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Bois forêt et développement durable (BFD)

RELATIONSHIP BETWEEN ANATOMICAL STRUCTURE
AND MECHANICAL ADAPTATIONS OF WOOD FORMED
AFTER THINNING IN BEECH (*FAGUS SYLVATICA* L.)



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Presentation of the host institute

L'Institut national de la recherche agronomique (INRA) was established in 1946 in response to demand from society to “feed France”. Current challenges such as climate change, the nutritional status of populations, the ecological equilibrium of rural areas and the competitiveness and sustainability of production are global in nature, and agriculture plays a key role in overcoming them. INRA's researches are at the heart of these issues. INRA has 17 regional centers, at the heart of regional activities and involved in the European Research Area and international relations. Research in INRA Lorraine is structured around two axes: forest-wood-territories and engineering and food safety.

Lerfob is one of INRA's units in Lorraine. Lerfob is a joint research unit composed of staff from INRA and AgroParisTech. Lerfob develops research on the ecological dynamics of forest resources, combining different disciplines (ecology of species and plant communities, modeling and simulation of the growth and production of forest stands, tree biomechanics and wood formation and its relation to environmental or phylogenetic constraints).

Context of the study

The general context of this internship is a LABEX ARBRE project focused on how wood acclimates to forest disturbances. More precisely, this internship is an integral part an ongoing PhD of Estelle Noyer which aims at finding wood markers to indicate the history of canopy disturbances in beech (*Fagus sylvatica* L.). As an integral part of the PhD work, the first two parts of results concerned with the reaction of beech poles to canopy opening are confidential and not allowed to publish otherwise that in this report. Beech is one of the most important tree species in Europe, with a wide distribution in the region of Western and central Europe (Alvarez-Gonzalez et al. 2010). Beech is generally used for furniture, packaging, plywood and decorative veneers. There are two major defects in Beech that affect the timber value in the industry, the red color and high growth stresses that lead to log end splitting, checked, board warping, and woolly grain in sawmills (Saurat & Gueneau 1976, Knoke et al. 2006, Yang & Waugh 2001, Jullien et al. 2013).

Intensive production of growth stresses is often related to early ontogenetic stages and/or small tree diameters (Dassot et al. 2012). In the present study, we investigate the reaction of old but small diameter beech poles to canopy opening. The viewpoint of the growth stresses issue is therefore functional and not technological although final results may be useful to forest managers because it allows them to know if these trees have more or less tension wood than others. Besides the study of relationships between the tree morphology, thinning treatment and growth stresses, the aim is also to calibrate the relationship between growth stresses; measurable only at the tree periphery; and the anatomical structure in order to allow for the retrospective evaluation of the growth stresses throughout the tree life.

Abstract

In the present study, we investigated the reaction of small diameter but old beech poles to canopy opening with particular interest in occurrence of growth stresses which allows the tree to maintain or correct its spatial position. We studied the relationships between growth stresses and (i) tree morphology, (ii) thinning treatment and (iii) anatomical structure. Forty-two beech poles were used for the study, half of which were thinned in 2007. We measured the tree morphological characteristics; growth stresses indicators (GSI) at eight positions around the trunk periphery and wood anatomical characteristics including proportion of G fibers and vessel characteristics.

Among the tree morphological descriptors, only crown eccentricity showed a slight correlation with the growth stress asymmetry *i.e.* the intensity of tension wood. Diameter and slenderness (height to diameter ratio) did not exhibit any relationship with the growth stress average value and asymmetry in beech poles. It seems therefore difficult to anticipate the beech pole growth stress level from its diameter and slenderness. Surprisingly, thinning treatment did not affect the average growth stress level and asymmetry in old beech poles. This unexpected result may be related to the high age of these trees and short time scale observation. Considering the relationship between the proportions of G fiber and the level of growth stresses, a significant positive correlation was found in agreement with previous studies on other species. Further, a negative correlation was found between vessel surface area and GSI level. Vessel frequency was also decreased with the increasing GSI level and proportion of G fibers.

Résumé

Dans la présente étude, nous avons examiné la réaction des perches de hêtre de petits diamètres mais âgées de 60 à 100 ans à l'ouverture de la canopée en portant l'accent sur la présence des contraintes de croissance qui permettent à l'arbre de maintenir ou corriger sa position dans l'espace. Nous avons étudié les relations entre les contraintes de croissance et (i) la morphologie de l'arbre, (ii) l'ouverture de la canopée et (iii) la structure anatomique du bois. Quarante-deux perches de hêtre ont été utilisées pour l'étude dont la moitié a été éclaircie en 2007. Nous avons mesuré les caractéristiques morphologiques des arbres, les indicateurs de contrainte de croissance (ICC) à huit positions autour de la circonférence de chaque arbre et les caractéristiques anatomiques y compris la proportion des fibres G et les caractéristiques des vaisseaux.

Parmi de descripteurs morphologiques des arbres, seulement l'excentricité du houppier a montré une légère corrélation avec l'asymétrie des contraintes de croissance. Le diamètre et l'élancement (ratio hauteur/diamètre) ne présentaient pas de relation significative avec la valeur moyenne et l'asymétrie des contraintes de croissance. Il semble donc difficile d'anticiper le niveau des contraintes de croissance à partir du diamètre et de l'élancement des perches. L'éclaircie n'a pas affecté le niveau et l'asymétrie des contraintes de croissance chez les perches. Ce résultat inattendu peut être lié à l'âge élevé de ces arbres et le court temps d'observation. En accord avec des études antérieures sur d'autres espèces, une corrélation positive a été trouvée entre la proportion des fibres à G et le niveau de contraintes de croissance. Par ailleurs, une corrélation négative a été observée entre la surface des vaisseaux et le niveau des ICC. La fréquence de vaisseaux a diminué avec augmentation du niveau d'ICC et la proportion de fibres de la G.

1. Introduction

1.1. *Growth stresses: their generation and role in living trees*

In contrast with the majority of man-made structures, tree stems exhibit a complex field of internal stresses resulting from the growth process (Kubler 1987). These so-called growth stresses result from an overlap of two components: accumulation of support stresses and maturation stresses. Gradual increase in crown weight induce compression stress (Spatz & Bruechert 2000) while the maturation of the newly formed wood layer lead to the tensile pre-stresses called maturation stress (Fournier et al. 1990). Maturation stresses appear after cell lignification. During the maturation of the newly formed wood, the cells, which grow every year on the stem periphery, contract longitudinally while the lignified wood cells already formed impede this contraction.

Pre-stresses are useful for living trees, since they improve the mechanical resistance of the stem against temporary bending loads. Wood has a high-tensile strength parallel to fiber direction but is relatively weak in compression. When wood is subjected to local axial compression, axial buckling can be avoided by tensile pre-stresses (Bonser and Ennos 1998). Tensile pre-stresses at the tree periphery therefore compensate the relatively low compressive strength of green wood. Pre-stresses are also important for the tree postural control. Its asymmetrical distribution around the tree circumference provides a motor system allowing the postural control of the tree and the stems and branches reorientation.

1.1.1. **Reaction wood: tissue specialized in a posture control function**

Trees control the spatial position of their axes (stem or branches) by generation of asymmetrical stress (Fournier et al. 1994; Clair et al. 2013). Asymmetry of maturation stresses induces a bending moment which maintains (growing branches) or corrects (accidentally tilted stem) the spatial position of axes (Alméras et al. 2006). To achieve an important bending moment, trees are pushed to produce an unusual level of maturation stresses. Tissues with the unusual level of maturation stresses is called reaction wood. Occurrence of reaction wood is most often associated with branches or tilted trees; however, it is also frequently reported in straight stems in a number of species including Beech (Gartner 1997, Washusen et al. 2003, Jullien et al. 2013).

Posture control differs between deciduous trees and conifers. While deciduous trees generate highly tensile stressed tissues called tension wood on the upper side of leaning axes, conifers produce so called compression wood on the lower side of leaning axes (Yoshida et al. 2002, Clair et al. 2003, Fang et al. 2008, Abasolo et al. 2009). Apart from the high levels of maturation stresses, tension wood presents some distinctive physical and anatomical features when compared to 'normal wood' (IAWA 1964). Tension wood has high longitudinal shrinkage, wider rings, low lignin, and high crystallinity (Ruelle et al. 2007, Mellerowicz & Gorshkova 2011).

1.1.2. Relationship between maturation strain and anatomical features

In many species of hardwoods such as beech, poplar, oak and chestnut, tension wood contains fibers with a special morphology and chemical composition due to the development of gelatinous layer (Clair et al. 2010, Fang et al. 2008, Clair et al. 2006). This layer usually used as a tool to identify the presence of tension wood in hardwoods. However, this layer is not always present in tension wood (Clair et al. 2006). Figure 1 shows the appearance of gelatinous layer in tension wood. Gelatinous layer has a jelly-like appearance with low MFA (Washusen et al., 2001, Ruelle et al., 2007), high mesoporosity (Chang et al. 2009), high crystalline cellulose, and low lignin content (Mellerowicz & Gorshkova 2011).

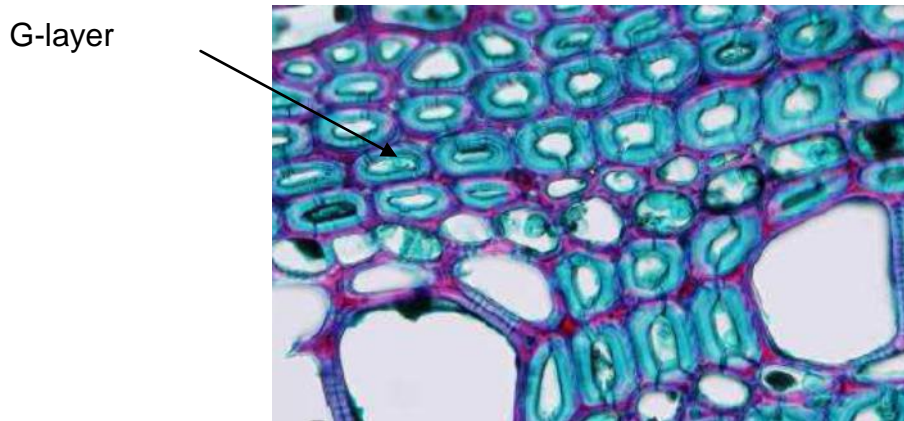


Figure 1. Gelatinous layer

Previous reports have shown that in chestnut and poplar there is a significant relationship between the proportion of the gelatinous layer and growth stresses (Figure 2). The higher the proportion of the gelatinous layer in tension wood, the higher the growth stress in trees. It indicates that the amount of G-layer is largely controls the stress level in trees (Fang 2008, Clair 2003, Dassot et al. 2012).

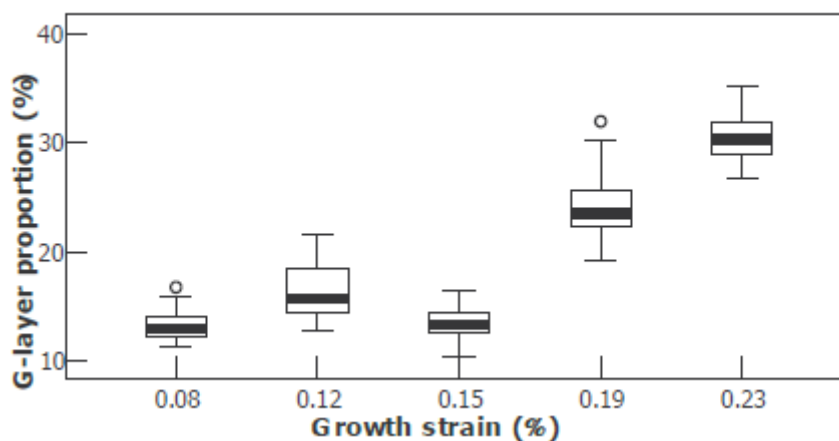


Figure 2. Relation between G-layer area ratio and growth strain (Fang 2008)

Besides the G-layer, a decrease in the frequency of vessels in tension wood was reported by Ruelle et al. (2006) in 21 tropical tree species. Jourez (2001) also found decrease in vessel

frequency and porosity in tension wood of poplar indicating a possible trade-off between the mechanical and hydraulic performances of the tension wood tissue.

1.2. Tree morphology, ontogeny, thinning and growth stresses

As explained above, one of the roles of maturation stress is to increase the stem resistance in bending. In the case of a straight tree, the main loading factor resulting in the bending moment is the wind. When the tree morphology is well acclimated to high wind loads *i.e.* the height to diameter ratio also called slenderness is low (height is the arm of the bending moment while diameter governs the stem resistance), the need for high maturation stress should be limited. This may explain the positive relationship between the slenderness and level of maturation stresses in beech trees reported by Jullien et al. (2013).

Generation of asymmetric maturation stress is a priori related to the asymmetry of external load inducing a bending moment (crown asymmetry, leaning stems) and we can therefore expect their level and intensity to be related with the external tree morphology. Jullien et al. (2013) reported that crown asymmetry resulted in a larger stress dissymmetry within trees. They also found that trunk inclination has a strong negative significant correlation with growth stress level until 2.5 % inclination but decreases rather abruptly after that and remains more or less flat until the highest tree leaning.

However, when thinking about the efficiency of the tree stem reorientation one needs to keep in mind that such a process is strongly dependent on the tree size as the inertia of stem section increases with the fourth power of its diameter. Therefore, the thicker the stem, the more difficult the bending movement and the slower the reorientation process. The impeding effect of the tree size on the amount of tension wood was clearly reported by Dassot et al. (2012). The question that remains open is how strong the ontogenetic effect on the efficiency of reorientation is *i.e.* if small but old trees are able to react to the change of their environment.

It is well known that silvicultural treatments such as thinning affect the tree morphology. Thinning tends indeed to reduce height growth and stimulates diameter growth which is in general explained by the increased post-thinning wind loads (Evans & Jackson 1972; Mitchell 2000) as thinning will open the canopy, increase the canopy roughness, decrease the sheltering effects from surrounding trees and increase the tree exposure to wind (Zhu et al., 2003; Washusen, 2005). This will lead to higher stress to the stem and may stimulate the tension wood production. However, thinning was reported to improve the tree stability by long-term effects on growth and development of trees (Polge 1981, Ferrand 1982). Some research shows that higher spacing of trees seems to be a good solution to lower the level of growth stress in beech stands and heavy thinning are to be made to reduce growth stresses in beech stands (Polge 1981, Jullien et al. 2013) while some others claim the opposite (Bruchert 2000, Washusen et al 2005).

Stress growth measurements performed on the stem periphery. The measurement is based on the displacement caused by release strain after cutting. There are two commonly used methods of measurement, single hole method developed by CIRAD, France and two-grooves method (Fournier et al. 1994, Yoshida and Okuyama 2002). Single hole method is the fastest method of measurement that is suitable for the rapid assessment of forest

stands. Two-grooves provide a local and direct method's strain measurement. This method is expensive and time consuming (Jullien & Gril 2008).

1.3. Objectives of the study

Objectives of this internship are the following:

- 1) Analyze the state of the art of the topics related to our study
- 2) Measure maturation strains in a wide sample of beech poles that have been thinned or not 6 years ago
- 3) Examine if growth stresses level and asymmetry were affected by the thinning treatment
- 4) Examine whether growth stresses level and asymmetry in beech poles are related to morphological characteristics of standing trees such as diameter, slenderness, and crown eccentricity.
- 5) Measure anatomical features usually associated to tension wood (as the amount of gelatinous fibers) in a subsample covering the whole range of growth stresses in order to calibrate that the relationship between maturation strains to wood anatomical features and allow for retrospective evaluation of growth stresses otherwise measurable only at the tree periphery.
- 6) Investigate the relationship between vessel parameters and growth stresses to see if there is any trade-off between the mechanical and hydraulic function of wood tissues.

2. Material and Method

2.1. Site location and tree selection

Trees for the present study were harvested in Grand Poiremont, Haute Saône, France from stands with natural regeneration forest consisting of beech, oak, spruce, maple, and birch. Stands are located at altitude of 470 meters above sea level with 1218 mm rainfall (ONF 2014). Forty-two beech poles aged from 60 to 100 years were used for the study, with diameters ranging from 9.5 to 20.9 cm and heights from 11 to 25 m. Half of them were released from the competition (3 or 4 competitor trees and felling trees with diameter 30 cm or more which was in contact with the Beech pole so that in radius 12 m from thinned trees there is no competitor) 6 years before harvesting while the other half continued to growth in high competition. One of the released poles has buckled so that only twenty treated poles are considered in the following analysis.

2.2. Tree morphology characteristics

The total tree height was measured in 2007, 2010 and 2013 while the diameter at breast height of 130 cm (DBH) was monitored every year from 2007 to 2013. Crown eccentricity was measured in 2014. To measure the crown eccentricity, several sticks were placed vertically below the points describing the crown periphery. The positions of these sticks were recorded by their orientation to north and the distance to the tree trunks. The distance between the center of projection of the crown and stem (crown eccentricity, CE) provides an indication of the crown eccentricity associated with the base of the tree.

2.3. Growth stress measurement and modeling the distribution of GSI

Stresses growth indicators were measured using the single hole method (Fournier et al. 1994). This method consists in measuring the displacement of two pins (initial distance is 4.5 cm) caused by the stress release after a 2 cm hole has been drilled between the pins. Outer layer up to the cambial layer is removed before the measurement. Two pins are fixed in a stem along the fiber direction using a template. A frame equipped with a micrometer is then mounted on the pins and the micrometer is set to zero (Figure 3). A 10 mm deep hole is drilled between the pins to release the stress leading to displacement of the two pins recorded by the micrometer. This displacement expressed in μm is called growth stress indicator (GSI) and is directly proportional to longitudinal growth stress at the trunk periphery, the conversion factor depending on each species mechanical properties (Sassus 1998). As such, values of GSI are good indicators of the relative growth stresses level for intraspecific comparison (Clair et al. 2003).

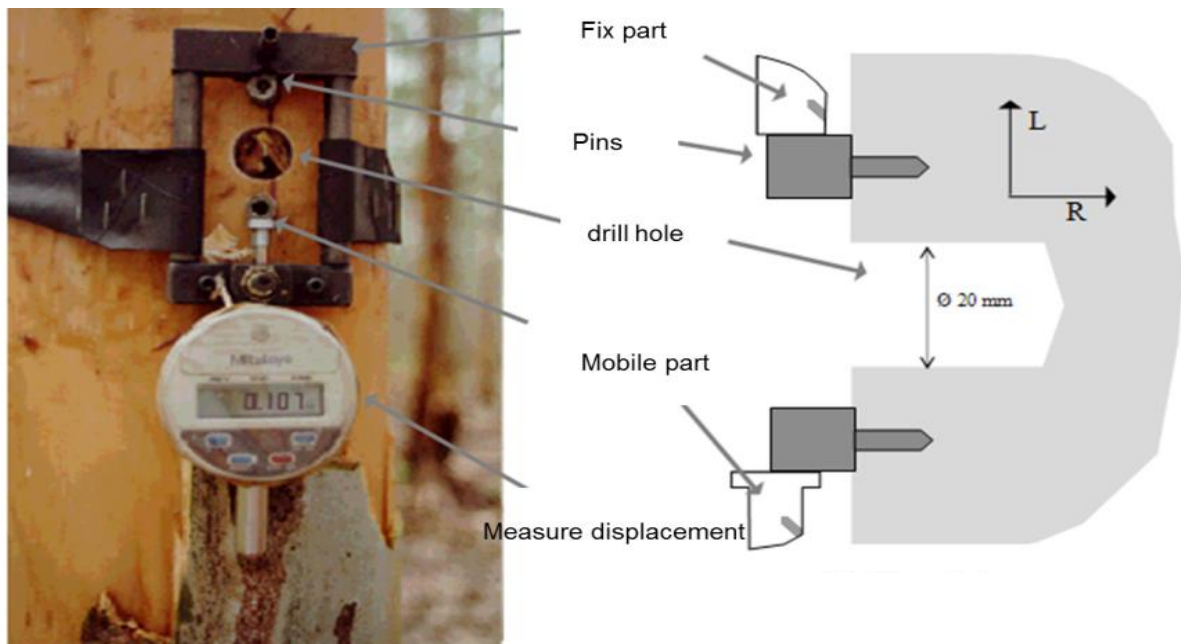


Figure 3. Single hole method for GSI measurement at the tree periphery

The GSI measurements were done at the 1.3 m height at eight positions equally distributed around the stem circumference (Figure 4a). The objective was to characterize the distribution of the GSI and determine the location of tension wood. The first measurement was done at the upper side of the tree at position of maximal tilt angle estimated with an inclinometer prior to the GSI measurements. The azimuth of the first GSI point was also measured. Measurements were conducted in February - March 2014 before the beginning of the growth season.

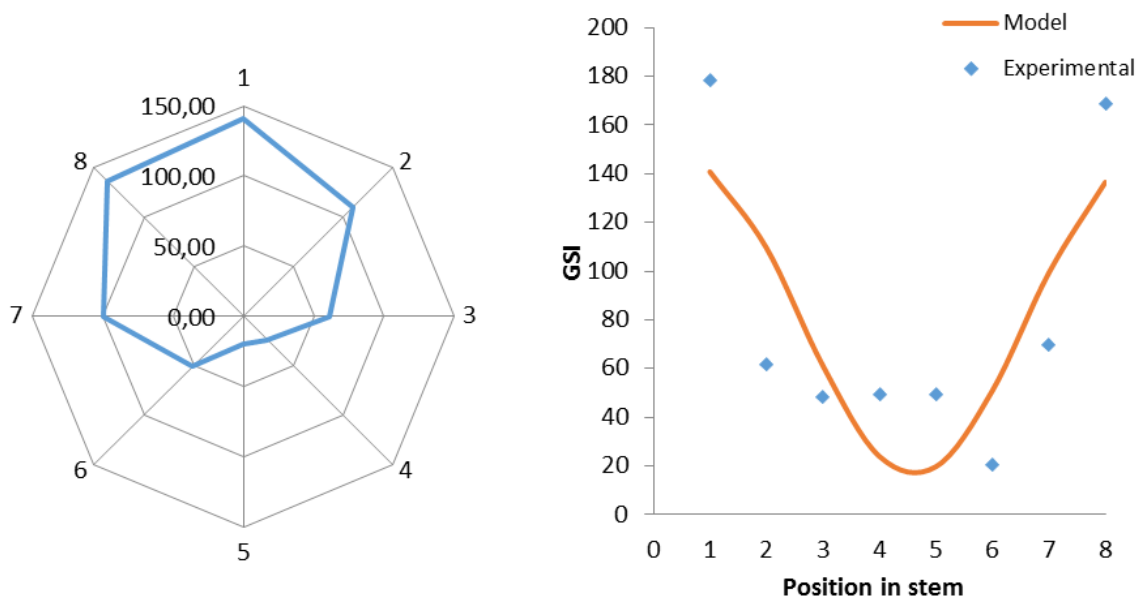


Figure 4. (a) Distribution of GSI around the stem circumference, position from 1 to 8 indicate the GSI measurements; (b) example of the correspondence between the cosine model and experimental values.

As the first position is expected to correspond to tension wood, the distribution of GSI around the stem circumference was described by a cosine function:

$$y = A + B \cos(\varnothing + \pi)$$

where A is the average value of GSI, B is the difference between the maximal and minimal value of GSI divided by two or the magnitude of GSI asymmetry, and \varnothing is the angular difference between the position of the GSI peak as estimated from the tilt measurement and the position of the estimated maximal value. Estimation of the \varnothing value is important for further measurements of the tension wood properties (not done in this study). An example of the agreement between experimental data and the cosine model is shown in Figure 4b.

2.4. Anatomical measurements

2.4.1. Selection of samples

After the measurement of GSI, trees were felled and a 5 cm thick disc was collected at the breast height (Figure 5). Specimens for the anatomical measurements were selected based on the histogram of all the GSI values recorded. The aim was to cover the complete range of GSI observed in beech poles. GSI values were classified in 14 classes. When possible, 3 thinned and 3 control trees were chosen from each class, and all specimens were used in GSI classes with frequency lower than six. In total, 64 specimens were used for anatomical observations.

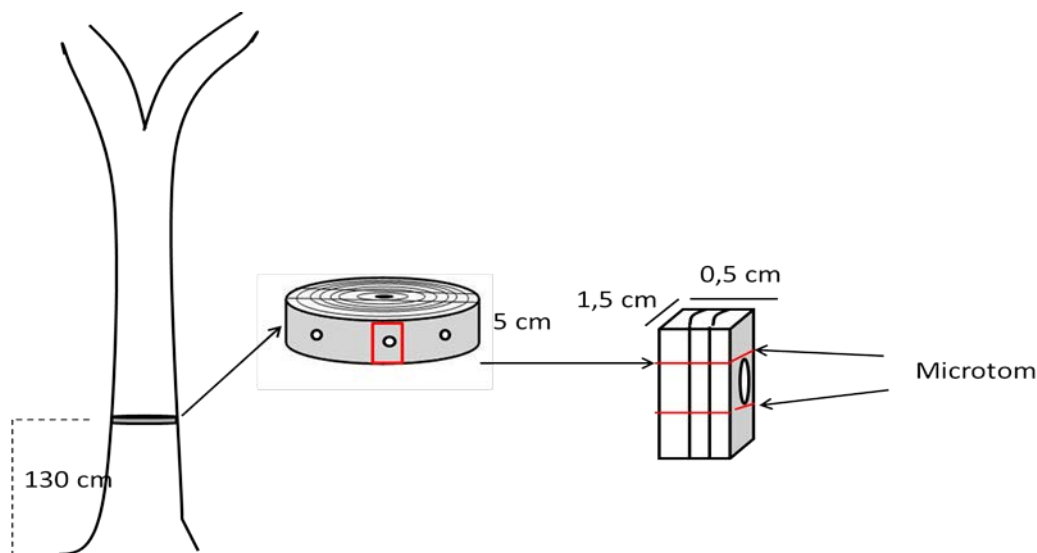


Figure 5. Specimen preparation for anatomical observation

2.4.2. Proportion of G fibers

To characterize the anatomical structure as close as possible to the GSI measurements, small blocks of (0,5 x 1,5 cm; R x T) were extracted from the disk. Cross

sections approximately 20 μm thick were cut with a microtome and double-stained with safranin and blue astra to highlight the presence of the G-layer in blue as illustrated in Figure 6b. To determine the proportion of fibers with G-layer i.e. G-fibers, one single image was taken of each sample covering the whole sample surface. Image capture was performed using a digital camera (Sony XCD-U100CR). Image-J software was then used to quantify the area occupied by G-fibers in the section. The algorithm was based on the subtraction of the red component of the image from the blue one. This operation enhances the distinction between G-fibers and other tissues. A common threshold was then used to separate them. The percentage of G-fibers value was deduced without ambiguity from histograms where pixels were identified as belonging to G-fibers and other tissues. This method was developed by Badia et al. (2005).

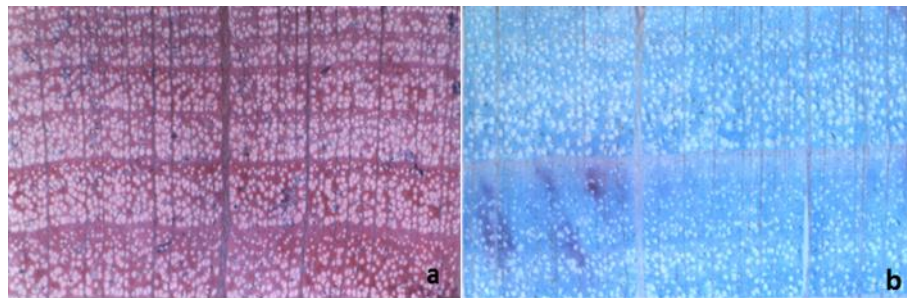


Figure 6. (a) Transverse sections of wood without G-fiber (b) Transverse sections of wood with G-fiber

2.4.3. Vessel anatomical characteristics

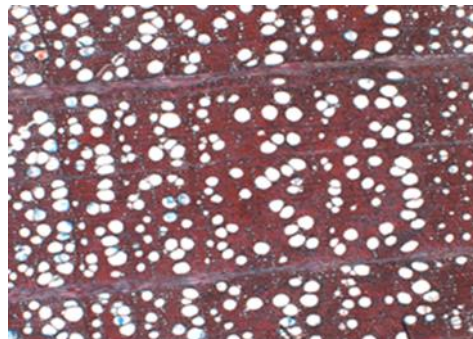


Figure 7. Vessels in Beech

The samples used were the same sample for proportion of G-fiber but images were taken at a magnification 5x to enable finer analysis of the vessel morphology (figure 7). Seven photos were taken at 7 different positions distributed evenly on each sample. Proportion of vessel was calculated as total vessel area/total surface of image. Vessels radius and vessel frequency were also calculated to estimate the hydraulic performances of wood tissues.

3. Results

3.1. Effect of thinning on the growth and the GSI distribution and asymmetry in beech poles

3.1.1. Growth response

Figure 8a shows a comparison of the increase in diameter of the thinned and control trees after thinning in 2007. First two years after thinning, thinned trees experienced accelerated diameter growth which seems however to stabilize afterwards. Figure 8b shows increase in height in control and thinned trees from 2007 to 2013. It shows that both treatment increase trees height. Also it shows higher increase in height in thinned trees.

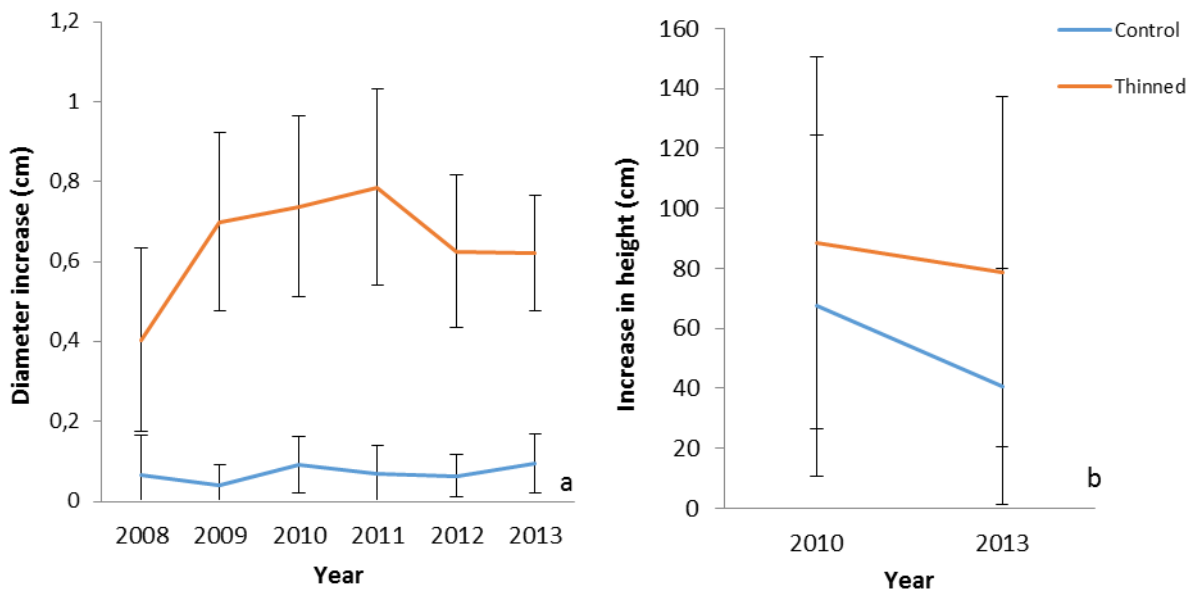


Figure 8. (a) Diameter growth for thinned and control trees after thinning in 2007 (b) Height growth for thinned and control trees after thinning in 2007

To assess the effect of thinning on the balance between the height and diameter growth kinetics, it is interesting to plot the evolution of slenderness ratio *i.e.* the ratio of height to diameter (H/D) as shown in Figure 9a. We can see that control trees have higher slenderness than thinned trees. Slenderness is stable in control trees while in thinned trees, slenderness decrease after the thinning. Figure 9b shows a negative correlation observed between initial slenderness (H/D 2007) with change in slenderness from 2010 to 2013 in thinned trees. It shows that higher initial slenderness tends to induce higher change in the slenderness ratio in thinned trees while no correlation is observed in control trees.

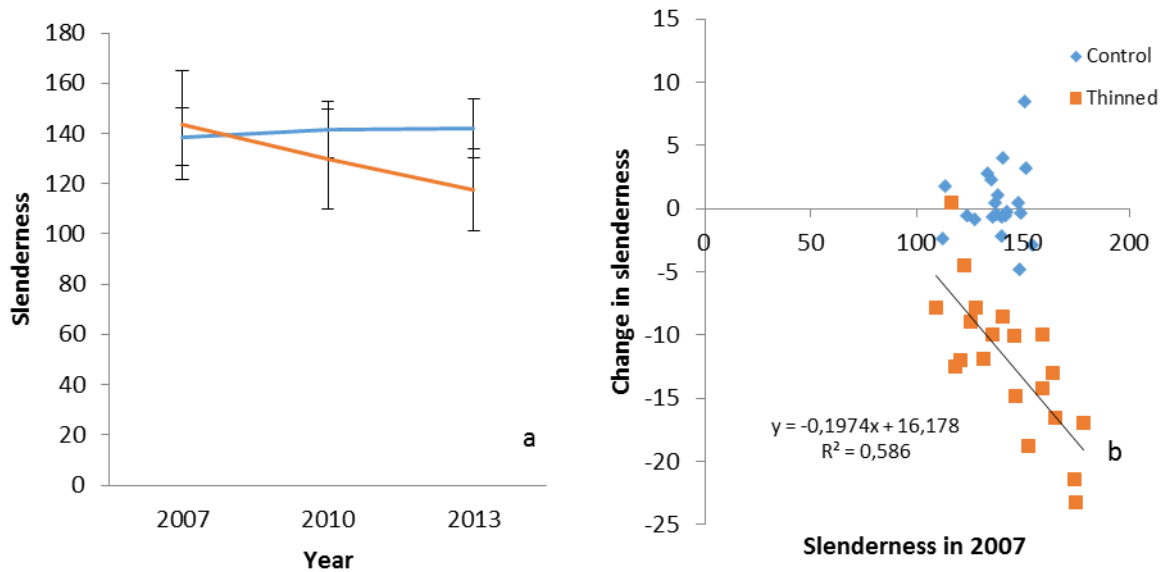


Figure 9. (a) Evolution of slenderness ratio in control and thinned trees; (b) correlation between initial slenderness (H/D 2007) with change in slenderness from 2010 to 2013

3.1.2. Suitability of the cosine model to describe the GSI distribution around the stem circumference

Figure 10 shows the agreement between the modeled and experimental values of average GSI (A) and the intensity of reaction (B). It shows that the A values are very well predicted by the model while the agreement is lower for B values which may be related from the bias of the peak of tension wood estimation *i.e.* parameter ϕ . Globally, cosine model fits well the experimental data (average $R^2 = 0,95$).

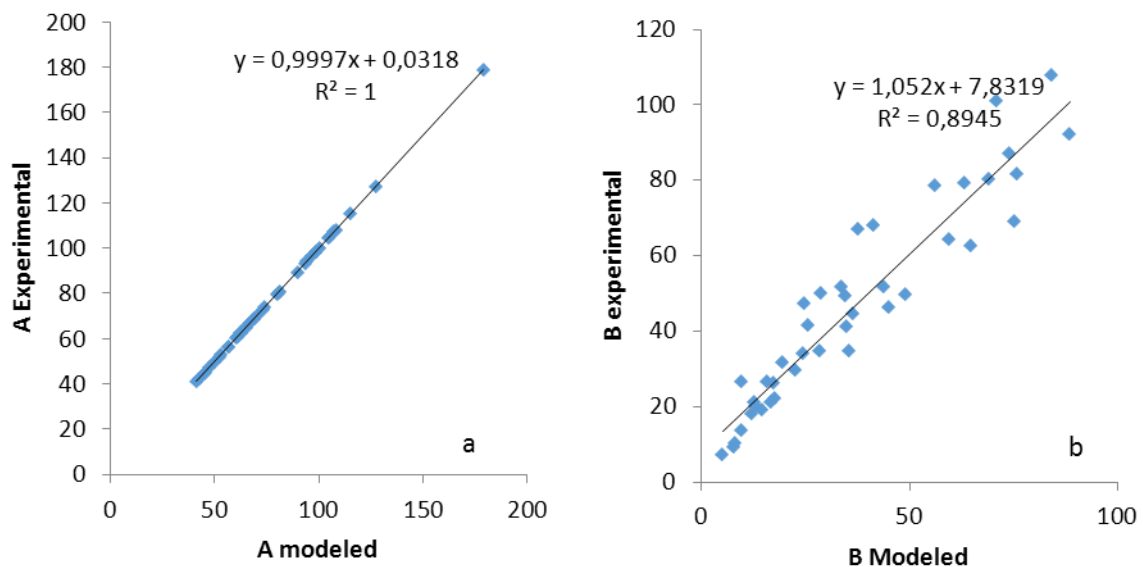


Figure 10. (a) Agreement between average measured and modelled GSI values, (b) agreement between measured and modelled GSI asymmetry.

3.1.3. GSI in control and thinned trees

To know whether there is a difference in GSI between thinned and control trees, we compared the average GSI and GSI asymmetry in both treatments. Figure 11 shows that there is no statistical difference in GSI average and GSI asymmetry wood between thinned and control trees.

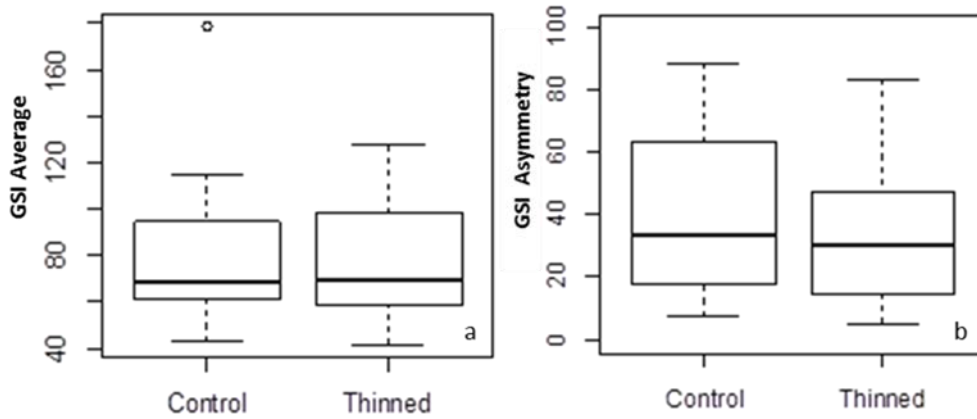


Figure 11. (a) Average GSI between control and thinned trees. (b) GSI asymmetry between control and thinned trees.

3.2. Tree morphological parameters potentially affecting the GSI

3.1.1. Stem diameter at the breast height

To see the effect of diameter to GSI, we plotted the GSI average and GSI asymmetry in function of the diameter. Figure 12 shows that there is no relationship between the diameter and the GSI average and GSI asymmetry regardless the treatment.

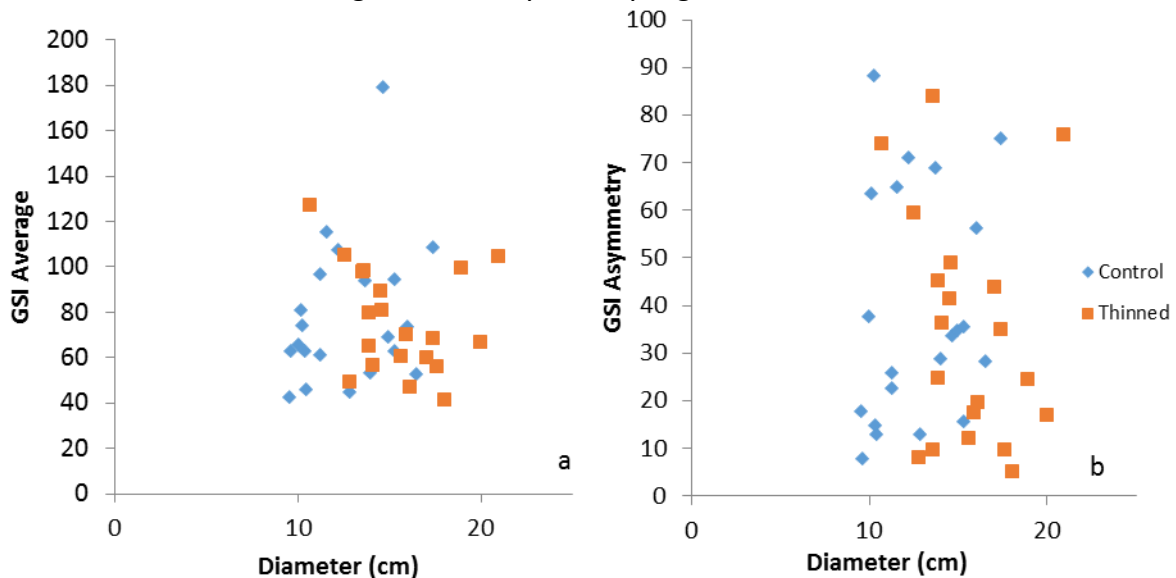


Figure 12. (a) Relationship between diameter and GSI in thinned and nonthinned trees (b) Relationship between Diameter and GSI asymmetry

3.1.2. Slenderness and GSI

Figure 13 shows the relationship between the slenderness and GSI average and GSI asymmetry. It appears that there are no correlation between slenderness of trees (H/D) with GSI average and intensity of the reaction.

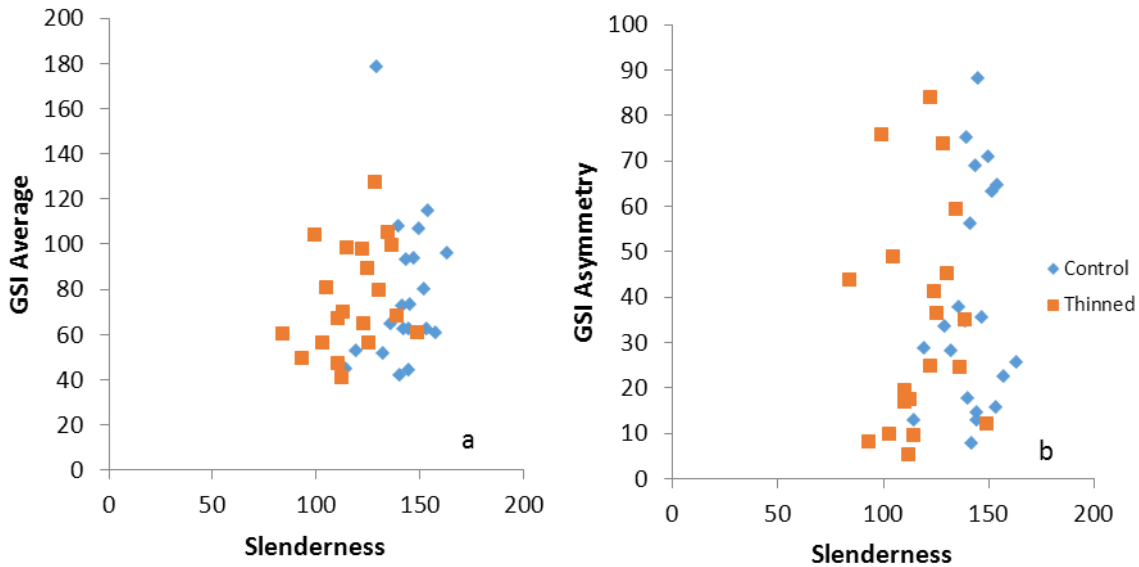


Figure 13. (a) Relationship Between tree slenderness and GSI Average, (b) Relationship Between tree slenderness and GSI asymmetry

3.1.3. Crown Eccentricity and GSI

To study the relation between crown eccentricity and GSI asymmetry we plot both in figure 14a. The result shows that there is a weak correlation between these variables. The higher the crown eccentricity, the greater the GSI asymmetry in the trunk.

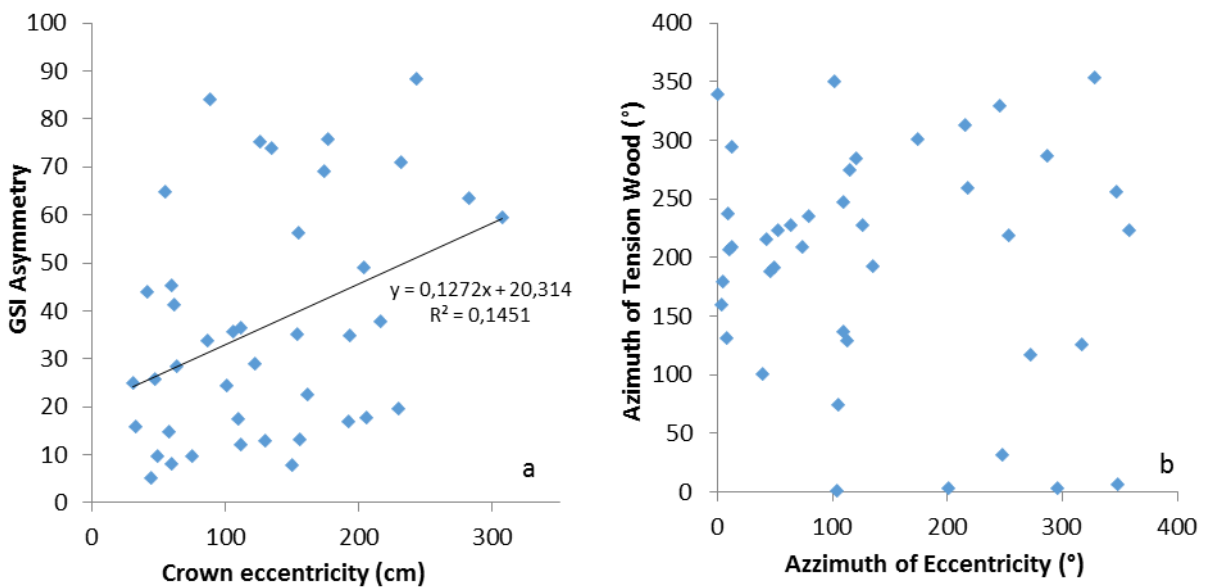


Figure 14. (a) Relationship between crown eccentricity and intensity of the reaction (b) Relationship between azimuth of crown eccentricity and azimuth of TW

To see the relation between direction of tension wood and the direction of eccentricity we plot azimuth of both variables (figure 14b). It appears that there is no correlation between both of them.

3.3. Relationship between GSI and anatomical features

3.3.1. Proportion of G fibers and GSI

In figure 15 we plot the proportion of G fibers with GSI. It shows a positive relationship, the larger the G-fibers proportion, the higher the GSI values.

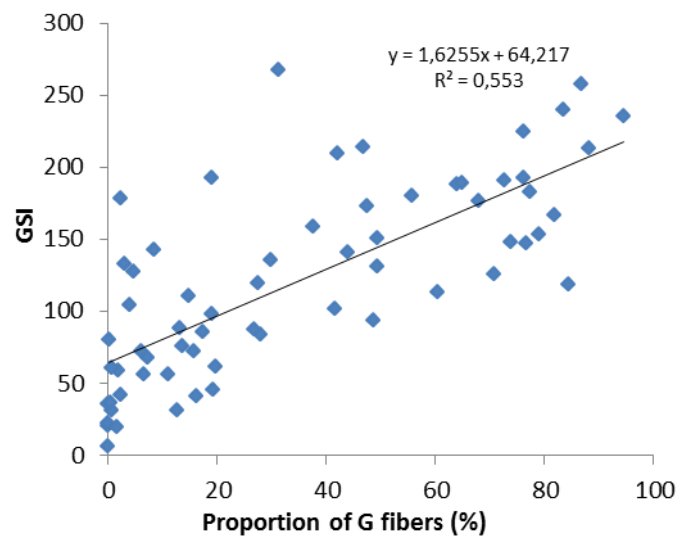


Figure 15. Relationship between proportion of G-layer fibers and GSI

3.3.2. Vessel with proportion of G fibers and GSI

Figure 16 shows the relation between GSI and proportion of G-fibers with vessel proportion. The results in figure 16 indicate a negative correlation between vessel proportion and GSI as well with proportion of G fibers. The larger the G-fibers proportion and GSI values, the lower the vessel proportion.

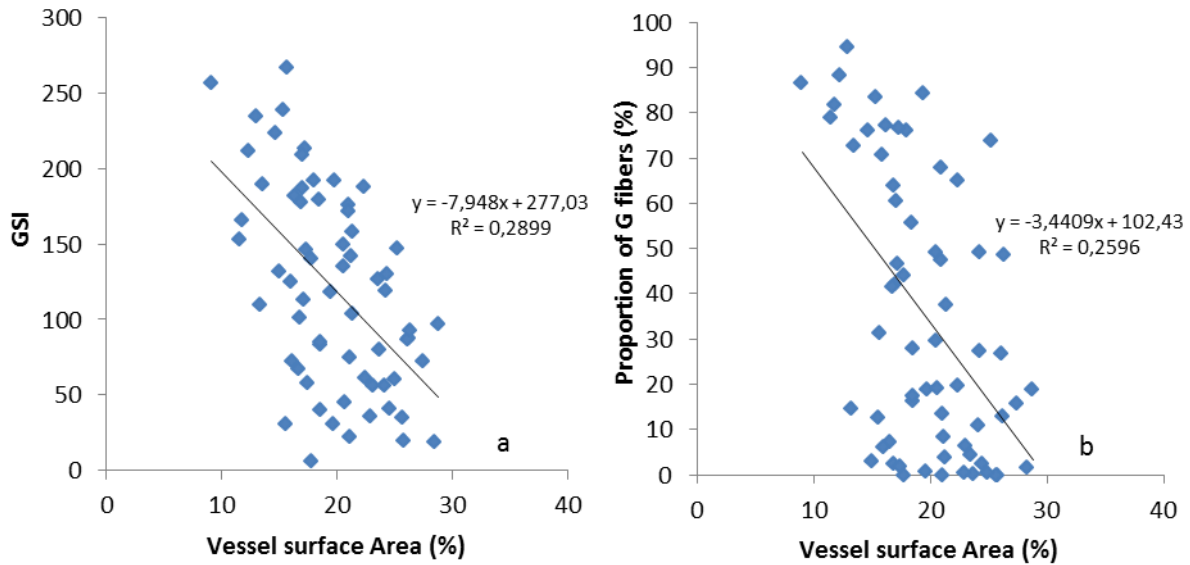


Figure 16. (a) Relationship between vessel lumen surface area and GSI (b) Relationship between vessel lumen surface area and proportion of G fibers

Relationship between GSI and vessels frequency is shown in figure 17a. It shows a slight negative relation between both variable. Figure 17b shows the relation between proportion of G-fibers and vessels frequency. It shows a slight negative correlation between both variable. It shows that vessel frequency is lower when the GSI level and proportion of G-fibers are higher. Proportions of G fibers and vessel frequency have better correlation than GSI and vessels frequency.

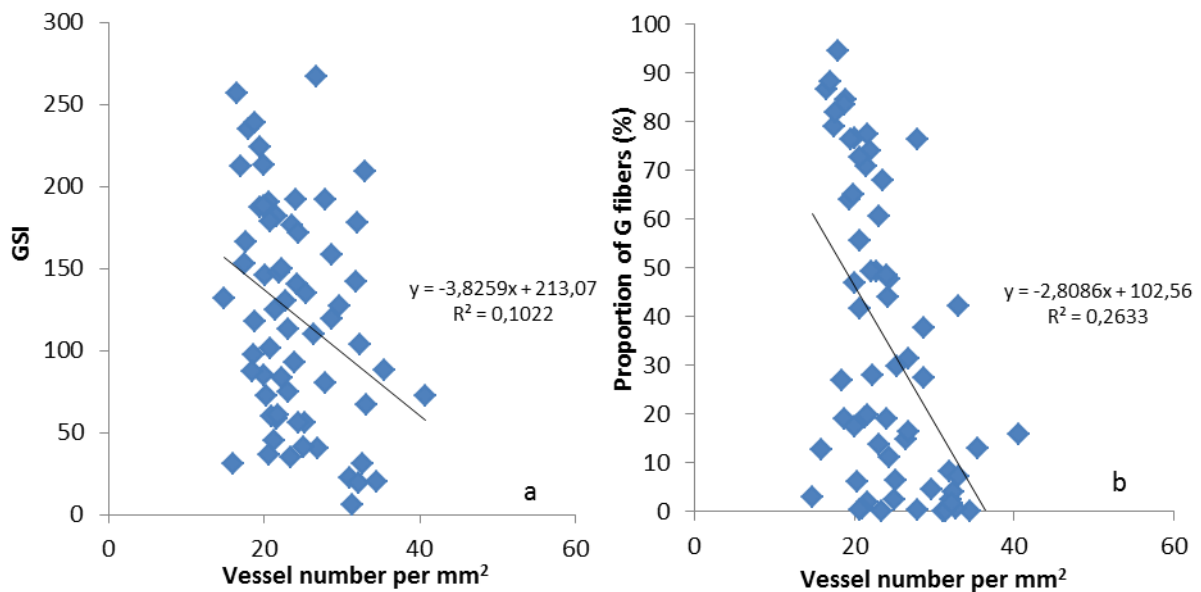


Figure 17. (a) Relationship between vessel frequency and GSI (b) Relationship between vessel frequency and proportion of G fibers

4. Discussion

4.1. *Growth response to canopy opening in old beech poles*

Diameter growth is significantly accelerated in thinned trees. This occurs because the reduction in competition improves the tree access to light and nutrients so that trees grow faster (Hale 2003, Blanco et al. 2009). Our results show that in spite of their high age (60-100 years), beech poles are still able to take benefit from the resource abundance after the canopy opening.

Concerning the allocation of the biomass, while diameter growth is accelerated the height growth also increase after thinning. But the slenderness ratio in thinned trees decreases. This is consistent with previously reported results (Boncina et al. 2007) and is generally interpreted as increase in wind firmness to resist increased wind loads (Mitchell 2000). Change in trees slenderness from 2010-2013 is negatively correlated to initial slenderness. It shows that the higher the initial slenderness, the higher correction is applied by the trees.

4.2. *Effect of thinning to GSI distribution and asymmetry in old beech poles*

Our results show that there is no effect of thinning on the GSI average value and their asymmetry. This result differs from results of some previous studies. For example Polge (1981) found that heavy thinning reduced growth stresses in 35-year-old beech trees that had been thinned 3 times since seedlings. Another report by Jullien et al. (2013) confirms findings by Polge. It shows that higher spacing between trees induced higher growth rates related to lower growth stresses. Different result was found by Washusen *et al.* (2005) who studied the effect of short period of thinning (4 years) to tension wood in *Eucalyptus globulus*. Thinning was done when the trees were 8 years old. He concluded that thinning contribute to the formation of tension wood through greater exposure of individual retained trees to wind following thinning. Therefore it seems that at short time scale thinning tends to increase the amount of tension wood and on the contrary at long time scale to decrease the amount of tension wood.

The observation time scale in our study is rather short. As the GSI is measured by single hole method, results indeed integrate the information about the growth stresses in the peripheral 10 mm of wood approximately. As such, several years are included for control trees and two last years in thinned tree. According to results by Washusen et al. (2005), we should therefore observe an increase in tension wood i.e. increase in the asymmetry of GSI values which is not the case. The lack of changes in the GSI asymmetry in our poles may be related to their high age. We can expect that 60 – 100 years old poles may react differently to the canopy opening when compared with young trees. Another possible explanation is related to the social status of our trees. As suppressed trees, the poles may need to often reorient their stems in order to benefit from each light pocket compared to well establish dominant trees leading to high tension wood occurrence before thinning.

4.3. Tree morphology and GSI

In general, the results showed the presence of asymmetry of GSI in most of the trees measured. To examine whether the GSI level in beech poles could be anticipated from observations on standing trees, some descriptors of the tree morphology as diameter, slenderness, and crown eccentricity have been measured. Our results show that there is no effect of diameter to GSI average value and its asymmetry. It is different with some literature. Dassot et al. (2012) observed decrease in tension wood percentage with increasing diameter however much wider diameter range was investigated. He showed that tension wood is higher at the younger ages (small diameter). Similarly, the study by Jullien et al. (2013) in beech stand with diameter more than 45 cm with 110-150 years old ages indicates a weak negative correlation between the diameter of the GSI average and slight positive correlation between diameter and GSI asymmetry. Big diameter was a favorable factor that in general leads to a moderate to low level of growth stress. The lack of relation between the diameter and the GSI in our study may be however due to very limited diameter range going from 9,5 to 20,9 cm.

No relation was found between slenderness and GSI value and its asymmetry. This is in contrast with the results of several studies indicating that there is a relationship between these two variables. A large slenderness was found as predictor of a large growth stress (Polge 1981, Ferrand 1982, Julien 2013). Explanation of this discrepancy may be as mentioned already above the high age of studied beech poles and/or high initial occurrence of tension wood due to the suppressed growth condition.

Further, the GSI asymmetry was positively correlated with the crown eccentricity (Pearson's $R = 0.381$; level of significance 0.05). On the contrary, the tension wood was not formed in the same direction as the azimuth of the crown eccentricity. That is probably due to the fact that formation of the tension wood is very local while crown eccentricity is measured at the whole tree level. There are also many factors that affect the GSI asymmetry in addition to crown eccentricity.

4.4. Beech anatomical features and GSI

Our result shows the relationship between proportion of G-fibers and GSI. Similar results were reported for example by Fang et al. (2008) who found that the amount of G-fibers per unit of tissue area was significantly correlated to growth stress values (Pearson $r=0.846$). R^2 in the report by Fang is slightly higher than in this study (0,7464 in Fang et al. 2008 and 0,553 in this study). This difference can be explained by the differences between the methods of GSI measurements. Fang et al (2008) used the strain gauge method which is a direct and more localized measure of maturation stresses when compared to single hole method used in our study. Another study by Clair et al. 2003 also shows the relationship between proportion of G-fibers and growth stresses.

Our result also shows that vessel proportion decreases when GSI increase. Vessel frequency is also decreasing with the increase of GSI and the proportion of G -fibers. No relation was found between size of vessels and GSI or proportion of G fibers. It suggests that lower vessel proportion is due to a lower vessel frequency and not to a change in size of the vessel elements. These results are consistent with research by research Jourez (2001) who

found the vessel elements decreasing in frequency in tension wood of poplar. A decreasing in the frequency of vessel in tension wood was found also by Ruelle et al. (2006) in 21 tropical trees. Christensen-Dalsgaard et al. 2007 study the changes in vessel anatomy in response to mechanical loading in six species of tropical tree. She found that the smallest vessels and the smallest vessel frequency were found in the parts of the trees with greatest stresses or strains. These changes appear to be an adaptation towards reinforcing mechanically loaded areas.

5. Conclusion

Thinning treatment did not affect the GSI level and asymmetry in old beech poles. This unexpected result may be related to the high age of these trees and short time scale observation. Among tree morphological descriptors, only the crown eccentricity showed a slight correlation with the GSI asymmetry i.e. the intensity of tension wood. Diameter and slenderness did not exhibit any effect to GSI average value and asymmetry in beech pole. It seems therefore difficult to anticipate the beech pole GSI level from its diameter and slenderness. Considering the relationship between the proportions of G- fibers and the level of GSI, a significant positive correlation was found in agreement with previous studies on other species. Further, a negative correlation was found between vessel proportion and GSI level. Vessel frequency is also decrease by the increasing of GSI level and proportion of G-fibers.

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