growth, such as the pipe model theory (Lehnebach et al. 2018). These laws can be related to the “uniform stress theory” (Morgan and Cannell 1994), which predicts an optimal allometric allocation of growth along the stem. This principle involves equalizing the distribution of stresses throughout the structure, thereby preventing local concentrations of stress from exceeding the strength of the constitutive material. While typically referred to as the "uniform stress theory", it could be also described as a "constant safety theory" (Moulia and Fournier-Djimbi 1997; Dean et al. 2013).

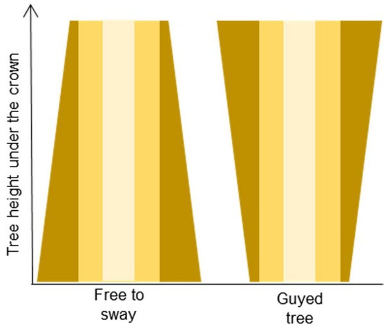

Fig. 2 Distribution of the radial growth increment along the tree height in free to sway and guyed trees. Schematic representation derived from the results obtained by Dongmo et al. (2022a). Light yellow is the initial tree shape, yellow is the radial growth allocation before thinning, and dark yellow is the biomass allocation after thinning and guying

The effect of wind-induced strains on root development in forest conditions has been less investigated. Acclimation of root systems was observed in windy sites (Nicoll and Ray 1996) or mountain context (Marchi et al. 2022; Costa et al. 2023). In particular, the cambial growth at the bases of scaffold roots was increased. By comparing guyed vs free-swaying individuals, Dongmo Keumo Jiazet et al. (2022a) found an 80% increase in the radial growth of major roots in response to wind loads.

Beside stimulating cambial activity, stem bending changes wood differentiation, leading to a special wood called “flexure wood” (Telewski 2016; Roignant et al. 2018) with increased wood density and higher mechanical resilience (Niez et al. 2020). This may be less generic than the growth-allocation effect. Indeed, several cases of lack of flexure wood induction have been reported in some provenances or genotypes (Telewski 2016). It was also found that beech poles submitted to increased mechanical loading did not exhibit significant changes in wood structure or properties, relying solely on

Table 1 Thigmomorphogenetic component of the radial stem and root growth in forest stand in acclimated condition and after a disturbance (thinning). DBH stands for diameter at breast height, stem or root radial growth ratio is the ratio between the difference in growth increments of free to sway (ΔDf) and guyed trees (ΔDg) and the growth increment in guyed trees

	Species	Tree age (yrs)	Tree height (m)	DBH (cm)	Stem height growth	Stem radial growth ratio (ΔDf-ΔDg)/ΔDg	Roots radial growth ratio (ΔDf-ΔDg)/ΔDg	Branch mass	Duration of the study
Acclimated condition									
Moore et al. (2014)	*P. radiata* D Don	13	17.5-23	39.5	-	80%	-	-	
Meng (2006)	*P. contorta* Dougl. ex Loud. var. latifolia Engelm.	50-55	15.3	11.3	-43%	-	-	-	
Defossez et al. (2021)	*P. pinaster*	16	9.4	15.0	-	33%	-	-	3yrs
Dongmo et al. (2022)	*F. sylvatica* L.	30	13.3	12.8	ns	131%	82%	ns	4yrs
After thinning									
Nicoll et al. (2019)	*P. sitchensis* (Bong.) Carr.	10	5.3	7.5	ns	40%	54%	-22%	4yrs
Defossez et al. (2021)	*P. pinaster*	16	9.4	15.0	-	20%	-	-	3yrs
Liu et al. (2003)	*P. contorta* Dougl. ex Loud.	17-22	4	3.65	-12%	20%	-	-	4yrs
Dongmo et al. (2022)	*F. sylvatica* L.	30	13.3	12.8	ns	74%	51%	ns	4yrs

Moore et al. (2014), Meng (2006), Defossez et al. (2022), Dongmo Keumo Jiazet et al. (2022a and b), Nicoll et al. (2019), Defossez et al. (2021), Liu et al. (2003)

geometrical adjustments possibly related to their bigger size (Dlouhá et al. 2024a).

1.3 Adaptive biomechanical performance and its thigmomorphogenetic acclimation: beyond wood density

In ecological studies, there is a need to identify traits that can be easily measured in situ on a large number of individuals. Variation in these traits can be then interpreted as (i) a genetic adaptation of the different species, or (ii) a phenotypic acclimation to the prevailing environmental conditions along tree life. Wood density is often held as a functional trait associated with wind resistance (Chave et al. 2009). The rationale behind this hypothesis is that (i) wood density scales with wood stiffness and strength and (ii) wood properties determine the wind resistance at the tree level. However, both items have been questioned by detailed biomechanical studies (Larjavaara and Muller-Landau 2010, 2012). The relationship between wood density and wood mechanical properties is broadly true at the interspecific level over a wide range of wood densities, but at the intraspecific level the relationship is less tight (Alteyrac et al. 2006; McLean et al. 2016; Dlouha et al. 2018). Upscaling stiffness from the material to the stem level requires the consideration of the cross-section geometry. The bending rigidity of the stem is computed as follows:

$$E \cdot I = \frac{E\pi D^4}{64} \tag{5}$$

where E is the modulus of stiffness and I is the moment of inertia. However, the tree resistance to wind makes relationship with the environmental factor of wind, aligning with the definition of ecological performance impacting directly plant fitness (Violle et a. 2007). In the primer to biomechanics, we introduced a strain-based formulation of the tree resistance to wind (Eq. 3 yields an equivalent of the tree safety against wind loads when divided by strain at break (Fournier et al. 2013)). This tree safety factor is a non-linear combination of elementary traits measured at different levels—tree size, shape, and material properties. In particular, the tree dimensions play an important role as stem diameter is elevated at the power of three. Therefore, direct multivariate statistical analysis of traits such as wood density or stem diameter, height or relative growth rate to deduce biomechanical performance or its variation is not informative because it assumes an additive combination of these traits.

How much is the tree safety against wind acclimated by wind-induced thigmomorphogenesis, and other environmental factors, and whether there may be different ecological strategies in such acclimation is an active area of research. If thigmomorphogenesis may lead to the production of flexure wood (Niez et al. 2020), its properties and production were found variable among species (Telewski 2016; Dlouhá et al. 2024a). As illustrated by Read et al. (2011) examining wood properties, tree morphology, and growth increments from species evolving in cyclone-prone environment, tree resistance to wind may be achieved by different combinations of morphological and wood traits. The range of variation of these parameters differs at interspecific and intraspecific level. For example, the variation range of wood density is reduced at intraspecific level and therefore other traits such as structural arrangement of the cell wall may be as important as density (Alteyrac et al. 2006; Ivkovic et al. 2009). Besides, wood density is influenced by many other environmental factors, in addition to wind-induced thigmomorphogenesis.

Species may differ in the combination of traits used to adjust their wind resistance (e.g., material properties, growth allocation) as well as in their sensitivity to thigmomorphogenesis which is likely related to their ecological strategy. For instance, pioneer species are expected to be highly sensitive due to their high exposure to wind loads. Significant interspecific variability in thigmomorphogenetic efficiency is linked to the need to maintain an acceptable security margin against wind (Coutand et al. 2010). To investigate the dynamics of acclimation process at both intra and interspecific levels, monitoring the amount of strain perceived by trees in stands with different wind exposure and/or after canopy opening could be a good candidate trait but requires long-term in situ instrumentations of forest stands. Such monitoring would also inform about the mechanical security margins of individual trees and their change during the tree life and canopy disturbance.

1.4 Adaptive thigmomorphogenesis after canopy disturbance in forest conditions

So far, we have only considered the response to different wind exposure and intensity in a stand that has not been disturbed for a long time. Since the thigmomorphogenesis in trees is related to the sensing of bending strains, changes in stand density, for example, in connection with windthrow clearings or with natural and artificial thinning, also leads to a change in wind-induced stimulation (Dongmo Keumo Jiazet 2022b). The mechanical strains induced by wind on remaining trees are also increased as tree-to-tree support through crown contacts is reduced (Milne 1991). The relative thigmomorphogenetic component of the radial growth increase after such a disturbance is between 20 and 74% depending on the species and thinning intensity (Table 1). Beyond the radial expansion recorded at breast height (DBH), the biomass allocation along the stem (Dongmo Keumo Jiazet et al. 2022a, Fig. 2) and among tree compartments (Dlouhá et al. 2024b) is also modified after thinning. The thinning effect on growth is not only due to sharing resources among fewer trees; it also has an equally strong mechanobiological component related to wind.

This example of thinning reflects the duality of wind effects on trees, as depending on time. In the short term (typically a few years), thinning significantly increases the damage during strong wind episodes (Valinger and Fridman 2011; Albrecht et al. 2012; Wallentin and Nilsson 2014). Nevertheless, the increased mechanical vulnerability is transient. In a long-term perspective, previously thinned stands in general exhibit higher wind resistance (Kamimura et al. 2017), which is interpreted as a result of mechanosensitive acclimation. Thanks to wind-induced strain sensing and thigmomorphogenesis, individual trees are able to restore its margin of safety after a disturbance to keep it constant (this state is referred to as acclimated conditions (Table 1)). However, we still lack a global evaluation of the value of this safety margin (as it has been done for example for hydraulic failure under water-stress (Choat et al. 2012; Delzon and Cochard 2014)). And modeling is required to estimate both, its level and how long it takes for the thigmomorphogenetic reaction to efficiently restore this mechanical security margin. To sum-up, the increase of the wind-induced strain after a canopy disturbance reflects on one hand the reduced tree resistance against wind and on the other hand, variation of the signal triggering the thigmomorphogenesis.

Changes in the upwind landscape also affects the wind loads on trees and hence their thigmomorphogenetic response. A clear illustration of this is the effect of forest edges. Trees at an edge exposed to wind receive a higher wind load than trees sitting within the stand (although the wind above the stand is more turbulent). Recently made edges are known to be very prone to wind damages. An extreme case occurs during a storm: newly created edges (downwind of already windthrown trees) during the storm itself result in the overloading of the remaining trees facing the wind, leading to large alleys of storm damage (Seidl et al. 2014b; Dupont et al. 2015). On the contrary trees at old forest edges (Gromke and Ruck 2018) are more resistant to wind. This may be due to a higher access to resources. However, based on the findings related to the response to thinning, thigmomorphogenesis is a prime candidate to explain the discrepancies between short-term and long-term wind effects on the stability of trees against wind.

Thigmomorphogenetic acclimation takes place over tree growth which also depends on many other environmental factors (irradiance, temperature, soil conditions…). Tree and forest growth models have been instrumental in combining these effects. These models however barely consider thigmomorphogenesis despite its large effects on growth. Recent advances on thigmomorphogenetic effects in forest conditions therefore now need to be integrated in models of tree and forest growth.

2 Integrating thigmomorphogenesis with other factors over tree and forest growth: updating models

For a long time, empirical models of forest growth at the stand level formed the backbone of sustainable management for both planted and naturally regenerated forests. These models inherently assume stable climatic conditions and in general, they do not consider wind effects on growth. An exception to that is the work by Dean et al. (2013). They showed that integrating an allometric law derived from the "uniform stress" theory could improve the empirical models of forest growth. The allometric predictions of the uniform stress theory are however derived for thigmomorphogenetic reactions in monospecific, even-aged stands that are fully acclimated under a steady climate (and no disturbance).

Empirical models will no longer be able to accurately predict growth under changing climate conditions. Indeed, they are neither adapted to integrate effects of climate change (Cuddington et al. 2013); nor are they capable of handling the increased complexity of the forest stand structure (shift from monospecific to mixed forests, expected to provide a higher resilience to global changes (Pardos et al. 2021)). This explains the recent emphasis on the process-based forest growth or vegetation models. These models include explicit rules for different ecological and eco-physiological processes governing tree growth, life, and mortality as well as interspecific interactions. Moreover, there is currently a shift from the "source modeling" where environmental factors only constraint photosynthesis to a "sink-driven approach" in which the direct response of carbon sink activity, in particular primary and secondary meristems, to environmental signals or conditions is found more limiting for the plant growth and development than for photosynthesis itself (Fatichi et al. 2014). Despite this, in all studies investigating constraints on meristem functioning due to environmental factors (Fatichi et al. 2014; Guillemot et al. 2017; Hartmann et al. 2020), the influence of wind as growth factor through thigmomorphogenesis is not addressed. Wind is, at most, only considered as a risk factor responsible for storm damage, thereby reducing the carbon balance of the forest (Scheller and Mladenoff 2004; Ancelin et al. 2004), and trees are still considered inert towards the change in their mechanical environment.

The research agenda needs however to be focused on producing a process model of tree growth that accounts for wind-induced thigmomorphogenetic effects and their effects on growth and allometries. To do so, the most straightforward would be probably to rely on functional-structural plant models (Louarn and Song 2020) that are easily compatible with mechanistic models like the sum of strain-sensing model for thigmomorphogenesis developed by Moulia et al. (2011, 2015) but imply an explicit description of tree architecture. We should aim at designing a generic model that will allow to generalize the experimental results (that cannot sample all the combinations of species*developmental stage*growth conditions). We think that this is feasible given the fact that controlled studies have shown that thigmomorphogenesis can be observed in a wide range of plant species (see in Biddington 1986; Morel et al. 2012).

A pioneer example of this is the development of a functional-structural plant model for trees and forest by Eloy et al. (2017). They were able to show in silico that the thigmomorphogenetic driver of secondary growth is of high adaptive value, and even a requisite for the acquisition of an erected habit. Many other issues should be addressed, like the kinetics of acclimation to the novel wind loads after wind-induced disturbances or damages in different wind climates and under different resource availabilities. It would be also interesting to analyze if the sink strength is modulated by thigmomorphogenesis. However, because their focus was on evolution, their model was not designed to predict growth or to assess wind risk in real forests.

Including a generic thigmomorphogenetic module of the biomass allocation in "real forest" growth models presents several challenges.

First, we need to build a transfer function that enables to transform the meteorological factor that is wind speed (easily obtained from a nearest meteorological station) into a sensed internal variable driving the growth response, i.e., the wind-induced strain. During this step, the wind-induced strain needs to be continuously monitored on the studied tree using strain gauges (Dongmo Keumo Jiazet 2022b). Mechanical models may help predict this transfer function but for the moment, we clearly lack time series of wind-induced strains. Therefore, we need to set a large-scale monitoring of the strain perceived by trees of different species and in different climatic and sylvicultural contexts to gather data to build a generic transfer function.

In the second step, we need to solve the problem of temporal integration of the mechanical signal under natural conditions and its use for triggering of the growth response. This consists in solving the issue of chronic signals' filtering and identification of the threshold triggering the thigmomorphogenetic response, threshold being dependent on the tree loading history (Bonnesoeur et al. 2016).

The last step consists in the building of a biomass allocation law inside the tree taking into account thigmomorphogenesis. This allocation law is not expected to be a binary response but a continuous control of the growth allocation in function of the sum of strains perceived by differentiating tissues (Bosc et al. 2017). In this step, we meet the challenge of thigmomorphogenesis' modulation by resource availability. Indeed, plant growth reflects compromises between different functions: interception of irradiance, water uptake and transportation, self-support, and resistance to wind. And therefore, it is under the direct or signal-mediated influence of all these factors. Some pioneer works in controlled conditions have shown that resource availability affects the amount of growth (quantitative effect) while thigmomorphogenesis affects the growth allocation (qualitative effect) regardless the resource availability (Niez et al. 2020). However, results from natural forests indicate that altering the hierarchy of environmental constraints through thinning leads to changes in allocation patterns along the tree stem, creating discrepancies with empirically established laws (Dongmo Keumo Jiazet et al. 2022a), and between different tree compartments (Dlouhá et al. 2024b). We must revisit allocation patterns within individual trees and potentially among trees, taking into account the influence of all environmental factors and their relative importance in shaping growth allocation trajectories. If transition periods are key to predicting mechanical risks, the degree of thigmomorphogenetic control under acclimated conditions underscores the need to consider thigmomorphogenesis continuously alongside other environmental factors. For instance, the site index, typically used to assess the forest stand productivity, should be broken down into components such as soil fertility and its interaction with climatic factors.

2.1 Moving forward to an acclimation growth—risk assessment loop after a disturbance

Hybrid mechanistic/empirical wind risk models, designed for predicting forest and peri-urban wind damage (Gardiner et al. 2000, 2008, 2024) have been widely and successfully used over the last decades. However, they have undergone recent refinements to transition from stand-level to individual-tree wind risk prediction. This shift incorporates the competition index, a measure of the local tree environment, to predict increased wind exposure following local disturbances (Hale et al. 2012; Duperat et al. 2021).

Trees from wide spaced plots with higher wind penetration are predicted to be more resistant to storms compared to highly packed stands (Gardiner et al. 1997; Achim et al. 2005; Locatelli et al. 2016; Torita and Masaka 2020). However, confrontation of the model predictions with observations showed difficulties to extend the prediction over areas for which direct measurements of model parameters such as root anchorage and soil condition are not available and in which these parameters need to be predicted by the model (through competition index) (Kamimura et al. 2016). In recently thinned plots, estimation of the wind damage predicted by GALES did not fit with the observed damage. It is likely due to the model not accounting for the influence of neighboring trees and the degree of mechanical tree acclimation to the change in local wind loading after thinning (Kamimura et al. 2017). Indeed, the change in the competition index after thinning accounts for the increase of the wind exposure because of the increased wind penetration in the vicinity of the target tree (Duperat et al. 2022). The function relating the competition index and change in wind exposure is in general assumed to be linear and continuous while it is likely discontinuous at the moment of a shift from the system to an isolated tree behavior (Kamimura et al. 2022). Further, at the longer time scale the acclimation process of the tree growth allocation (inside the stem, between the tree compartments, etc.) fundamentally affects the change of the mechanical risk level. Therefore, integrating the acclimative growth-wind risk assessment loop into wind risk tools, particularly in post-canopy opening scenarios, would significantly improve the precision of predicting the duration of increased mechanical vulnerability. This involves coupling wind risk models with growth models that account for wind-induced thigmomorphogenesis, as previously discussed.

3 Conclusion

Consideration of wind as a hazard has widely shaped our thinking about the wind action over forests. However, wind-induced mechanical signals (strains) are also sensed by trees and affect their growth. In this paper, we highlight the surprisingly high magnitude of mechanosensitive control over the tree growth in real forest condition. The sensing of wind-induced strains by trees explained indeed 33–131% of the radial growth at breast height for three common forest species (two conifers, one hardwood) in acclimated conditions (no recent disturbance) and 20–74% of radial growth at breast height after a disturbance (thinning). It was also shown that mechanosensing strongly affects the biomass distribution along the tree height, therefore tuning the tree allometry, as well as biomass allocation between the tree compartments acting on the root-shoot ratio. Diameter at breast height and its growth is the reference value for most of forest tree growth and wind risk models. Diameter at breast height is also used for prediction of other tree morphological descriptors through allometric laws and to follow response to environmental stresses. Since the impact of thigmomorphogenesis is primarily concentrated in the basal part of the stem, particularly at DBH, we advocate for its integration alongside established environmental factors into all of the aforementioned models. This involves revisiting allometric laws in relation to all environmental factors that influence tree growth, as well as their changes over time and/or with alterations in forest structure. We also stress the importance of monitoring mechanical strain in forest stands equipped to track the effects of environmental factors on tree growth. To effectively address the challenges posed by global change on forests, including their growth, vulnerability, and ecology, interdisciplinary research is essential, with thigmomorphogenesis playing a key role in this effort.

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Code availability
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Authors' contributions
Writing—original draft preparation: Jana Dlouhá; writing—review and editing: Jana Dlouhá, Bruno Moulia, Meriem Fournier, Eric Badel, Thiéry Constant. The authors read and approved the final manuscript.

Data availability
All data used for this paper are already published and corresponding references are cited.

Declarations

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Not applicable.

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