



Article

The Effects of Wind Exposure on Scots Pine Trees: Within-Stem Variability of Wood Density and Mechanical Properties

Arkadiusz Tomczak ^{1,*}, Tomasz Jelonek ¹, Witold Pazdrowski ¹, Witold Grzywiński ¹, Przemysław Mania ² and Karol Tomczak ¹

- ¹ Department of Forest Utilization, Faculty of Forestry and Wood Technology, Poznań University of Life Sciences, Wojska Polskiego 71A, 60-625 Poznań, Poland; tomasz.jelonek@up.poznan.pl (T.J.); kul@up.poznan.pl (W.P.); witold.grzywinski@up.poznan.pl (W.G.); karool.tomczak@gmail.com (K.T.)
- ² Department of Wood Science and Thermal Technics, Faculty of Forestry and Wood Technology, Poznań University of Life Sciences, Wojska Polskiego 38/42, 60-627 Poznań, Poland; przemyslaw.mania@up.poznan.pl
- * Correspondence: arkadiusz.tomczak@up.poznan.pl

Received: 15 September 2020; Accepted: 12 October 2020; Published: 14 October 2020

Abstract: Survival in variable conditions of wind exposure depends on the strategy of trees in adapting to environmental constraints. There are many studies investigating the effect of wind on the adaptation of trees, but little attention is paid to the properties of the wood, particularly withinstem variability. In the present work, an analysis was made of within-stem variability of the density and mechanical properties of Scots pine wood from parts of stands with different wind exposure (stand edge, forest interior). The research was carried out in north-western Poland, in seven selected pine stands (without other species in the canopy) aged from 82 to 87 years. In each stand, three trial plots were marked, each at a different distance from the edge of the stand. The first plot was immediately adjacent to the edge (0-20 m), the second was at a distance of 30-50 m, and the third was at a distance of 60-80 m. Generally, wind exposure, defined by the distance from the windward edge, did not significantly affect the tree morphology and wood properties. A statistically significant difference was found only for the modulus of elasticity (MOE), between stand edge and forest interior. Trees growing at a distance from the stand edge compensate for their greater stem slenderness with higher elasticity. A certain growth response to wind loads is also represented by the within-stem variability of wood. We found that within-stem variability of wood at the stand edge is higher than in the forest interior. At various points along the stem, the wood density and strength were generally higher on the eastern radius (on the leeward side of the stem). Different wind resistance requirements at the stand edge and in the interior lead to combinations of tree architecture and wood properties that enable the best resistance to wind loads.

Keywords: growth; adaptation; tree stability; compressive strength longitudinal to grain; modulus of rupture; modulus of elasticity

1. Introduction

Wind is one of the most important abiotic factors acting on forests [1–3]. In extreme cases, this action leads to very serious disturbances to the functioning of forest ecosystems and generates huge economic losses [4–7]. Mainly for these reasons, attempts are made to assess levels of risk, and simulations are performed with the aim of developing management models that minimise the risk of

damage [8–17]. Such damage often occurs on a large scale, and is linked by some researchers to climate change [18–21].

On encountering an obstacle such as a forest, wind changes its direction (rises) and loses some of its speed and strength [22,23]. The change of direction is associated with turbulence [24,25]. In passing the obstacle, air masses fall and strike the crowns of trees. The load is particularly strong on rows of trees growing close to the edge of the stand. The force exerted by the wind on a forest edge depends on its shape and tightness. The pressure increases when the stand edge is a dense, containing a large number of trees with long crowns. The pressure decreases when the structure enables air masses to rise relatively freely or to flow freely under the tree crowns [23]. Generally, the most heavily loaded part of the stand is the canopy. For this reason, many studies of the tree–wind relationship focus on the crowns. In this regard, analyses are made of—among other things—movements of air and the resistance coefficient [26–29] and the stability of trees [30,31]. In the case of broadleaf stands, the leaves make an important contribution to the resistance [32–35].

The reaction of plants to mechanical signals is called thigmomorphogenesis [6,36–39]. Persistent action of the wind on forests and trees gives rise to reactions which may be regarded as adaptive [40,41]. These are changes in the structure, growth, or condition of stands, or in tree morphology [6,25,41–52]. Mechanosensitive control over growth and morphogenesis is an adaptive trait, reducing the risks of breakage or explosion [53,54]. In the 1950s, Jacobs [55] carried out an experiment which involved immobilising the lower part of a tree stem. The swaying upper part of the stem, just above the point of immobilisation, grew significantly faster than the immobilised part below that point. Following the removal of the fastenings, the differences in radial growth were not significant. Telewski and Jaffe [56,57] noted further that the direction of action of the force is important. If the direction remains the same, then a certain part of the stem cross-section is subject to greater compressive and tensile stresses, which have a stimulating effect on the activity of the cambium. There is a change in the pattern of radial growth, and thus the shape of the stem cross-section is altered [58–60].

Another response to mechanical stress may be a change in the structure and properties of the wood [56,57,61,62]. A typical example of a tree's response mechanism is the development of reaction wood [63]. Detailed study of this phenomenon has shown primarily what role in the process is played by static loads (gravitropism). Wind pressure on a tree additionally generates what are called dynamic loads. These occur periodically, and their size depends on the wind strength and speed and on the effect of wind exposure. In a stand, wind exposure depends mainly on the distance from the forest edge [64]. Brüchert [65] showed that the differences in wood properties between trees growing close to the edge and in the interior of a forest were not significant. Particularly interesting, however, is the variation in properties over a cross-section of the stem, between the windward and leeward sides [58,66]. On the one hand, the disproportions between the sides of the stem increase with age; on the other, the effect depends on the distance from the edge of the stand—the greater the distance, the smaller the differences [67].

In real conditions, and in the case of mature trees in a forest, it is hard to obtain empirical evidence of relationships between wood properties and biomechanical constraints [68]. In fact, many properties responsible for the mechanical structure are closely correlated, and in natural conditions, there are limited possibilities of measuring them and making a comprehensive analysis of them [69,70]. For this reason, many existing studies of the tree–wind relationship focus mainly on analysis of the morphological traits of trees and the related resistance to dynamic loads [71,72]. Wood structure and properties have been studied mainly in terms of the resistance of trees to extremely strong destructive loads. Experimenters have attempted to initiate damage to trees in a controlled manner [65,73,74] and have compared the properties of wood from damaged and undamaged trees [75–79].

The significance of wood properties, particularly density, for the life strategy, adaptation, and long-term stability of trees continues to be debated [80–82]. Loehle [83] believes that tree architecture is an effect of constraints that result from the wood properties. Simply, a tree produces wood of limited strength. We aimed to determine in precise quantitative terms how trees, under the influence

of position and mechanical forces, adapt to the microclimate in the stand. We focus particularly on the properties as features resulting indirectly from the dynamics of secondary growth, because in conifer species, these are strongly correlated traits. In addition, wood properties have previously been studied chiefly through experiments that simulate mechanical forces. Our research took place in commercial stands, where the parameters of the model cannot be directly measured and calibrated [69]. The response of secondary growth to mechanical forces is the easiest to measure, particularly if the research is focused on adaptive changes over a long time. Mature stands, exposed to prevailing winds, were studied because a process of acclimatisation must have taken place as the trees aged. In fact, long-term stability represents a complex of situations and variables, often unknown and uncontrolled. Nonetheless, in this way we can give an indication of how trees in a stand adapt to real wind loads.

The aim of the study was to analyse within-stem variability of the density and mechanical properties of the wood of Scots pine, the most significant species in Polish forests. Research was carried out in wind-exposed stands. We proposed the hypothesis that: (i) wind induces asymmetric stresses that are sensed by trees, resulting in higher wood density and strength on the leeward side of the stem (the side subject to stronger and more frequent mechanical loads); (ii) trees growing at a distance from the stand edge are subject to smaller loads (lower growth response to mechanical loads) compared with those growing close to the edge, and as a result, the wood properties on their windward and leeward sides are similar; (iii) the variability of wood properties is an adaptation to the real wind loads on mature trees in the forest. Account must be taken of the specific conditions of our experiment, including the species, age, and structure of the stand.

2. Materials and Methods

2.1. Stand Selection

The study was carried out in the north-western part of Poland, in seven mature stands of Scots pine (*Pinus sylvestris* L.) (Figure 1). In this area, the annual average wind speed is 3.9 m/s, the average temperature is 8.2 °C, and annual rainfall is 795 mm.



Figure 1. Location of the study (number explanation in Table 1).

One of the basic criteria for selecting areas for study was their closeness to open area (without trees or other obstacles). In view of the prevailing winds in this part of Europe, the windward forest edge was on the side facing west or in a similar direction (north-west or south-west). The selected stands consisted of pine trees (with no other species in the canopy) and were similar in terms of age and other features. The age of the stands ranged from 82 to 87 years. The mean diameter at breast height ranged from 31 to 37 cm, and the height from 24 to 27 m (Table 1). The average stand density per plot (per hectare): A 62 (312), B 61 (305), C 59 (293).

No.	Forest District	Age	dbh	Height	Coordina	Direction of the	
		0					Stand Edge
			(cm)	(m)	Ν	Ε	
1	Miastko I	84	34	26	53°58′28″	16°58′3″	N-S
2	Miastko II	89	36	26	54°0′56″	16°53′59″	N-S
3	Warcino	86	31	25	54°12′37″	16°52′28″	NW-SE
4	Czaplinek	87	35	27	53°37′35″	16°11′57″	N-S
5	Łupawa	83	37	24	54°23′11″	17°17′40″	N-S
6	Świdwin	83	32	26	53° 53′3″	15°44′18″	N-S
7	Czarnobór	82	31	24	53°36′59″	16°40′37″	NE-SW

Table 1. Characteristics of stands, in which mean sample plots were located.

Note: dbh-diameter at breast height.

2.2. Selection of Model Trees

Within each stand, three trial plots were marked out in the shape of rectangles, of which the longer sides, of length 100 m, were parallel to the stand edge. The shorter side of each rectangle

measured 20 m. The trial plots were located at different distances from the stand edge: the first was adjacent to it (plot A: trees growing to 20 m from the stand edge, without first row), the second was at a distance of 30–50 m (plot B: trees growing between 30 and 50 m from the stand edge), and the third was at a distance of 60–80 m (plot C: trees growing between 60 and 80 m from the stand edge) (Figure 2). This meant that the studied trees were subject to different levels of wind exposure, because the average wind speed rapidly decreases from the edge to the interior of the stand [22].



Figure 2. Location plots in stand and sampling procedure.

On each trial plot, selected morphological traits of the trees were measured: diameter at breast height (dbh), tree height (th), and height of the first living branch of the crown. Trees growing on the forest edge (first row), growing in the second storey of the stand, or heavily inclined were excluded from the measurements. Dbh (in bark) was measured with a calliper to an accuracy of 1 cm, in opposite directions (minimum and maximum diameters, and in the north–south and east–west directions). Tree height (th) and the position of the first living branch of the crown were measured with an accuracy of 0.1 m using a Nikon Forestry Pro laser rangefinder. The crown length (cl) was obtained by subtracting the height of the first living branch from the total height of the tree. The trees were further characterised using selected structural indicators: the slenderness ratio (tree height/dbh) and relative crown length (tree height/length of crown).

In each stand, six model trees were selected, two from each trial plot. Hence 14 trees were selected in total from each plot, giving 42 trees in all (Table 2). Average distance of model trees from the stand edge: 11 m (plot A); 39 m (plot B), 67 m (plot C).

Table 2. Numbers of model trees, logs, and samples.



model trees	14	14	14	42
logs for wood samples	70	70	70	210
samples for wood density (WD)	421	403	421	1245
samples for compressive strength (CS)	421	409	434	1273
samples for modulus of rupture (MOR)	420	400	440	1260
samples for modulus of elasticity (MOE)	419	400	438	1257

2.3. Sampling Procedure

From each model tree, five logs were cut from different parts of the stem. Each log was located at a different height (level). The first was cut from breast height level, and the second and subsequent logs were taken from 20%, 40%, 60%, and 80% of the height of the tree (Figure 2).

Samples with normalised cross-section $(20 \times 20 \text{ mm})$ were located adjacently along the W and E radii, omitting the core (Figure 2). In this way, information was obtained on mean values for the whole cross-section of the stem, and the effect of cambial age on wood properties was eliminated. All samples were free of structural defects. In order to characterize the experimental material (for compressive strength test), numbers and the width of annual rings were measured on the cross-sections of the wood samples.

2.4. Measurement of Wood Properties

Wood density was determined for wood samples of size 20 (R) × 20 (T) × 30 (L) mm³, serving to determine the compressive strength of the wood along the fibres. The sample densities were determined according to the method recommended in ISO 13061-2:2014 [84]. The mass of each sample was measured on an analytical balance with ± 0.001 g accuracy. The dimensions were measured with a digital calliper to an accuracy of ± 0.01 mm.

To ensure that the results approximated the properties of wood in the stems of growing trees, strength tests were carried out at moisture contents higher than 30% (above the saturation point of the fibres). The limiting moisture of the membranes was obtained by immersing the samples in water until their dimensions stabilised; that is, until the increment in the individual dimensions of the sample, measured at a 72-h interval, was equal to or less than 0.2 mm.

Experimental tests were performed using the TIRA TEST 2000 wood testing machine. The compressive strength of the wood in a longitudinal direction (or stress to failure, CS) was determined in accordance with ISO 13061-17:2017 [85] on 20 (R) × 20 (T) × 30 (L) mm³ rectangular samples.

For modulus of rupture (MOR) and modulus of elasticity (MOE), the three-point bend test was carried out in accordance with PN-77/D-04103 [86]. The samples (20 (R) \times 20 (T) \times 300 (L) mm³) were placed on the machine support pins separated by a distance of 240 mm in such a way that the forced deflection was always in the tangential direction. The load was applied at the midpoint of the sample on the radial surface.

Modulus of rupture (MOR) was calculated using Equation (1):

$$MOR = \frac{{}_{3}F_{max}L}{2bh^2} (MPa), \tag{1}$$

where F_{max} is the maximum (breaking) force (N), L is the distance between supports (mm), and b and h are the width and height, respectively, of the test samples (mm).

Modulus of elasticity (MOE) was calculated using Equation (2):

$$MOE = \frac{3(F_{n+1} - F_n)L^3}{64bh^3(f_{n+1} - f_n)}$$
(MPa), (2)

where $F_{n+1} - F_n$ is the increment in load within the linear region of the load–deflection curve (N), and $f_{n+1} - f_n$ is the increment in deflection corresponding to $F_{n+1} - F_n$ (mm).

2.5. Statistical Analyses

In order to compare the physical and mechanical properties of wood with respect to the experimental variables, in the first step, the Lilliefors test was used to examine the normal distribution

Forests 2020, 11, 1095

of data. The data in the analysed groups were of different quantities and had no normal distribution. Because of this, for three or more independent observations, the non-parametric Kruskal–Wallis test was carried out, followed by a Dunn test for multiple comparisons of means from each group of data. Statistical inference was performed at the significance level $\alpha = 0.05$. The experimental data were analysed using Statistica 13.1 (TIBCO Software Inc., Palo Alto, CA, USA).

3. Results

The trees in the forest interior were higher by approximately 3 m than those growing on the stand edge, but the differences were not statistically significant. The slenderness ratio for trees growing in the 20 m strip at the stand edge (plot A) was 78; for the zone of moderate wind exposure (B) it was 81; and for the zone furthest from the stand edge (C) it was 85. There were no statistically significant differences. The variation in the slenderness ratio—the ratio of the height of a tree to its diameter at breast height—may be expected, since the mean dbh values of trees in the different wind exposure zones were very similar, ranging from 32 to 34 cm. The crown lengths of the studied trees decreased with increasing distance from the stand edge, from 8.4 m in the edge zone to 6.3 m. The relative crown length decreased similarly: at the stand edge, the living crown accounted for more than one-third of the length of the stem, while in the interior, it was approximately one-quarter. In the case of this indicator of the morphological structure of trees, statistically significant differences were found between the plots of greatest exposure (A) and low exposure (C). Crown diameter varied in an entirely different manner than the aforementioned features: the widest crowns (4.3 m) were those of trees at the stand edge, and moderately wide crowns (4.0 m) were found on the trees least exposed to the action of the wind, growing at the greatest distance from the stand edge (Table 3).

	A (0–20 m)	B (30–50 m)	C (60–80 m)
	Mean ± SD	Mean ± SD	$Mean \pm SD$
tree height (th) (m)	23.8 ± 1.2	25.9 ± 2.7	26.9 ± 3.3
diameter at breast height (dbh) (cm)	32 ± 6.9	34 ± 5.9	33 ± 7.5
height-to-diameter-ratio (h:d)	78 ± 16.5	81 ± 17.8	85 ± 15.1
radius E d1.3—leeward (cm)	17.8 ± 4.3	16.7 ± 4.5	15.7 ± 3.7
radius W d1.3—windward (cm)	13.2 ± 2.6	13.1 ± 2.7	12.1 ± 2.9
crown length (cl) (m)	8.4 ± 2.0	7.1 ± 2.2	6.3 ± 2.2
crown ratio (cl:th) (crown length/tree height)	$0.35\pm0.08~^{\rm C}$	0.27 ± 0.07	0.23 ± 0.06 $^{\rm A}$
crown diameter (cd) (m)	4.3 ± 1.3 ^B	3.3 ± 1.4 ^A	4.0 ± 1.8

Table 3. Model trees characteristics.

Note: different superscripts denote a statistically significant difference between plots.

3.2. Differences of Wood Properties Between Stand Edge and Forest Interior

There were no statistically significant differences in the mean oven-dry density (WD), compressive strength longitudinal to grain (CS), or modulus of rupture (MOR). The trees growing close to the stand edge (A) and at the greatest distance from it (C) had wood with similar density and strength. Of the analysed properties, only MOE exhibited significant differences, and only between plots A and C. The value of MOE increased with increasing distance from the stand edge (Table 4).

Table 4. Wood	properties	characteristics.
---------------	------------	------------------

	A (0–20m)	B (30–50 m)	C (60–80 m)
	$Mean \pm SD$	$Mean \pm SD$	Mean ± SD
oven-dry density (WD) (kg/m ³)	495 ± 76	490 ± 82	491 ± 83
compressive strength longitudinal to grain (CS) (MPa)	23.7 ± 4.5	23.2 ± 4.4	23.6 ± 4.6
modulus of rupture (MOR) (MPa)	48.8 ± 10.5	48.3 ± 10.0	48.5 ± 10.5
modulus of elasticity (MOE) (GPa)	4.98 ± 1.23 ^C	5.03 ± 1.29	5.23± 1.25 ^A

Note: different superscripts denote a statistically significant difference between plots.

3.3. Variability of Wood Properties Across the Stem

WD, CS and MOR were higher in the eastern (leeward) part of the stem cross-section, while MOE was higher on the western (windward) part. The greatest differences were observed in plot A (statistically significant for all properties). In relative terms, the difference was 3.5% for WD, 6.1% for CS, 4.2% for MOR, and 3.9% for MOE. In the forest interior (plot B), the differences between the parts of the stem were smaller and statistically insignificant: 0.6% for WD, 3.1% for CS, 3.0% for MOR, and 3.8% for MOE. The wood from trees in zone C was found to be homogeneous, with identical or nearly identical values for the analysed properties on the western and eastern sides; the relative differences were 0.2% for WD, 0.4% for CS, and 0% for MOR, and MOE. There were no statistically significant differences between the zones (Figure 3a–d).





Figure 3. Differences between windward (radius W) and leeward (radius E) side of the tree stem: (**a**) oven-dry density; (**b**) compressive strength longitudinal to grain; (**c**) modulus of rupture (MOR); (**d**) modulus of elasticity (MOE). Note: stars denote a statistically significant difference between radii.

3.4. Variability in Wood Properties Along the Stem

In plot A, the largest relative differences in the value of WD between the E and W radii (5.0%) were recorded at dbh (Figure 4a). For the other properties, the largest differences were found for CS

at 20% (7.1%) and 40% relative height (7.0%), for MOR at 40% (8.3%) and 80% relative height (8.6%), and for MOE at dbh (9.8%) and 80% relative height (9.5%) (Figures 5a, 6b and 7c). In plot B, the largest differences were found for WD at 80% relative height (3.6%), for CS at dbh (6.0%) and 20% relative height (6.7%), for MOR at 40% relative height (5.4%), and for MOE at 60% relative height (15.1%) (Figures 4b, 5b, 6b, and 7b). In plot C, the largest differences were found for WD, CS, and MOR at 80% relative height (respectively 4.8%, 5.3%, and 5.8%) and for MOE 40% relative height of the tree (4.5%) (Figures 4c, 5c, 6c, and 7c).



Figure 4. Variability in oven-dry density (WD) along the stem (the lines represented ± standard deviation): (**a**) plot A (0–20 m); (**b**) plot B (30–50 m); (**c**) plot C (60–80 m).



Figure 5. Variability in compressive strength longitudinal to grain (CS) along the stem (the lines represented ± standard deviation): (**a**) plot A (0–20 m); (**b**) plot B (30–50 m); (**c**) plot C (60–80 m).



Figure 6. Variability in modulus of rupture (MOR) along the stem (the lines represented ± standard deviation): (**a**) plot A (0–20 m); (**b**) plot B (30–50 m); (**c**) plot C (60–80 m).



Figure 7. Variability in modulus of elasticity (MOE) along the stem (the lines represented ± standard deviation): (**a**) plot A (0–20 m); (**b**) plot B (30–50 m); (**c**) plot C (60–80 m).

4. Discussion

Wind exposure, defined by distance from the windward edge of the stand, does not have a significant effect on tree morphology. Above all, the trees had similar diameters at breast height. It is possible that in a stand without gaps, the susceptibility of trees to the wind does not need to be compensated by an increase in the stem diameter. The presence of neighbouring trees has a favourable effect on stability. Particularly smaller trees are sheltered by larger neighbouring trees. Nevertheless, during storms with strong winds, the response of individual trees is highly irregular, and the shelter effect from larger trees might not be as effective [49,87]. It is known that the stresses induced in the stem under wind load increase radial growth [6]. In this case, the stem cross-sections become oblate. While narrower annual rings (shorter radii) were observed on the windward

(western) side of the stem, the differences from the leeward (eastern) side were not statistically significant.

Another effect of the action of the wind on trees is a reduction in upward growth [6]. Although the absolute difference in height between the stand edge (A) and the forest interior (C) was approximately 3 m, it was not statistically significant. Similarly, significant differences were not found in the case of crown length. Both the height of the tree and length of the crown are found to be factors affecting tree stability [8]. However, a more appropriate indicator is the ratio of crown length to tree height (the crown ratio). In this case, there was a statistically significant difference between the stand edge (A) and the forest interior (C). Trees growing further from the edge had longer crowns. They also had slightly lower slenderness ratios. In combination, these two indicators show that the stability of trees gradually decreases from the edge of the stand to the interior. Similar results were reported by Bascuñán et al. [67] and by Bruchert and Gardiner [64]. According to those authors, both the shape of the stem and the wood properties vary depending on wind exposure, although Brüchert [65] notes that the differences in the wood properties are not statistically significant. We obtained similar results. We did not observe significant differences in wood density, compressive strength, or MOR. A statistically significant difference was found only for MOE between plot A (stand edge) and C (forest interior). The more exposed trees, growing on the edge of the stand, are less tall and have more tapered stems. Those growing in the interior are taller and more slender. The stems of trees on the stand edge are more rigid in the lower part and more flexible in the crown part. Trees growing at a distance from the edge compensate for their greater stem slenderness with higher elasticity [64,67].

A certain growth response to wind loads is represented by the variability of wood properties between the windward and leeward sides of the stem [58,66]. The disproportions between the sides of the stem increase with age, and the effect also depends on the distance from the stand edge: the greater the distance, the smaller the differences [67]. The stands included in our study were of similar age. However, like Bascuñán et al. [67], we noted that with increasing distance from the windward edge of the stand, the differences between the windward and leeward sides decreased. We observed statistically significant differences only in plot A, closest to the stand edge. In this case, the mean values characterised the whole stem. Analysing the differences between the sides at different positions along the stem, we found the differences to be noticeable, but not statistically significant.

Generally, along the stem, higher wood density and strength were recorded on the eastern radius. This is a pattern that quite well describes the variability of wood properties in plots A and B. However, in the case of trees growing in plot C, both density and strength decrease in the direction from the base to the top of the stem, but in different parts, higher values were recorded either on the windward side (W) or on the leeward side (E). The longitudinal pattern of variation in wood properties and the decreasing trend with height on the stem were in accordance with previous studies on Scots pine and other softwood species [88–91].

Uninherited features, shaped under the influence of the environment, are an expression of adaptive processes. Phenotypic variability is a condition for trees' survival in different conditions of growth and development. Growth responses involve both eccentric wood growth around the trunk, stiffening as wood matures, and change in the modulus of elasticity of new wood [60,92-94]. According to Sellier and Fourcaud [95], however, the material properties play a limited role in tree dynamics, and architecture is more significant. Generally, wind-exposed trees have greater safety margins than protected trees [96]. Our experiments were carried out in the relatively small areas into which commercial stands are divided. These provide highly uniform conditions for growth and development. We assumed that trees growing several tens of metres from the stand edge would be subject to smaller loads (lower growth response to mechanical loads) than those growing close to the edge. In such conditions, according to Moore et al. [68], it may be difficult to obtain empirical evidence of relationships between the wood properties and biomechanical constraints. The biomechanics of a tree consist of a complicated system of relations between features, which in natural conditions are closely correlated, and there are limited possibilities of measuring these and subjecting them to comprehensive analysis [69]. Different requirements relating to wind resistance at the stand edge and in the forest interior cause tree architecture and wood properties to be combined in such a way as to provide the best resistance to wind loads. In zones subject to the strong action of the wind, the trees are less tall, their stems are more tapered, the crowns are lower, and the wood properties exhibit greater variation. The stability of a tree thus depends not only on morphological traits: the degree of within-stem variability will also play an important role.

Within-stem variability of wood is a natural feature and is probably determined by the physiological and biomechanical functionality of plant tissues. The changes observed in the structure and properties of wood would appear to be linked to changes occurring in the biomechanics of a tree as it grows and develops. Based on the results obtained, it may also be assumed that the differences are the result of a process of acclimatisation, which leads to the formation of an optimum biostructure in both physiological and mechanical terms. Because of such within-stem variability of wood properties, the stability of the tree, as well as the ability of the stem to transfer static and dynamic loads, would appear to be much greater than in the case of wood with a homogeneous structure and properties.

5. Conclusions

The mean values (for the whole of the stem) of the density, compressive strength, and modulus of rupture of the wood, for trees growing at different distances from the windward edge of the stand, did not exhibit statistically significant differences. Only the MOE increased with increasing distance from the edge, similarly to the mean tree height and slenderness. This means that trees growing at a distance from the stand edge compensate for their increased slenderness with greater stem elasticity. A certain growth response to wind loads was the variability in wood properties between the western and eastern sides of the stem. This effect was particularly marked in trees subject to high wind exposure, growing closest to the stand edge. With increasing distance from the edge, the differences in density and strength between the windward and leeward sides gradually decreased. Comparing different sections along the stem, it was found that higher wood density and strength on the eastern (leeward) radius generally occurred in the lower part of the stem. This shows that the different requirements relating to wind resistance at the stand edge and in the forest interior lead the tree architecture and wood properties to combine in a way that enables the best resistance to wind loads. It may be assumed on this basis that the effect of exposure will also be visible in the structure of the wood (tracheid length, cell wall thickness, microfibrils angle, etc.). However, this needs to be verified in future research, which should also consider other species of tree. This is one of the paths to understanding the different strategies used by trees to adapt to environmental constraints and the non-uniform growth response to those strategies.

Author Contributions: Conceptualization, A.T.; methodology, A.T., T.J., and W.P.; formal analysis, A.T., T.J., W.G., P.M., and K.T.; data curation, A.T. and T.J.; writing—original draft preparation, A.T., T.J., W.P., W.G., P.M. and K.T.; writing—review and editing, A.T., T.J., W.G., and P.M.; visualization, A.T.; supervision, A.T. All authors have read and agreed to the published version of the manuscript.

Funding: Publication was co-financed within the framework of the Polish Ministry of Science and Higher Education's program: "Regional Initiative Excellence" in the years 2019–2022 (No. 005/RID/2018/19).

Acknowledgments: The authors would like to acknowledge anonymous reviewers for commenting and improving scientific quality of this paper.

Conflicts of Interest: The authors declare no conflicts of interest.

References

- 1. Ennos, A.R. Wind as an Ecological Factor. *Trends Ecol. Evol.* **1997**, *12*, 108–111, doi:10.1016/S0169-5347(96)10066-5.
- Ulanova, N.G. The Effects of Windthrow on Forests at Different Spatial Scales: A Review. For. Ecol. Manag. 2000, 135, 155–167, doi:10.1016/S0378-1127(00)00307-8.
- Tomczak, A.; Jelonek, T.; Jakubowski, M. Changes in the Structure and Properties of Wood as an Effect of the Impact of Wind on Trees. Sylwan 2012, 156, 776–783.

- 4. Schelhaas, M.-J.; Nabuurs, G.-J.; Schuck, A. Natural Disturbances in the European Forests in the 19th and 20th Centuries. *Glob. Chang. Biol.* **2003**, *9*, 1620–1633, doi:10.1046/j.1365-2486.2003.00684.x.
- Mitchell, S.J. Wind as a Natural Disturbance Agent in Forests: A Synthesis. Forestry 2013, 86, 147–157, doi:10.1093/forestry/cps058.
- Gardiner, B.; Berry, P.; Moulia, B. Review: Wind Impacts on Plant Growth, Mechanics and Damage. *Plant Sci.* 2016, 245, 94–118, doi:10.1016/j.plantsci.2016.01.006.
- Forzieri, G.; Pecchi, M.; Girardello, M.; Mauri, A.; Klaus, M.; Nikolov, C.; Rüetschi, M.; Gardiner, B.; Tomaštík, J.; Small, D.; et al. A Spatially Explicit Database of Wind Disturbances in European Forests Over the Period 2000–2018. *Earth Syst. Sci. Data* 2020, *12*, 257–276, doi:10.5194/essd-12-257-2020.
- Peltola, H.; Kellomäki, S.; Väisänen, H.; Ikonen, V.P. A Mechanistic Model for Assessing the Risk of Wind and Snow Damage to Single Trees and Stands of Scots Pine, Norway Spruce, and Birch. *Can. J. For. Res.* 1999, 22, 647–661, doi:10.1139/x99-029.
- Valinger, E.; Fridman, J. Models to Assess the Risk of Snow and Wind Damage in Pine, Spruce, and Birch Forests in Sweden. *Environ. Manag.* 1999, 24, 209–217, doi:10.1007/s002679900227.
- Ancelin, P.; Courbaud, B.; Fourcaud, T. Development of an Individual Tree-Based Mechanical Model to Predict Wind Damage Within Forest Stands. *For. Ecol. Manag.* 2004, 203, 101–121, doi:10.1016/j.foreco.2004.07.067.
- Scott, R.E.; Mitchell, S.J. Empirical Modelling of Windthrow Risk in Partially Harvested Stands Using Tree, Neighbourhood, and Stand Attributes. For. Ecol. Manag. 2005, 218, 193–209, doi:10.1016/j.foreco.2005.07.012.
- Gardiner, B.; Byrne, K.; Hale, S.; Kamimura, K.; Mitchell, S.J.; Peltola, H.; Ruel, J.-C. A Review of Mechanistic Modelling of Wind Damage Risk to Forests. *Forestry* 2008, *81*, 447–463, doi:10.1093/forestry/cpn022.
- 13. Heinonen, T.; Pukkala, T.; Ikonen, V.-P.; Peltola, H.; Venäläinen, A.; Dupont, S. Integrating the Risk of Wind Damage into Forest Planning. *For. Ecol. Manag.* **2009**, *258*, 1567–1577, doi:10.1016/j.foreco.2009.07.006.
- Hanewinkel, M.; Peyron, J.L. The Economic Impact of Storms. In *Living with Storm Damage to Forests: What Science Can Tell Us;* Gardiner, B., Schuck, A., Schelhaas, M.-J., Orazio, C., Blennow, K., Nicoll, B., Eds.; European Forest Institute: Joensuu, Finland, 2013; pp. 55–63.
- Hale, S.E.; Gardiner, B.; Peace, A.; Nicoll, B.; Taylor, P.; Pizzirani, S. Comparison and Validation of Three Versions of a Forest Wind Risk Model. *Environ. Model. Softw.* 2015, 68, 27–41, doi:10.1016/j.envsoft.2015.01.016.
- Anyomi, K.A.; Mitchell, S.J.; Ruel, J.-C. Windthrow Modelling in Old-Growth and Multi-Layered Boreal Forests. *Ecol. Model.* 2016, 327, 105–114, doi:10.1016/j.ecolmodel.2016.02.003.
- Morimoto, J.; Nakagawa, K.; Takano, K.T.; Aiba, M.; Oguro, M.; Furukawa, Y.; Mishima, Y.; Ogawa, K.; Ito, R.; Takemi, T.; et al. Comparison of Vulnerability to Catastrophic Wind Between Abies Plantation Forests and Natural Mixed Forests in Northern Japan. *For. Int. J. For. Res.* 2019, *92*, 436–443, doi:10.1093/forestry/cpy045.
- Dale, V.H.; Joyce, L.A.; McNulty, S.; Neilson, R.P. The Interplay Between Climate Change, Forests, and Disturbances. *Sci. Total Environ.* 2000, *262*, 201–204.
- Dale, V.H.; Joyce, L.A.; McNulty, S.; Neilson, R.P.; Ayres, M.P.; Flannigan, M.D.; Hanson, P.J.; Irland, L.C.; Lugo, A.E.; Peterson, C.J.; et al. Climate Change and Forest Disturbances. *BioScience* 2001, 51, 723, doi:10.1641/0006-3568(2001)051[0723:CCAFD]2.0.CO;2.
- Blennow, K.; Andersson, M.; Sallnäs, O.; Olofsson, E. Climate Change and the Probability of Wind Damage in Two Swedish Forests. *For. Ecol. Manag.* 2010, 259, 818–830, doi:10.1016/j.foreco.2009.07.004.
- Seidl, R.; Thom, D.; Kautz, M.; Martin-Benito, D.; Peltoniemi, M.; Vacchiano, G.; Wild, J.; Ascoli, D.; Petr, M.; Honkaniemi, J.; et al. Forest Disturbances Under Climate Change. *Nat. Clim. Chang.* 2017, *7*, 395–402, doi:10.1038/nclimate3303.
- Stacey, G.R.; Belcher, R.E.; Wood, C.J.; Gardiner, B.A. Wind Flows and Forces in a Model Spruce Forest. Bound. Layer Meteorol. 1994, 69, 311–334, doi:10.1007/BF00708860.
- Dupont, S.; Brunet, Y. Impact of Forest Edge Shape on Tree Stability: A Large-Eddy Simulation Study. Forestry 2008, 81, 299–315, doi:10.1093/forestry/cpn006.
- Irvine, M.R.; Gardiner, B.A.; Hill, M.K. The Evolution of Turbulence Across A Forest Edge. Bound. Layer Meteorol. 1997, 84, 467–496, doi:10.1023/A:1000453031036.
- 25. de Langre, E. Effects of Wind on Plants. *Annu. Rev. Fluid Mech.* **2008**, 40, 141–168, doi:10.1146/annurev.fluid.40.111406.102135.

- 26. Marcolla, B.; Pitacco, A.; Cescatti, A. Canopy Architecture and Turbulence Structure in a Coniferous Forest. *Bound. Layer Meteorol.***2003**, *108*, 39–59, doi:10.1023/A:1023027709805.
- Cescatti, A.; Marcolla, B. Drag Coefficient and Turbulence Intensity in Conifer Canopies. Agric. For. Meteorol. 2004, 121, 197–206, doi:10.1016/j.agrformet.2003.08.028.
- Dupont, S.; Brunet, Y. Edge Flow and Canopy Structure: A Large-Eddy Simulation Study. Bound. Layer Meteorol. 2008, 126, 51–71, doi:10.1007/s10546-007-9216-3.
- 29. Queck, R.; Bernhofer, C. Constructing Wind Profiles in Forests from Limited Measurements of Wind and Vegetation Structure. *Agric. For. Meteorol.* **2010**, *150*, *724–735*, doi:10.1016/j.agrformet.2010.01.012.
- Ciftci, C.; Brena, S.F.; Kane, B.; Arwade, S.R. The Effect of Crown Architecture on Dynamic Amplification Factor of an Open-Grown Sugar Maple (*Acer saccharum* L.). *Trees* 2013, 27, 1175–1189, doi:10.1007/s00468-013-0867-z.
- Ver Planck, N.R.; MacFarlane, D.W. Branch Mass Allocation Increases Wind Throw Risk for Fagus Grandifolia. For. Int. J. For. Res. 2019, 92, 490–499, doi:10.1093/forestry/cpz001.
- Frederick, R.H. A Study of the Effect of Tree Leaves on Wind Movement. *Mon. Wea. Rev.* 1961, 89, 39–44, doi:10.1175/1520-0493(1961)089<0039:ASOTEO>2.0.CO;2.
- Vogel, S. Drag and Reconfiguration of Broad Leaves in High Winds. J. Exp. Bot. 1989, 40, 941–948, doi:10.1093/jxb/40.8.941.
- Dellwik, E.; Bingöl, F.; Mann, J. Flow Distortion at a Dense Forest Edge. Available online: https://rmets.onlinelibrary.wiley.com/doi/abs/10.1002/qj.2155 (accessed on 14 May 2020).
- 35. Angelou, N.; Dellwik, E.; Mann, J. Wind Load Estimation on an Open-Grown European oak Tree. *For. Int. J. For. Res.***2019**, *92*, 381–392, doi:10.1093/forestry/cpz026.
- Jaffe, M.J. Thigmomorphogenesis: The Response of Plant Growth and Development to Mechanical Stimulation: With Special Reference to Bryonia Dioica. *Planta* 1973, 114, 143–157, doi:10.1007/BF00387472.
- 37. Jaffe, M.J.; Forbes, S. Thigmomorphogenesis: The Effect of Mechanical Perturbation on Plants. *Plant Growth Regul.* **1993**, *12*, 313–324, doi:10.1007/BF00027213.
- Coutand, C.; Martin, L.; Leblanc-Fournier, N.; Decourteix, M.; Julien, J.-L.; Moulia, B. Strain Mechanosensing Quantitatively Controls Diameter Growth and *PtaZFP2* Gene Expression in Poplar. *Plant Physiol.* 2009, 151, 223–232, doi:10.1104/pp.109.138164.
- Bonnesoeur, V.; Constant, T.; Moulia, B.; Fournier, M. Forest Trees Filter Chronic Wind-Signals to Acclimate to High Winds. *New Phytol.* 2016, 210, 850–860, doi:10.1111/nph.13836.
- Lundström, T.; Jonas, T.; Volkwein, A. Analysing the Mechanical Performance and Growth Adaptation of Norway Spruce Using a Non-Linear Finite-Element Model and Experimental Data. J. Exp. Bot. 2008, 59, 2513–2528, doi:10.1093/jxb/ern116.
- Rodriguez, M.; Langre, E. de; Moulia, B. A Scaling Law for the Effects of Architecture and Allometry on Tree Vibration Modes Suggests a Biological Tuning to Modal Compartmentalization. Available online: https://bsapubs.onlinelibrary.wiley.com/doi/abs/10.3732/ajb.0800161 (accessed on 13 May 2020).
- Valinger, E. Effects of Wind Sway on Stem Form and Crown Development of Scots Pine (*Pinus sylvestris* L.). Aust. For. 1992, 55, 15–21, doi:10.1080/00049158.1992.10676094.
- Telewski, F.W. Wind-Induced Physiological and Developmental Responses in Trees. In Wind and Trees; Coutts, M.P., Grace, J. Eds.; Cambridge University Press: Cambridge, UK, 1995; pp. 237–263.
- 44. Telewski, F.W. Is Windswept Tree Growth Negative Thigmotropism? *Plant Sci.* 2012, 184, 20–28, doi:10.1016/j.plantsci.2011.12.001.
- Telewski, F.W. Flexure Wood: Mechanical Stress Induced Secondary Xylem Formation. In Secondary Xylem Biology; Kim, Y.S., Funada, R., Singh, A.P., Eds.; Academic Press: Boston, MA, USA, 2016; pp. 73–91, ISBN 978-0-12-802185-9.
- Nicoll, B.C.; Ray, D. Adaptive Growth of Tree Root Systems in Response to Wind Action and Site Conditions. *Tree Physiol.* 1996, 16, 891–898, doi:10.1093/treephys/16.11-12.891.
- Jiao-jun, Z.; Zu-gen, L.; Xiu-fen, L.; Matsuzaki, T.; Gonda, Y. Review: Effects of Wind on Trees. J. For. Res. 2004, 15, 153–160, doi:10.1007/BF02856753.
- Tamasi, E.; Stokes, A.; Lasserre, B.; Danjon, F.; Berthier, S.; Fourcaud, T.; Chiatante, D. Influence of Wind Loading on Root System Development and Architecture in Oak (*Quercus robur* L.) Seedlings. *Trees* 2005, 19, 374–384, doi:10.1007/s00468-004-0396-x.
- 49. Schindler, D.; Bauhus, J.; Mayer, H. Wind Effects on Trees. *Eur. J. For. Res* **2012**, *131*, 159–163, doi:10.1007/s10342-011-0582-5.

- 51. Kašpar, J.; Hosek, J.; Treml, V. How Wind Affects Growth in Treeline Picea Abies. *Alp. Bot.* 2017, doi:10.1007/s00035-017-0186-x.
- 52. Tomczak, A.; Jelonek, T.; Pazdrowski, W. Characteristics of Selected Morphological Traits of Trees in Mature Scots Pine Stands Exposed to Wind. *Sylwan* **2014**, *158*, 183–191.
- Moulia, B.; Der Loughian, C.; Bastien, R.; Martin, O.; Rodríguez, M.; Gourcilleau, D.; Barbacci, A.; Badel, E.; Franchel, G.; Lenne, C.; et al. Integrative Mechanobiology of Growth and Architectural Development in Changing Mechanical Environments. In *Mechanical Integration of Plant Cells and Plants*; Wojtaszek, P., Eds.; Springer: Berlin/Heidelberg, Germany, 2011; pp. 269–302, ISBN 978-3-642-19091-9.
- 54. Moulia, B.; Coutand, C.; Julien, J.-L. Mechanosensitive Control of Plant Growth: Bearing the Load, Sensing, Transducing, and Responding. *Front. Plant Sci.* **2015**, *6*, doi:10.3389/fpls.2015.00052.
- Jacobs, M. The Effect of Wind Sway on the Form and Development of Pinus Radiata D. Don. Aust. J. Bot. 1954, 2, 35–51.
- Telewski, F.W.; Jaffe, M.J. Thigmomorphogenesis: Field and laboratory studies of Abies Fraseri in Response to Wind or Mechanical Perturbation. *Physiol. Plant.* **1986**, *66*, 211–218, doi:10.1111/j.1399-3054.1986.tb02411.x.
- Telewski, F.W.; Jaffe, M.J. Thigmomorphogenesis: Anatomical, morphological and mechanical analysis of genetically different sibs of Pinus taeda in response to mechanical perturbation. *Physiol. Plant.* 1986, 66, 219–226, doi:10.1111/j.1399-3054.1986.tb02412.x.
- 58. Robertson, A. Centroid of Wood Density, Bole Eccentricity, and Tree-Ring Width in Relation to Vector Winds in Wave Forests. *Can. J. For. Res.***1991**, *21*, 73–82, doi:10.1139/x91-011.
- Pruyn, M.L.; Ewers, B.J., III; Telewski, F.W. Thigmomorphogenesis: Changes in the Morphology and Mechanical Properties of Two Populus Hybrids in Response to Mechanical Perturbation. *Tree Physiol.* 2000, 20, 535–540, doi:10.1093/treephys/20.8.535.
- Alméras, T.; Fournier, M. Biomechanical Design and Long-Term Stability of Trees: Morphological and Wood Traits Involved in the Balance Between Weight Increase and the Gravitropic Reaction. *J. Theor. Biol.* 2009, 256, 370–381, doi:10.1016/j.jtbi.2008.10.011.
- 61. Koch, G.; Bauch, J.; Puls, J.; Schwab, E. Biological, Chemical and Mechanical Characteristics of "Wulstholz" as a Response to Mechanical Stress in Living Trees of *Picea abies* [L.] Karst. *Holzforschung* **2000**, *54*, 137–143, doi:10.1515/HF.2000.024.
- Kern, K.A.; Ewers, F.W.; Telewski, F.W.; Koehler, L. Mechanical Perturbation Affects Conductivity, Mechanical Properties and Aboveground Biomass of Hybrid Poplars. *Tree Physiol.* 2005, 25, 1243–1251, doi:10.1093/treephys/25.10.1243.
- Fournier, M.; Alméras, T.; Clair, B.; Gril, J. Biomechanical Action and Biological Functions. In *The Biology of Reaction Wood*; Springer Series in Wood Science; Gardiner, B., Barnett, J., Saranpää, P., Gril, J., Eds.; Springer: Berlin/Heidelberg, Germany, 2014; pp. 139–169, ISBN 978-3-642-10814-3.
- 64. Bruchert, F.; Gardiner, B. The Effect of Wind Exposure on the Tree Aerial Architecture and Biomechanics of Sitka Spruce (*Picea sitchensis*, Pinaceae). *Am. J. Bot.* **2006**, *93*, 1512–1521, doi:10.3732/ajb.93.10.1512.
- 65. Brüchert, F. *The Influence of the Site Factor Wind Exposure on Wood Quality;* Forestry Commission, Northern Research Station: Roslin, Scotland, 2000; p. 119.
- Zipse, A.; Mattheck, C.; Gräbe, D.; Gardiner, B. The Effect of Wind on the Mechanical Properties of the Wood of Beech (*Fagus sylvatica* L.) Growing in the Borders of Scotland. *Arboric. J.* 1998, 22, 247–257, doi:10.1080/03071375.1998.9747208.
- Bascuñán, A.; Moore, J.R.; Walker, J.C.F. Variations in the Dynamic Modulus of Elasticity with Proximity to the Stand Edge in Radiata Pine Stands on the Canterbury Plains, New Zealand. N. Z. J. For. 2006, 51, 4– 8.
- Moore, J.; Gardiner, B.; Sellier, D. Tree Mechanics and Wind Loading. In *Plant Biomechanics: From Structure to Function at Multiple Scales*; Geitmann, A., Gril, J., Eds.; Springer International Publishing: Cham, Switzerland, 2018; pp. 79–106, ISBN 978-3-319-79099-2.
- 69. Fournier, M.; Dlouhá, J.; Jaouen, G.; Almeras, T. Integrative Biomechanics for Tree Ecology: Beyond Wood Density and Strength. J. Exp. Bot. 2013, 64, 4793–4815, doi:10.1093/jxb/ert279.

- Jelonek, T.; Tomczak, A.; Karaszewski, Z.; Jakubowski, M.; Arasimowicz-Jelonek, M.; Grzywiński, W.; Kopaczyk, J.; Klimek, K. The Biomechanical Formation of Trees. *Drewno. Prace naukowe. Doniesienia. Komunikaty* 2019, 62, 5–22, doi:10.12841/wood.1644-3985.318.05.
- Petty, J.A.; Swain, C. Factors Influencing Stem Breakage of Conifers in High Winds. For. Int. J. For. Res. 1985, 58, 75–84, doi:10.1093/forestry/58.1.75.
- 72. Nishimura, T.B. Tree Characteristics Related to Stem Breakage of Picea Glehnii and Abies Sachalinensis. *For. Ecol. Manag.* **2005**, *215*, 295–306, doi:10.1016/j.foreco.2005.05.018.
- Peltola, H.; Kellomäki, S.; Hassinen, A.; Granander, M. Mechanical Stability of Scots Pine, Norway Spruce and Birch: An Analysis of Tree-Pulling Experiments in Finland. *For. Ecol. Manag.* 2000, 135, 143–153, doi:10.1016/S0378-1127(00)00306-6.
- 74. Peltola, H.M. Mechanical Stability of Trees Under Static Loads. Am. J. Bot. 2006, 93, 1501–1511, doi:10.3732/ajb.93.10.1501.
- Cameron, A.D.; Dunham, R.A. Strength Properties of Wind- and Snow-Damaged Stems of Picea Sitchensis and Pinus Sylvestris in Comparison with Undamaged Trees. *Can. J. For. Res.* 1999, 29, 595–599.
- Dunham, R.A.; Cameron, A.D. Crown, Stem and Wood Properties of Wind-Damaged and Undamaged Sitka Spruce. For. Ecol. Manag. 2000, 135, 73–81, doi:10.1016/S0378-1127(00)00299-1.
- Meyer, F.D.; Paulsen, J.; Körner, C. Windthrow Damage in Picea Abies is Associated with Physical and Chemical Stem Wood Properties. *Trees* 2008, 22, 463–473, doi:10.1007/s00468-007-0206-3.
- Tomczak, A.; Jelonek, T.; Jakubowski, M. Density of Scots pine (Pinus sylvestris L.) Wood as an Indicator of Tree Resistance to Strong Winds. *Sylwan* 2013, 157, 539–545.
- Jakubowski, M.; Jelonek, T.; Tomczak, A. Compressive Strength Parallel to Grain of Scots Pine Wood of Wind–Damaged and Undamaged Trees. Sylwan 2014, 158, 787–794.
- Larjavaara, M.; Muller-Landau, H.C. Rethinking the Value of High Wood Density. *Funct. Ecol.* 2010, 24, 701–705, doi:10.1111/j.1365-2435.2010.01698.x.
- Larjavaara, M.; Muller-Landau, H.C. Still Rethinking the Value of High Wood Density. Am. J. Bot. 2012, 99, 165–168, doi:10.3732/ajb.1100324.
- Dlouhá, J.; Alméras, T.; Beauchêne, J.; Clair, B.; Fournier, M. Biophysical Dependences among Functional Wood Traits. *Funct Ecol.* 2018, 32, 2652–2665, doi:10.1111/1365-2435.13209.
- Loehle, C. Biomechanical Constraints on Tree Architecture. *Trees* 2016, 30, 2061–2070, doi:10.1007/s00468-016-1433-2.
- ISO 13061-2:2014. Physical and Mechanical Properties of Wood—Test Methods for Small Clear Wood Specimens— Part 2: Determination of Density for Physical and Mechanical Tests; International Organization for Standardization: Geneva, Switzerland, 2014.
- ISO 13061-17:2017. Physical and Mechanical Properties of Wood—Test Methods for Small Clear Wood Specimens— Part 17: Determination of Ultimate Stress in Compression Parallel to Grain; International Organization for Standardization: Geneva, Switzerland, 2017.
- PN-77/D-04103 Wood. Determination of Static Bending Strength; Polish Committee for Standardization: Warsaw, Poland, 1977.
- Kamimura, K.; Gardiner, B.A.; Koga, S. Observations and Predictions of Wind Damage to Larix Kaempferi Trees Following Thinning at an Early Growth Stage. *For. Int. J. For. Res.* 2017, 90, 530–540, doi:10.1093/forestry/cpx006.
- Tomczak, A.; Jelonek, T.; Zoń, L. Comparison of Selected Physical Properties of the Juvenile and Mature Wood of Scots Pine (*Pinus sylvestris* L.) from Mature Stands. *Sylvan* 2010, 154, 809–817.
- Auty, D.; Achim, A.; Macdonald, E.; Cameron, A.D.; Gardiner, B.A. Models for Predicting Wood Density Variation in Scots Pine. *Forestry* 2014, 87, 449–458, doi:10.1093/forestry/cpu005.
- Horáček, P.; Fajstavr, M.; Stojanović, M. The Variability of Wood Density and Compression Strength of Norway Spruce (*Picea abies*/L./Karst.) Within the Stem. *Beskydy* 2017, 10, 17–26, doi:10.11118/beskyd201710010017.
- Tomczak, A.; Jelonek, T. Technical Parameters of Juvenile and Mature Wood in Scots Pine (*Pinus sylvestris* L.). Sylwan 2012, 159, 695–702.
- Alméras, T.; Thibaut, A.; Gril, J. Effect of Circumferential Heterogeneity of Wood Maturation Strain, Modulus of Elasticity and Radial Growth on the Regulation of Stem Orientation in Trees. *Trees* 2005, 19, 457–467, doi:10.1007/s00468-005-0407-6.

- 93. Coutand, C.; Pot, G.; Badel, E. Mechanosensing is Involved in the Regulation of Autostress Levels in Tension Wood. *Trees* 2014, 28, 687–697, doi:10.1007/s00468-014-0981-6.
- Pot, G.; Coutand, C.; Toussaint, E.; Le Cam, J.-B.; Saudreau, M. A Model to Simulate the Gravitropic Response and Internal Stresses in Trees, Considering the Progressive Maturation of Wood. *Trees* 2014, 28, 1235–1248, doi:10.1007/s00468-014-1033-y.
- Sellier, D.; Fourcaud, T. Crown Structure and Wood Properties: Influence on Tree Sway and Response to High Winds. *Am. J. Bot.* 2009, *96*, 885–896, doi:10.3732/ajb.0800226.
- King, D.A. Tree Form, Height Growth, and Susceptibility to Wind Damage in Acer Saccharum. *Ecol.* 1986, 67, 980–990, doi:10.2307/1939821.

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



© 2020 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (http://creativecommons.org/licenses/by/4.0/).