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RESEARCH PAPER

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No matter how much space and light are available, radial growth distribution in *Fagus sylvatica* L. trees is under strong biomechanical control

Joel Hans Dongmo Keumo Jiazet^{1*} , Jana Dlouha¹, Meriem Fournier¹, Bruno Moulia², François Ningre¹ and Thierry Constant¹

Abstract

Key message: This study presents the first attempt to quantify how the thigmomorphogenetic syndrome is involved in *Fagus sylvatica* L. tree growth responses to thinning. An experimental design preventing mechanosensing in half of the trees demonstrated that radial growth distribution in roots and along the tree stem is under strong biomechanical control.

Context: Studies on the mechanosensitive control of growth under real forest conditions are rare and those existing to date all deal with conifer species. In the current context of global changes, it is important to disentangle how different biotic and abiotic factors affect tree growth.

Aims: Whereas growth changes after thinning are usually interpreted as responses to decreased competition for resources, this study investigates the importance of how mechanosensing controls growth distribution inside the tree.

Methods: In an even-aged beech stand, 40 pole-sized trees (size class at first thinning) were selected, half of the plot was thinned and, within each sub-plot (thinned and unthinned), half of the tree were guy-wired in order to remove mechanical stimulations to the lower part of the stem. Four years later, all trees were felled and volume increment, ring width distribution along the tree height, and the largest ring width of the structural roots were measured. The effect of mechanical stimulation in the two treatments (thinned and unthinned) was assessed.

Results: Removal of mechanical stimulation decreased the volume increment in the lower part of the stem as well as radial root growth but did not affect axial growth. When mechanical strain was removed, the ring width distribution along the stem height changed drastically to an ice-cream cone-like distribution, indicating a strong mechanosensitive control of tree shape.

Conclusion: In a forest stand, the growth allocation inside the tree is under strong mechanical control. Mechanical stimulations explain more than 50% of the increment stimulated by thinning, whatever the growth indicator. A further

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challenge is to better understand how cambial cells perceive strains during growth in order to integrate mechanosensing into process-based tree-growth modeling.

Keywords: *Fagus sylvatica* L., Pressler's law, Thigmomorphogenesis, Thinning

1 Introduction

High winds have long been regarded as a factor of forest damage (Ennos 1997; Schelhaas et al. 2003; Gardiner et al. 2016). However, as pointed out by the pioneer paper by Ennos (1997), wind is also a factor of tree growth and plays an important role in forest ecology. Metzger (1893) first proposed wind as one of the most significant regulators affecting forest tree growth. Before that, Knight (1803) conducted the first experiments to observe the changes in stem morphology and growth in guy-wired vs wind-blown apple trees.

Unlike light or water, wind is not a direct resource for trees. It acts as a growth factor when wind loads in the crown produce signals transmitted to the living cells. First of all, in the same way a wind load in a sail transmits mechanical stresses to the mast and rigging, wind forces in the tree crown result in mechanical stresses and strains in the cambial cells (Mouliia 2013). Mechanosensing is the ability of living cells to perceive such strains, i.e., shortening or stretching. This perception of mechanical strain activates a biologically complex signaling chain allowing the whole tree to sense the strains. For instance, Coutand et al. (2008) showed that bending roots, without causing any movement in the apical zone is still able to very quickly inhibit apical growth, even though there is no mechanical stress or strain in the apical zone. This complex mechanosensing system triggers a series of growth responses, dubbed thigmomorphogenesis in 1973 (Jaffe 1973; Mouliia 2013). Responses include a decrease in apical growth, an increase in radial growth and an increased allocation from above-ground to below-ground tissues see Telewski (2021) for a general review of these mechanisms. Research in plant physiology is currently becoming more and more involved in better understanding molecular signaling and growth regulation (see Telewski (2021) and Mouliia et al. (2011) for reviews). A further question, though, is how these mechanisms act to shape trees in the real world of forest ecosystems, and what this means in terms of forest ecology? For instance, does thigmomorphogenesis significantly affect forest growth or forest resistance to winds? Indeed, even though mechanical stress cannot be compared to a resource like water or light, the way it affects the distribution of growth between roots and shoots, and between axial and secondary growth, calls for deeper investigations into thigmomorphogenesis from the point of view of forest ecology and management. There are only a few

studies on the role of mechanical signals from wind loads in forest processes. Some included wind among many other fertility factors such as soil conditions in their environmental analyses of site index changes from large scale inventory data (Watt et al. 2009; Farrelly et al. 2011); these authors showed a significant negative effect of wind speed on height growth. Other studies were based on field experiments where the way trees perceived mechanical loads was artificially disrupted (Jacobs 1954; Burton and Smith 1972; Telewski and Jaffe 1986; Valinger 1992; Nicoll and Ray 1996; Liu et al. 2003; Watt et al. 2005, 2009; Meng et al. 2006; Moore et al. 2014; Bonnesoeur et al. 2016; Nicoll et al. 2019).

Actually, practitioners (foresters or arborists) have long been aware that wind shapes trees (for example, Schimper (1898), cited by Telewski (2012), described the flag-shaped trees associated to strong, directional winds; Holroyd (1970) and Robertson (1987) presented how tree shape can be used as a biological indicator of prevailing wind direction and wind speed). Some modeling work (Mattheck and Kubler 1997; Dean et al. 2013; Eloy et al. 2017) assumed a thigmomorphogenetic hypothesis as an “axiom”, or even included more empirical laws such as the controversial constant-stress hypothesis stated by Metzger (1893) and widely developed by Claus Mattheck (e.g., Mattheck and Kubler, 1997), in order to suggest an optimal tree shape to avoid windfall risks. Forest researchers have observed ‘adaptive’ or ‘acclimative’ tree growth in response to mechanical stress (Telewski 1995; Ennos 1997; Badel et al. 2015; Fournier et al. 2015; Bonnesoeur et al. 2016). However, disentangling mechanical stress from other environmental factors is not easy merely through observation. So researchers have designed field experiments, often derived from protocols first used in controlled conditions, in order to change the mechanical stimuli without modifying other factors. One easy experimental design uses staking or guy-wiring to stabilize the tree. Provided that a perfectly rigid fixation is ensured, such treatments remove all mechanical stresses and strains in the trunk and roots below the fixation point. This makes it possible to compare control trees with staked or guy-wired trees growing in the same conditions, and allows the researcher to disentangle thigmomorphogenetic responses from other environmental factors of growth.

Among the numerous environmental factors affecting forest growth, the competition between trees for light

and other resources has been well documented from both theoretical and practical points of view (Biging and Dobbertin 1995; Coomes and Allen 2007). Competition between trees is assumed to limit individual tree growth. Therefore, thinning, one of the most popular silvicultural practices, is used to control competition between trees and increase radial growth. At the stand level, thinning is expected to have less effect on height growth. Consequently, at least in even-aged stands, the top height at a given age can be used as an integrative productivity index, independent of stand density and competition among trees (Skovsgaard and Vanclay 2008; Pretzsch 2009). However, thinning is not just a way to manipulate competition between trees: after thinning, the remaining trees are exposed to more available light and water but also to greater mechanical strains due to the wind (Rudnicki et al. 2003). The growth response to thinning lasts several years (Mitchell 2000) before stabilizing in a new stationary state. In a pioneer work on the mechanosensing aspects of thinning, Nicoll et al. (2019) observed growth responses in spruces after thinning, disentangling the effect of resource availability and wind sway by guy-wiring half of the trees. They found a huge effect of mechanical signaling since more than 50% of the radial growth near the ground was due to wind sway.

Distribution of radial growth along stems has interested forest scientists for decades. In the nineteenth century, M.R. Pressler published what is now known as Pressler's law: "Ring area growth (cross-sectional area of a single annual increment) at any one point on the stem is proportional to the quantity of foliage above this point" (Pressler, 1864 as cited by Larson, 1963). In the trunk below the crown, this law becomes simply "Ring area growth is constant below the first living branch". To explain this constant area, the need to ensure constant hydraulic conductivity between the crown and the root system is usually invoked. However, numerous authors have reported discrepancies between this theory and experimental observations (see Cruziat et al. (2002); Lehnebach et al. (2018)) for detailed reviews of these concepts), and such discrepancies have sometimes been attributed to mechanical strains (Gafrey and Sloboda 2001; Lehnebach et al. 2018). Nonetheless, no clear demonstration of thigmomorphogenetic control of vertical ring area distribution was given. Pressler's law assumes a constant ring area, consistent with hydraulic theories. However, if mechanical stress has a dominant effect, ring area is not a relevant variable since mechanical signaling is not a flux through a surface. Therefore, the local ratio of ring width (the response) to perceived strain (the stimulus) should be the relevant constant variable (Mouliat et al. 2011). The question is then how the stimulus (perceived strain) varies in cambial cells. Lacking

any accurate information on this point, we retained the Mattheck's uniform stress "axiom" (Mattheck and Kubler 1997) as our null hypothesis. Consequently, we assumed that the tree ring width would be uniform along the stem in accordance with the mechanical strains perceived by living cambial cells. This theory becomes irrelevant when mechanical stimuli are removed by guy-wiring; in this case, a constant ring area linked to hydraulic requirements would be expected.

2 Objectives and main hypotheses

This study, following Jacobs (1954), Nicoll et al. (2019), and Defossez et al. (2021), aims at proving that tree growth responses to thinning involve mechanosensing and thigmomorphogenesis, and not just competition for light and other resources. We set up an experiment (VENT ÉCLAIR) in a naturally regenerated beech stand, with 40 dominant trees, and used thinning and guy-wiring to disentangle the effects of competition and mechanosensing; we monitored the plot for 4 years. In this paper, we examine the growth responses that were studied through destructive experiments at the end of the 4-year monitoring period. We looked at axial growth, radial growth distribution along the trunk, volume growth, and also paid attention to root growth.

Whereas thinning increased the growth in aerial and root biomass and volume, with significant impacts on radial growth and fewer impacts on height growth, guy-wiring prevented mechanical strains below the fixation point and should have removed thigmomorphogenetic responses to a large extent. Based on what Jacobs (1954) observed in his pioneer work and according to our current knowledge of how living cells respond to mechanical strains, we expected the following effects of guy-wiring:

- An increase in axial growth (growth in the length of the dominant axis) leading to height growth. Greenhouse experiments have proved that the perception-response mechanism for axial growth integrates the sum of strains below the apex (Coutand and Mouliat, 2000; Mouliat et al. 2015). Guy-wiring removes strains below the fixation point, thus eliminating a significant part (although not the entirety) of the strains involved in the axial growth response;
- A decrease in root radial growth since guy-wiring prevents the transmission of strains from wind forces in the crown to the root system;
- A decrease in volume increment of the trunk under the fixation point of the guy rope.

We then interpreted the observed differences in growth after thinning between free and guy-wired trees, expressed as a percentage of growth response to thinning

(i.e., the difference between free thinned and unthinned trees) as the part of the growth response to thinning attributable to mechanosensing. We expected this part to be very large, not just statistically significantly different from 0, which would prove that mechanical strains are a major growth stimulus and not merely an environmental factor impacting growth among many others.

Lastly, we expected that not only would radial growth globally decrease below the fixation point, but the distribution of the radial growth along the trunk would also change.

3 Methodology

3.1 Site description

The “Vent-éclair” experimental site was set up during the winter of 2014/2015 in a 2-ha plot located in the north-eastern of France in the Haye National Forest (46,671,230° N 6,084,482°E). The plot consists mostly of beeches (*Fagus sylvatica* L.) with a few hornbeams (*Carpinus betulus* L.), maples (*Acer pseudoplatanus* L.) and ashes (*Fraxinus excelsior* L.). It was an even-aged (average age of 30 years), high-density stand issued from natural regeneration that had experienced no thinning. The stand is typical of naturally regenerated even-aged beech high forests in lowlands in this region, at the pole stage (called “phase de compression” in French, ONF 2005). The site climate is a degraded oceanic type with continental influence. Rainfall is heavy and well distributed over the year. Over the 4 years of the study, the mean annual rainfall was 700 mm, with the maximum and minimum rainfall years being 2018 (795 mm) and 2015 (537 mm) respectively.

The average wind speed during the 4-year period was 3 m/s. Dominant winds came mainly from the West, South-West, and South. The study plot was located on a plateau at an altitude of 340 m. The soil is a calcium brown type consisting of two main layers. The first, about 30–40 cm deep, is clay-silt and strongly prospected by the roots. The second, from 40 cm to 120–150 cm, is clay with a strong load of calcareous rocks (80–90% by volume) more or less arranged in strata (Bonnesoeur 2016). The estimated water reserves in the soil are about 60–70 mm. The soil is also rich from a trophic point of view due to the calcareous nature of the rock.

3.2 Plant material

In 2014, 40 dominant trees in the stand were selected according to the following criteria: a non-flexuous stem with a tilt angle $< 5^\circ$, with no low branches and a well-developed, balanced crown. The trees were split into four sub-groups of 10 trees each all in the same diameter range. The average tree circumference was 40.3 cm and average height was 13.3 m (Chaumet 2015).

3.3 Experimental design

During the winter of 2014/2015, thinning was performed; this was a few years later (more than 2 years) than the silvicultural recommendations. The presence of mechanical stimuli in the stem in half of the poles was controlled by guy-wiring. Four treatments were defined. Two were designed to disentangle the effect of mechanical stimulation during the growth usually observed after thinning: thinned, guy-wired trees (TG), and thinned trees free to sway (TF). The other two were controls: unthinned, guy-wired trees (uTG), and unthinned trees free to sway (uTF). Thinning was carried out by removing all the neighboring trees in a radius of 4 m around the target tree. Guy-wiring was performed by fixing three steel cables to the stem at the base of the crown (about 7 m above the ground) at 120° from each other. Each guy cable was then anchored in the ground by a loop passed around an iron rod driven obliquely into the limestone bedrock. As it is well known that the concentration of stresses near the attachment point increase growth (Patch 1987), we avoided taking radial growth measurements on the stem in the vicinity of the attachment point. Along the stem, the only significant strains and stresses are bending ones, and guy-wiring canceled them below the attachment point. To allow comparison between the free and guy-wired trees, we defined a virtual guy-wire height in the free trees (at 7 m above ground) and paired each guy-wire tree to a specific free tree, with a similar diameter and height.

3.4 Radial and axial stem growth

After harvesting the selected trees, we performed measurements at regular intervals along the tree stem below the guy-wiring point to estimate stem volume increment. For each tree, six cross-sectional discs were collected at regularly spaced heights between 1.3 m and 7 m, taking care to avoid the vicinity of the attachment point and the tree base since butt swells are not accounted for in Pressler’s law (Cortini et al. 2013). Indeed, butt growth is a stand-alone phenomenon in biomechanics (see Clair et al. 2003). After cutting, the discs were wrapped in a plastic film and taken to the laboratory where ten ring widths were measured from the bark inward on four perpendicular radii. After a preliminary analysis, the data from two trees were removed either because of an obvious problem with the guy-wiring, or a very high local stand density (in the unthinned treatment), which prevented free motion. We also removed two others trees to balance the number in each group.

To measure axial growth of the dominant axis, we observed growth units on the last 6 m of the tree stem. As beech sometimes exhibits several growth cycles during the year, errors can occur when identifying growth

units. When in doubt, we cut out the cross-sectional sample containing at the growth unit's edge and counted the rings on both sides of the disc.

3.5 Root growth measurement

The root systems of the felled trees were pulled out with an electric winch and cleaned in the forest with a gas-powered air compressor, then pressure-washed in the laboratory. We divided the root system into four quadrants according to the dominant wind direction (SW). For each quadrant, the largest root was sampled and its upper generatrix marked with a felt-tipped pen to recognize the root orientation once it was separated from the root system. For each of the major roots, a cross-sectional sample was taken at a distance of 0.25 m from the tree stem center. According to Nicoll et al. (2019), it is at this distance that the growth reaction to thinning and guy-wiring is the most pronounced. Moreover, many roots were broken off relatively close to the stump so we could not sample sections farther away from the stump. A total of 122 cross-sectional samples (68 thinned and 54 unthinned) were scanned with an optical scanner at a 600-dpi resolution. To obtain an indicator of annual root growth following thinning, we measured the maximum annual increment perpendicular to the previous annual ring limit (Fig. 1). As for ring shape, though the direction of the increment could differ slightly from the vertical (Fig. 1), globally they were from the bottom to the top of the cross-section. Measurements were carried out on the first 10 annual rings from the bark inward.

3.6 Analysis of the longitudinal distribution of radial growth: null hypotheses and relevant variables

As explained in the "Introduction" section, we analyzed longitudinal growth distribution according to two variables (ring width and ring area) associated to two null hypotheses of a constant value along the stem (i.e., no systematic increase or decrease). We expected tree ring width to be the relevant variable when the taper was assumed to be under mechanical control and tree ring area when no mechanical stimulation was present (guy-wired trees).

3.7 Statistical assessment

Statistical analyses were performed on R Core Team (2021). As a reminder, the purpose of our study was not to analyze individual tree growth, annual growth or variability; our objective was to analyze the ratios of growth increment 4 years before and 4 years after the treatment, similar to Meng et al. (2006), for example. We used linear mixed effects models (nlme packages) to assess the effects of thinning, guy-wiring, and their interaction on these growth ratios. Pairing was introduced as a random

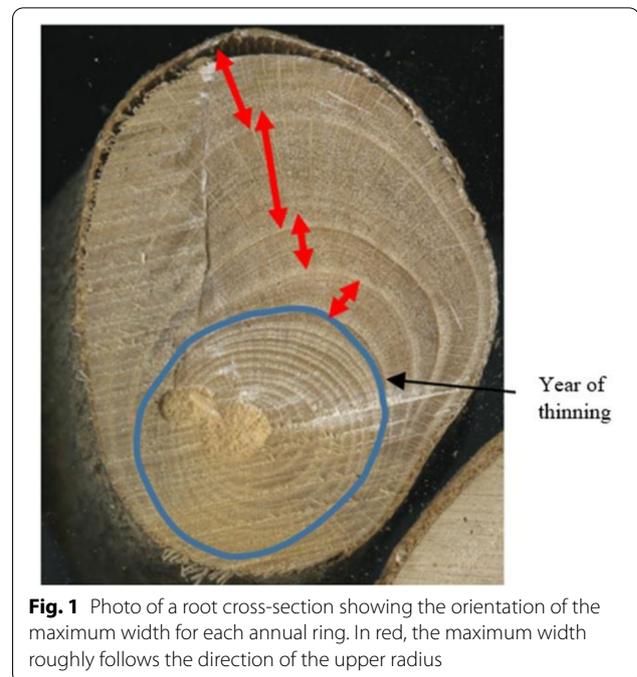


Fig. 1 Photo of a root cross-section showing the orientation of the maximum width for each annual ring. In red, the maximum width roughly follows the direction of the upper radius

effect. We assessed the normality of the data distribution (ratios of axial, root, and stem volume increments) with Q-Q plots, and homoscedasticity with standardized residuals against plotted fitted values. An ANOVA test was then performed to assess the significance of the main effects and their interaction, and relevant contrasts were tested with Tukey contrasts (multcomp package). The root-and stem volume-growth ratios that were not normally distributed were log transformed before ANOVA testing.

Linear mixed effects models were also used to assess how the slope of the relationship between ring width (or area) and tree height (and their interaction) changed with thinning, guy-wiring and period (before or after the treatment). For the pre-treatment period, we compared the slope of the regression to zero (according to the null hypothesis, ring width (or area) remains constant along the stem). Pairing and tree effects were considered nested random effects on the slope. Relevant contrasts were tested with Tukey pair-wise comparisons.

4 Results

4.1 Axial growth

The order of magnitude of the mean values of axial growth over the 4-year period after treatment was 1.8 m (precisely, 1.83 ± 0.25 m for TE, 1.82 ± 0.29 m for TG, 1.77 ± 0.46 m for uTG, 1.76 ± 0.26 m for uTF). The ratios of axial increment over the two 4-year periods before and after treatment are shown in Table 1. According to the factorial ANOVA, the effects of thinning ($F=0.03$,

Table 1 Means of growth ratios for beech poles submitted to different treatments (mean ± standard deviation; *n* = 9)

| Growth ratios | Treatments | | | | Differences between treatments (<i>p</i> value) | | | |
|---------------------------|---------------|--------------|--------------|--------------|--|---------|---------|---------|
| | TF | TG | uTF | uTG | TF/TG | uTF/uTG | TF/uTF | TG/uTG |
| Axial growth | 0.93 (±0.009) | 0.88 (±0.19) | 0.83 (±0.14) | 0.86 (±0.21) | | | | |
| Root radial growth | 1.87 (±0.38) | 1.24 (±0.29) | 0.71 (±0.11) | 0.39 (±0.08) | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| Volume increment | 2.26 (±0.45) | 1.58 (±0.24) | 0.97 (±0.11) | 0.66 (±0.10) | <0.0001 | <0.0001 | <0.0001 | <0.0001 |

The ratio of axial growth is the axial growth 4 years after treatment related to the axial growth 4 years prior to treatment. The ratio of root ring width is the root ring width 4 years after treatment related to the root ring width 4 years prior to treatment. The ratio of volume increment is the volume increment in the stem below the guy-wiring point 4 years after treatment related to the volume increment in the stem below the guy-wiring point 4 years prior to treatment. Ratios are dimensionless; a ratio of 1 means growth was unchanged. *TF* Thinned trees free to sway, *TG* Thinned and guy-wired trees, *uTF* Unthinned trees free to sway, *uTG* Unthinned and guy-wired trees. *P* values refer to Tukey test results

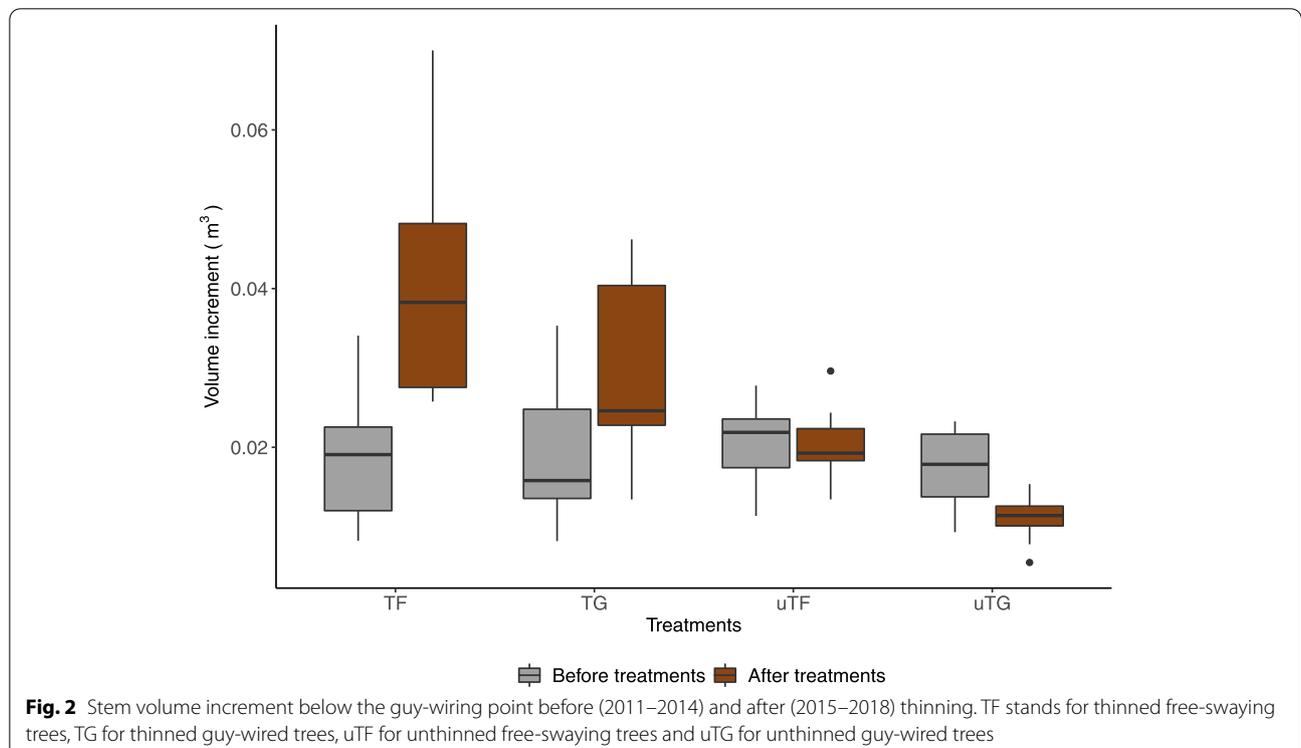
p = 0.87), guy-wiring (*F* = 0.52, *p* = 0.48) and their interaction were not significant (*F* = 0.60, *p* = 0.45).

4.2 Radial root growth

The factorial ANOVA on the ratios of root radial growth shows significant effects of both thinning (*F* = 165.79, *p* < 0.0001) and guy-wiring (*F* = 25.99, *p* < 0.001) while the interaction effect was non-significant (*F* = 3.20, *p* = 0.09). As expected, thinning increased root radial growth while guy-wiring systematically reduced root radial growth, even in the thinned treatment (Table 1).

4.3 Volume increment

Stem volume increment below the guy-wiring point was significantly affected by both thinning (*F* = 165.44, *p* < 0.001) and guy-wiring (*F* = 27.37, *p* < 0.001) while their interaction was non-significant (*F* = 0.17, *p* = 0.69). As expected, thinning strongly increased volume increment; the ratios were well over 1 (2.27 and 1.58 respectively in the free *TF* and guy-wired *TG* treatments). Growth was not affected in the *uTF* control (ratio *uTF* of 0.97 close to 1). Eliminating mechanosensing very significantly reduced volume increment for thinned and even unthinned trees (significant differences between *TF* and *TG* and between *uTF* and *uTG*). Figure 2 illustrates the



magnitude of volume increment before and after the different treatments: about 45% of the volume increment (after thinning) below the guy-wiring height was due to mechanosensing (45% is the value of $\frac{TF-TG}{TF-uTF}$).

4.4 Distribution of radial growth along the stem

Considering the variation of radial growth versus height along the tree stem, we compared the slopes in the graphs for both ring width and ring area to check that no differences existed among the treatments before 2014 (Table 2). Before applying the treatments, the slopes were positive for ring width and were significantly different ($p < 0.05$) from zero (except for TG). Concerning ring area, the slopes were negative but were not significantly different from zero ($p > 0.05$) (except for uTF). For ring area, all the slopes were significantly different (p value < 0.05) from zero after treatment (i.e., the area was not constant along the stem). For ring width, the slopes for free trees were not significantly different from zero (Table 2). As a main result, the sign (positive or negative) of the slopes was independent of the variable (width or area) and depended on mechanical stimulation and not on resource availability. In free trees (TF), tree ring width (or tree ring area) decreased with height (the slope was negative, see Table 2; Figs. 3 and 4) whereas in guy-wired trees (TG and uTG), tree ring width (or tree ring area) increased with height (the slope was positive, see Table 2; Figs. 3 and 4).

Lastly, for the thinned trees (T), where radial growth was greater, the differences between slopes before and

after the treatment were significant for both guy-wired and free trees and for both ring width and ring area.

5 Discussion

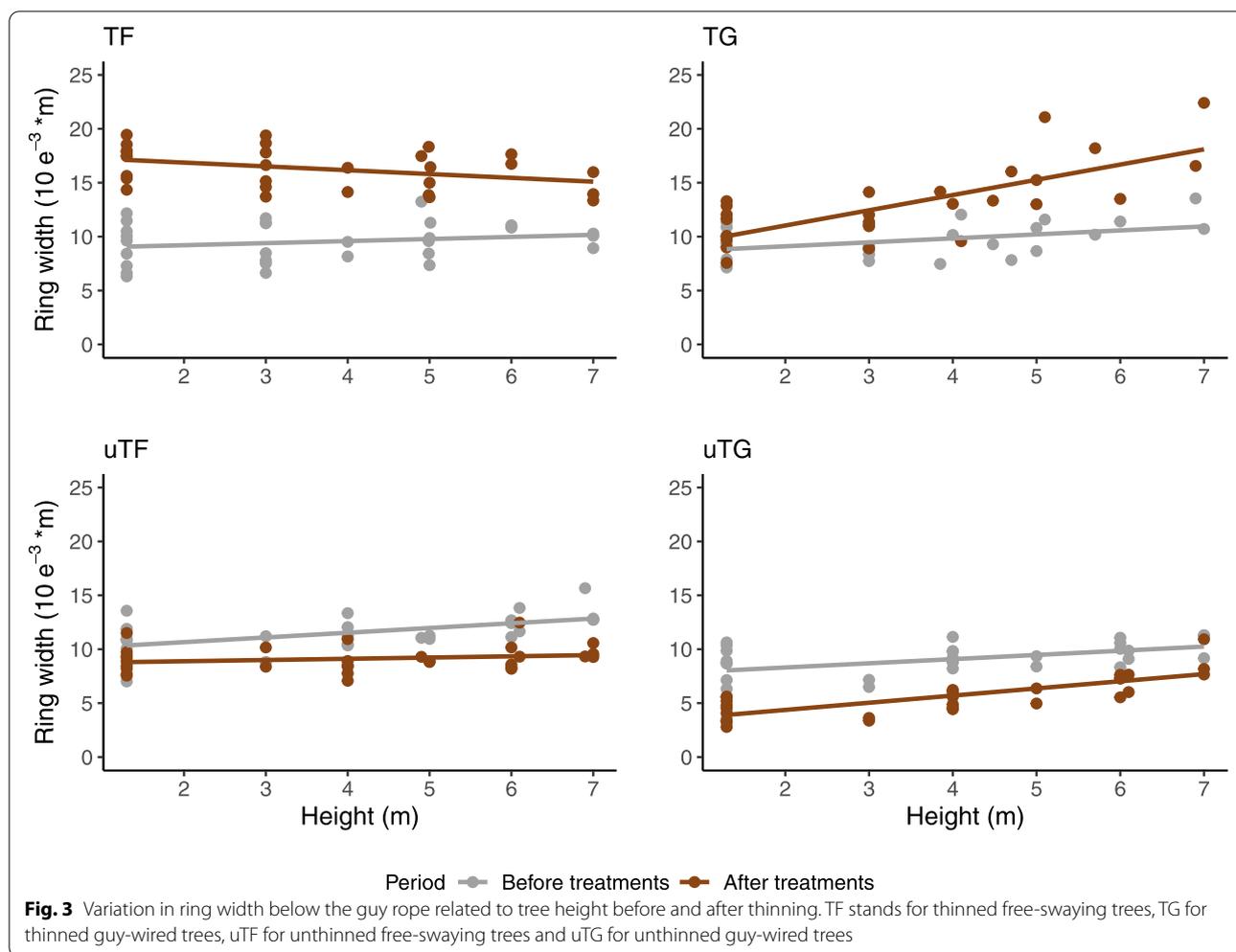
5.1 No mechanically induced change in axial growth was detected

The sum of strain model (S^3m) (Mouliat et al. 2015) assumes that axial growth is driven by the accumulation of local strains perceived at different heights along the tree stem. We significantly reduced the sum of perceived mechanical strains by guy-wiring certain trees, and therefore expected to find a decrease in axial growth. Indeed, many studies have reported a decrease in axial growth after mechanical stimulation in controlled conditions (Telewski 1995; Stokes et al. 1997; Braam 2005; Coutand et al. 2008; Mouliat et al. 2011; Niez et al. 2019) and in natural conditions (Meng et al. 2006). However, in our study, we did not detect any effect of guy-wiring on axial growth. This may be due to several reasons. First, in the studies mentioned above, the strain magnitude applied daily under controlled conditions to the mechanically stimulated plants was close to 1% (Niez et al. 2019), while the controls were completely free of mechanical stimulation. At our experimental plot, the wind-induced strain regime and the magnitude of strains stimulating radial growth had been carefully studied in a previous work (Bonnesoeur et al. 2016): under field conditions, daily stimulation was not zero in the control trees, and the greatest strains observed a few times in a year in these young dense stands were around 0.15%. This rather

Table 2 Regressions between the growth variable (ring width, ring area) and height along the stem

| Growth variable | Period | Treatment | Slope (mm/m or cm ² /m) | Null slope (p value) | Period effect (p value) | Treatment comparison | p value |
|-----------------|-----------|-----------|------------------------------------|-------------------------|----------------------------|----------------------|-------------------|
| Ring width | 2011–2014 | TF | 0.36 | 0.015 | | | 1 |
| | | TG | 0.25 | 0.068 | | | |
| | | uTF | 0.35 | 0.004 | | | |
| | | uTG | 0.41 | 0.001 | | | |
| | 2014–2018 | TF | −0.27 | 0.060 | 0.001 | TF-uTF | 0.193 |
| | | TG | 1.37 | 0.000 | < 0.001 | TG-uTG | < 0.001 |
| | | uTF | 0.12 | 0.331 | 0.382 | TF-TG | < 0.001 |
| | | uTG | 0.64 | 0.000 | 0.406 | uTF-uTG | 0.010 |
| Ring area | 2011–2014 | TF | −0.72 | 0.195 | | | 0.89 |
| | | TG | −0.95 | 0.075 | | | |
| | | uTF | −1.23 | 0.009 | | | |
| | | uTG | −0.23 | 0.615 | | | |
| | 2014–2018 | TF | −4.07 | 0.000 | < 0.001 | TF-uTF | < 0.001 |
| | | TG | 3.57 | 0.000 | < 0.001 | TG-uTG | 0.011 |
| | | uTF | −1.22 | 0.010 | 1 | TF-TG | < 0.001 |
| | | uTG | 1.38 | 0.003 | 0.007 | uTF-uTG | < 0.001 |

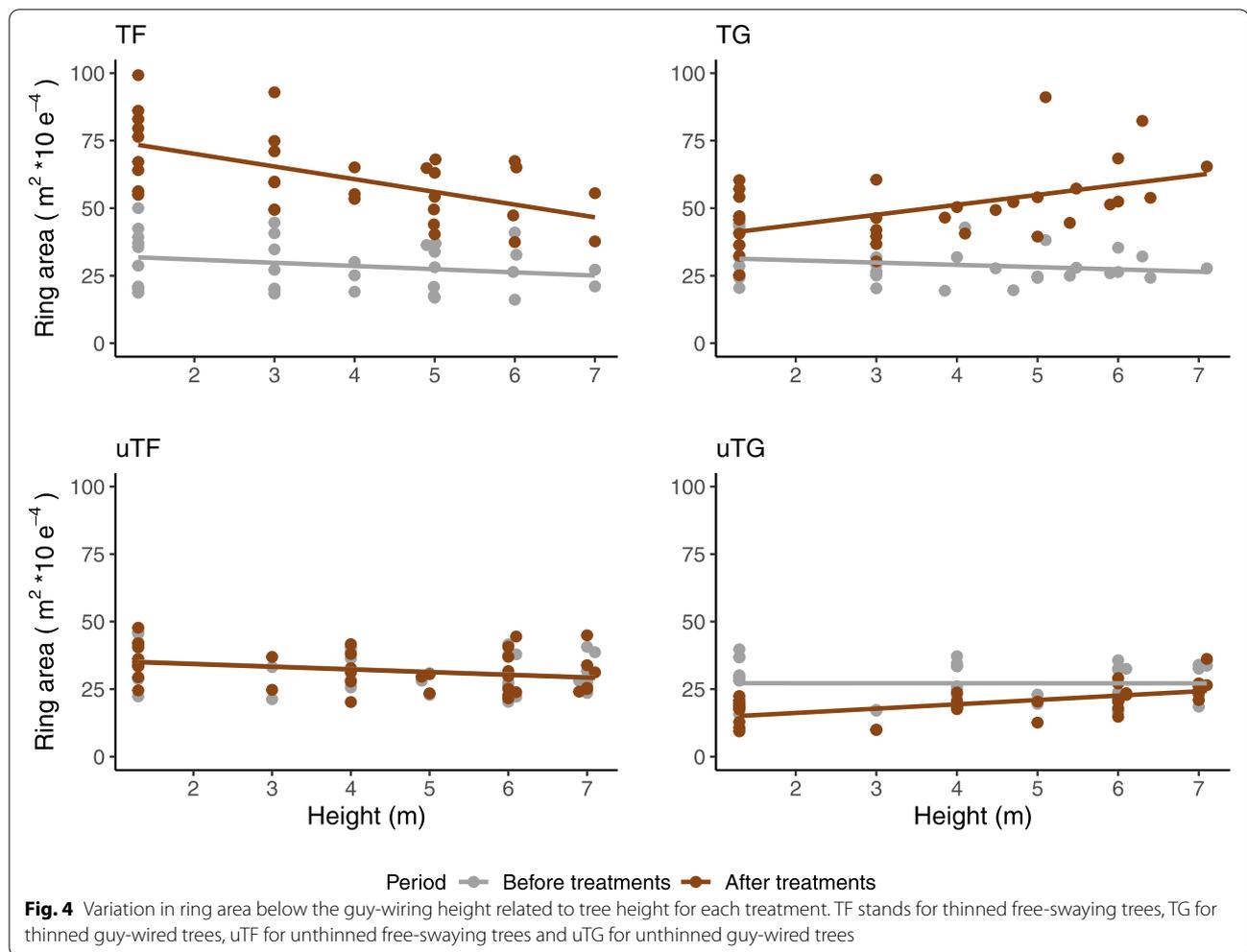
P values refer to the slope significance in the linear model (compared to zero) or Tukey contrasts (period and treatment effects). Significant values are in bold



low level of strain enhanced radial growth by 80% when applied several times during the growing season. Therefore, much lower strains than the ones typically applied in controlled experiments on axial growth are consistent with real strain regimes in the field, where they have proven to stimulate radial growth. However, there is no proof to date that such low levels can modify axial growth, as the physiological mechanisms are completely different between axial and radial growth responses. Our results point to further areas of research: (i) testing different ranges of magnitudes in controlled experiments, calibrated on the magnitude of experienced stimuli in natural conditions; and (ii) systematically measuring strains in field conditions to quantify the natural stimuli and to facilitate comparisons between field experiments.

Furthermore, to explain the differences in results concerning axial growth control between our experiment and those in controlled environments, the strains integrated over the whole plant could be responsible in S^3m (Mouliet et al 2015). However, this hypothesis was

derived from experiments on young seedlings with only a few large leaves and a streamlined structure, and can be strongly questioned in the case of adult broadleaf trees with a complex structure, many secondary axes and less obvious apical control. Guy-wiring does not restrain motion in the branches for secondary axis in the crown of adult trees. Nicoll et al. (2019) investigated the thigmomorphogenetic response in young thinned Norway spruce trees guy-wired at mid-height but with branches close to the ground; they did not detect any axial-growth response to guy-wiring. On the other hand, Meng et al. (2006) showed a strong increase in height in lodgepole pines whose overall motion, branches included, was constrained by roping a group of trees together at two thirds of the trees' height. These results suggest that more attention should be paid to mechanical strain perceived by branches, as already suggested by Coutand et al. (2008). Possible differences in apical control among species must be also considered, with different reactions expected in broadleaf species compared to conifers; different



tree architecture and geometry are highly responsible for resulting strain fields (Jackson et al. 2019). Furthermore, thigmomorphogenesis is not the only mechanism regulating axial growth; for example, shade avoidance responses push trees to grow in height in dense canopies and may also affect observed results (Huber et al. 2021).

5.2 Radial root growth requires mechanical stimulation by aerial forces

Thigmomorphogenetic responses increase root growth with increasing mechanical stimulation, as many studies have reported (Stokes et al. 1997; Nicoll and Dunn 2000; Ruel et al. 2003; Nicoll et al. 2019). Our results confirm that root radial growth is strongly driven by loads in the tree crown, which are transmitted by the lever arm of the trunk to the root system, and result in strains in the living cambial cells of the roots close to the trunk base. Indeed, 61% of the growth added after thinning is due to high levels of mechanosensing, proving how important mechanical strains derived from wind forces are in

improving anchorage. Further studies should focus more precisely on the strains located in different types of roots, using anchorage models (Yang et al. 2014). Researchers should find suitable methods to measure strains in roots in a non-destructive way: which roots are the most mechanically stimulated? Is there a threshold distance from the trunk base where strains become diluted and are no longer significant for thigmomorphogenesis?

5.3 Stem volume increment decreased and its distribution along the tree stem reversed when mechanical stimulation were restrained

In agreement with the thigmomorphogenetic assumption and as we expected, volume increment in the stem increased in the mechanically stimulated trees for both treatments (thinned and unthinned, see Fig. 2); this has also been observed in some other reports (Moore et al. 2014; Defosse et al. 2021). When we removed the mechanical stimuli, stem volume increment decreased, thus revealing the considerable influence of mechanical

stimulation on the distribution of radial growth within the trees. It is noteworthy that, as for root growth, the mechanical factor was not just significant, it was large: 45% of the volume increment added after thinning was due to mechanosensing. These results also emphasize that local mechanosensing is crucial to understanding the variations in the strength of the cambial-sink in relation to water and carbon fluxes. Unfortunately, mechanosensing is currently insufficiently taken into account in models for stem growth dynamics (Steppe et al. 2015). Lastly, thigmomorphogenetic growth, stimulated by routine, low level mechanical forces, seems to be necessary for the tree to ensure its resistance to occasional hazardous strong winds. Further work should investigate how both tree resilience and thigmomorphogenetic growth responses are linked to wind force regimes (with contrasting situations between strong and weak trees, between low and strong, or even extreme, stresses induced by winds, and between regular and sudden stress events).

5.4 A closer look into the distribution of ring area along the tree stem

Before guy-wiring and thinning, in three cases out of four (TF, TG, and uTG), there was no variation in the annual ring area along the trunk below the crown, in agreement with the Pressler's (empirical) law and the pipe model theory. Concerning ring width, its variation was virtually uniform in one case (uTF). Therefore, neither Pressler's law nor a uniform stress theory implying a growth response to mechanosensing seems perfectly relevant to describe the distribution of radial growth along the stem before thinning and guy-wiring. After thinning, growth distribution was no longer constant: we observed more growth in the lower stem (negative slope) in free (not guy-wired) trees. The negative slope was significant for both variables (width and area) so neither of the null hypotheses (a mechanical response under uniform stress or a constant area for hydraulic requirements) proved suitable.

However, our experiment did demonstrate that this negative slope was due to mechanosensing since the removal of the mechanical stimulations resulted in an opposite and significant positive slope, regardless of the treatment (thinned or unthinned trees). The lack of growth in mechanical stimulations inhibited growth in the lower part of the stem and induced more growth in the upper part, leading to an ice-cream cone distribution of ring width (or ring area). In the trees free to sway, Pressler's law was also disturbed after thinning but, contrary to the guy-wired trees, the ring area greatly decreased with height. This is in agreement with the well-known hypothesis linked to the uniform stress theory:

stem taper is governed by the mechanical need to ensure optimal trunk strength with more matter at the stem base where the lever arm is greater. However, a key question in tree ecology is to understand how this mechanism, designed to minimize risks from bending forces, relates to the adaptive growth response to environmental signals (and not resulting from a fixed genetically controlled design) (Mouliia et al. 2011). Our results demonstrate that, beyond the mechanical optimality of stem shape, the dynamics of radial growth and its distribution along the trunk is under strong thigmomorphogenetic control.

In our study, the observed preferential radial growth at the stem base after thinning (whereas growth was uniform before) suggests that thinning disturbs the uniform stress hypothesis, and that more intense strains are perceived at the stem base after canopy opening. Further studies should try to pinpoint when the constant stress state is valid (probably after a long process of adaptive growth without any disturbance of the strain regime) and when it is disturbed.

Lastly, as already mentioned, the biomechanical control of growth may explain some empirically observed deviations from Pressler's law. It is important to remember that the factors considered in these studies (e.g., Courbet 1999; Cortini et al. 2013) such as site effect, tree status, and stand density are also related to changes in wind exposure and tree structural traits, both of which influence the magnitude of the strains perceived by living cells in the cambium.

In addition to comparing the regression slopes, it is interesting to look at the minimal growth in case of guy-wiring since it must be sufficient to ensure hydraulic conductance. Lehnebach et al. (2018) proposed estimating the cross section of conducting xylem independently of mechanical effects just below the canopy because, even those some strains are present, the lever arm effect on mechanical strain magnitude is the most reduced at this location on the stem. Such a proposal is questionable because other structural characteristics are involved in mechanical strains, not only the lever arm effect. Indeed, the uniform stress hypothesis assumes that any part of the trunk is equally stressed since taper compensates for the lever arm). Our guy-wiring experiment ensured the absence of mechanical stimulations; therefore, the very small radial growth we observed far from the guy-wiring height is likely to represent changes linked to hydraulic needs. For unthinned guy-wired trees, basal growth (Fig. 4) was lower than the growth during the preceding period. For thinned guy-wired trees, the slight basal increment still overtook the growth during the preceding period; increasing hydraulic needs (more evapotranspiration associated to greater resource availability) after thinning could partly explain this result.

5.5 Toward a better integration of thigmomorphogenesis in forest growth modeling

Following earlier work, the present experiment demonstrates how important mechanical stimuli are in explaining growth allocation and carbon sinks inside trees. Nowadays, because climate change is shaping forests in previously unexperienced ways, forest growth modelling is integrating more and more eco-physiological process-based models (Pretzsch 2009; Fontes et al. 2010). However, the allocation of carbon among tree organs is poorly reflected in process-based models, although it is of great importance (Guillemot et al. 2017). By building on many previously cited works in tree biomechanics, this paper demonstrates how relevant mechanical strains and thigmomorphogenesis are in modelling issues.

The potential of biomechanics in forest growth modeling was investigated by (Dean and Baldwin 1996; Dean 2004; Dean et al. 2013). The authors used the constant stress hypothesis to calculate tree diameter from crown volume, which was assumed to be a load indicator. They also discussed the link between Reineke's stand-density index and the amount of bending strains generated by wind action on the canopy. However, their models were still based on the constant strain principle and allometry between load factors, size, and shape, and they do not take growth processes into account, i.e., the adaptive eco-physiological response over time of growth to mechanical stimuli. The challenge was then to adapt the S^3m model (Mouliat et al. 2015), which formalizes the dose–response curve with strains as stimuli and growth in length or diameter as a response. Although the S^3m model was developed for short durations and calibrated with greenhouse experiments on seedlings, it is already a functional structural model that integrates both the stimulus and the response at the whole tree level. However, one unsolved question remains: the accommodation process by which living cells stop responding to a repeated stimulus.

Our team's work on beech poles is designed to prefigure a new generation of forest growth models based on S^3m principles. We have already been able to accurately measure strains (Bonnesoeur et al. 2016) and quantify some responses (this paper and Constant et al., pers. com). Integrating S^3m into forest growth models requires two major steps. First, we must be able to model strains in living cells caused by wind flow in the canopy while taking forest and tree structures into account (see Gardiner et al. 2016 for a review of all the questions raised by such an approach). Note that such models have already been included in forest risk models (Gardiner et al. 2008). Second, we need a parsimonious and robust stimuli-response model, adapted from S^3m , that can account for time, stand type, tree species and size. Such

a process-based growth model should converge with optimal constant stress designs in steady state mechanical environments, and they should also model forest responses to changing wind exposure. We must remember that tree structure is the result of a long growth and wind exposure history. Changes in tree structure obviously result from silvicultural practices such as thinning but also from changing wind climates, a growing area of study for wind energy development (see Greene et al. 2010; Zeng et al. 2019).

Lastly, adaptive growth in response to wind-induced strains contributes to tree hardening and to improved forest resistance to extreme strong winds. For instance, the ice cream cone shape of incremental radial growth that appeared in guy-wired trees with no mechanical strains will certainly weaken the trees, putting them at risk if mechanical strains are reapplied later on. However, highly concentrated strains near the base could also trigger a rapid thigmomorphogenetic response to correct such a risky structure. As pointed out recently in a review by Gardiner (2021), a deeper understanding of tree acclimation to wind during growth is obviously a key issue for wind risk assessment. Designing risk and growth models that explicitly represent mechanical strains as factors of both growth and damage will be useful tools in this domain.

6 Conclusion

The effect of mechanical stimuli on plant biomass production is still under debate. Common sense may tell us that no changes are likely, as mechanical signaling is only a signal, not a resource like light, water or nutrients. However, signals can change crop production since they change the actual structure (architecture and morphology) of the system, which is in itself, an important component of crop functions and production (Vos et al. 2007).

As we show in the present study, removing mechanical stimulation in beech poles reduces root growth and stem volume increment in accordance with a thigmomorphogenetic process. However, we detected no effect of mechanical stimulations on axial growth; this was likely due to strain sensing in branches and a lower apical control in broadleaf trees than in conifers. The main contribution of our study is that we firmly proved that ring area distribution along the tree stem is under strong mechanical control. Generally speaking, mechanical signaling interacts with the water and carbon cycles to shape trees and tailor forest production. This argues in favor of introducing biomechanical variables (i.e., indicative of strains perceived by living cells) into both structural–functional, ecophysiological process-based models and dendrometric models of forest tree growth. The objective is to better understand

functional volume and taper equations in order to significantly improve the rules defining radial growth allocation along the stem, while also taking into account observed discrepancies in Pressler's law. Mechanical signals are shaped by tree architecture and other structural features and not just by wind speed. Therefore, integrating signal effects implies not just adding wind speed to statistical models as an additional environmental variable, but also selecting the proper stimulus variables (local or integrated strains) based on solid mechanics, as in mechanistic wind risk assessment. Overall, our study emphasizes that wind is a major driver of tree growth and therefore must be taken into account in forest growth models.

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Authors' contributions

TC, MF, and BM conceived the study. FN organized the conception of the field experiment in the context of forest management. JHDJ performed data collection and measurements, and wrote initial draft. JHDJ, JD, and TC contributed to data analyses. JHDJ, TC, MF, and JD contributed to the writing of the final draft. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets and Code generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

The authors declare that the study was not conducted on endangered, vulnerable or threatened species.

Consent for publication

All authors gave their informed consent to this publication and its content.

Competing interests

The authors declare that they have no conflict of interest.

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