Evolution des performances biomécaniques des perches de hêtres à l'ouverture de la canopée



4.1. Avant-propos

L'ouverture de la canopée implique une augmentation des sollicitations mécaniques auxquelles l'arbre doit s'adapter. Le changement d'allocation de la biomasse entre la croissance radiale et axiale couplé à une anisotropie de la croissance radiale au niveau de la section ou de la modification des propriétés matérielles du bois peuvent impacter les performances biomécaniques de l'arbre. Dans le chapitre précédent, l'accent était mis sur les changements de croissance des arbres à l'ouverture de la canopée. Dans ce chapitre, nous essayons de comprendre quel est l'intérêt de ces modifications pour la biomécanique de l'arbre en nous focalisant sur le contrôle postural et la motricité des tiges. Ce chapitre est divisé en trois parties :

- Dans une **première partie**, nous discutons sur une **méthode** d'évaluation des contraintes de maturation du bois en rétrospectif et de son utilisation dans l'étude à suivre.
- La **deuxième partie** traite des traits liés à la **motricité des tiges** et constitue l'Article 2 qui est en cours de préparation.
- La **troisième partie** est axée sur la **sécurité biomécanique** et est au stade d'avant-projet sous forme d'Article 3.

La contribution des co-auteurs pour chaque ébauche d'article est synthétisée dans le Tableau 4.1.

Auteurs	Contribution à l'Article 2	Contribution à l'Article 3
Estelle NOYER	Acquisition des données, analyse des résultats, principale rédactrice de l'article	Acquisition et analyse des données du site du Grand Poiremont, relecture de l'article
Jana DLOUHA	Analyse des résultats (modèle PC) et participation à la discussion et à la rédaction	Analyse des données, principale rédactrice de l'article
Mériem FOURNIER	Participation à la discussion et à la rédaction	
Thiéry CONSTANT Catherine COLLET	Participation à la discussion	Participation a la discussion
François NINGRE	Mise en place du site d'expérimentation du Grand Poiremont	-

Tableau 4.1 : Contribution	des co-auteurs a	aux Articles	2 et 3.
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4.2. Estimation rétrospective des contraintes de croissance

L'objectif de cette partie est d'évaluer de façon rétrospective les contraintes de croissance du bois de hêtre, qui sont dues au retrait de maturation des cellules du bois et aux contraintes de support. Actuellement, les méthodes du trou unique et des jauges permettent la mesure des contraintes de croissance périphériques (Fournier *et al.*, 1994). La méthode du trou unique évalue indirectement ces contraintes en se basant sur le déplacement mesuré après la libération des contraintes de croissance qui dépend entre autres des propriétés du bois tandis que la méthode des jauges permet une mesure directe de la déformation (déformations résiduelles longitudinales de maturation, DRLM). Après avoir écorcé le tronc, deux pointes sont plantées dans le sens longitudinal à une distance de 45 mm, un capteur développé par le CIRAD est installé (Fig. 4.1a). Un trou de 20 mm de diamètre sur 10 mm de profondeur est réalisé ce qui permet la libération des contraintes et engendre un déplacement des pointes qui est mesuré en μ m par le capteur de déplacement (Fig. 4.1b). Une couronne de mesures uniformément réparties autour de la circonférence de l'arbre permet la caractérisation de la répartition des contraintes de croissance sur la périphérie du tron (Fig. 4.1c).



Figure 4.1 : Mesures des ICC par la méthode du trou unique. a : mise en place des pointes et du capteur CIRAD. b : réalisation du trou. c : répartition des mesures le long de la périphérie du tronc. (Source : INRA)

Ce déplacement est proportionnel à la déformation longitudinale due à la maturation des cellules nouvellement formées du bois. En connaissant les propriétés du bois, il est possible de convertir le déplacement mesuré en déformation (Sassus, 1998). Ici, nous nous baserons sur la relation observée par Fournier *et al.* (1994) entre les mesures réalisées par la méthode des jauges (mesure directe) et la méthode du trou unique (mesure indirecte) sur le hêtre. Pour cette espèce, la déformation est égale à 15.8 µdef par micromètre de déplacement mesuré. Lorsqu'il s'agit d'une mesure indirecte, le déplacement mesuré en µm est généralement désigné comme indicateur de contraintes de croissance (ICC, ou GSI en anglais) (Clair *et al.*, 2003).

Dassot et al. (2012) proposent une estimation rétrospective des contraintes de croissance du bois de hêtre. En se basant sur la principale caractéristique du bois de tension des angiospermes qui est son état de tension élevé (Trenard & Guéneau, 1975; Fang *et al.*, 2008), et son aspect visuel, *i.e.* l'aspect nacré des fibres G du bois de tension, les auteurs identifient rétrospectivement le pourcentage de bois de tension par cerne (Barbacci *et al.*, 2008). Des photographies des rondelles réalisées sous une lumière rasante permettent de mettre en évidence les plages de bois de tension (Fig. 4.2a). Suite à une analyse d'images, les pixels correspondant au bois de tension apparaissent en bleu tandis que les pixels de bois sans fibres G sont rouges (Fig. 4.2b). En sectorisant la surface des rondelles analysée, la proportion du nombre de pixels bleu permet d'obtenir un pourcentage de bois de tension par secteur (Fig. 4.2c). En combinant ce pourcentage de bois de tension obtenu aux valeurs d'ICC obtenues par la méthode du trou unique, il est possible de calibrer l'état de tension du bois à un pourcentage de bois de tension et *infine* d'obtenir, en rétrospectif, l'état de tension du secteur considéré du cerne.



Figure 4.2 : Succession d'étapes permettant la détection du bois de tension sur une rondelle.

a : rondelle originale, le bois de tension présente un aspect nacré. b : étape de seuillage, le bois de tension apparaît en bleu. c : étape de sectorisation radiale et angulaire de la surface de la rondelle, plus le secteur est bleu, plus le pourcentage de bois de tension est élevé. (Source : INRA)

Dans notre étude, les ICC ont été mesurées sur 8 points répartis de façon homogène sur la circonférence du tronc à 1.30 m avant l'abattage (Fig. 4.1c). Une rondelle prélevée à cette hauteur et conservée à -20°C a permis la réalisation de la cartographie du bois de tension. Pour la calibration entre pourcentage de bois de tension et ICC, nous avons délimité des secteurs périphériques lors du traitement des images des rondelles (Fig. 4.2c) pour recaler la position de chaque trou de mesure d'ICC. Différentes tailles de secteurs ont été testées, allant de la taille du trou réalisé (20 mm de longueur d'arc x 10 mm de profondeur) à une taille minimale de 5 mm x 5 mm, de façon à correspondre au mieux à la surface qui contribue le plus à la libération des contraintes de croissance qui est de 8 mm x 8 mm (Sassus, 1998). Finalement, le secteur de 10 mm x 5 mm de profondeur donnant la meilleure qualité de la droite de régression, a été retenu.

La Figure 4.3 présente la droite de régression entre les ICC (μ m) et le pourcentage de bois de tension pour les 8 mesures de 42 perches. La relation est significative mais la qualité de l'ajustement est faible (R² = 0.18). L'origine à l'ordonnée nous informe qu'un bois sans fibres G, i.e. le bois normal, présente une valeur d'ICC de 68.75 μ m. La pente est de 1.44. La dispersion des valeurs est très importante surtout pour les secteurs avec un pourcentage limité de bois sans fibres G.



Figure 4.3 : Relation entre les valeurs des ICC (μ m) et du pourcentage de bois de tension.

En comparant ces résultats avec Dassot et *al.* (2012), il est observé que les perches présentent une plus forte valeur d'ICC pour le bois normal, ainsi que des ICC maximales plus élevées. Les conditions de croissance de ces deux lots d'arbres sont différentes. Or ce sont les conditions de croissance qui conditionnent la forme de l'arbre. Il a été démontré que la forme de l'arbre, notamment l'asymétrie du houppier ou le ratio hauteur/diamètre, influence l'amplitude des valeurs des ICC, même à l'échelle intraspécifique (Jullien *et al.*, 2013). Nous suggérons donc que ces valeurs sont spécifiques au matériel végétal étudié.

Des fortes valeurs d'ICC ont déjà été observées dans des secteurs avec peu de bois de tension (Trenard & Guéneau, 1975; Fang *et al.*, 2008), et celles-ci ont été attribuées à des hétérogénéités de taux de fibres G. Une mauvaise détection du bois de tension lors du traitement d'images peut aussi en être la cause. En effet, un trop fort seuillage réduit drastiquement le nombre de pixels détectés comme bois de tension. De plus, la qualité de sciage des rondelles altère la qualité des images. Dans notre cas, des coupes anatomiques permettraient d'évaluer le pourcentage de fibres G plus précisément et de s'affranchir des artefacts engendrés par la méthode cartographique. Néanmoins, une telle approche est expérimentalement lourde. Des coupes anatomiques ont été réalisées sur un rayon du bois normal. La coloration des coupes avec le protocole standard, celui utilisé sur des semis ou des arbres dominants de hêtre, n'est pas adéquate pour le bois de perches de hêtre.

En raison de la faible qualité de la régression entre les ICC et la quantité de bois de tension, nous avons choisi de ne pas estimer rétrospectivement les contraintes de croissance. Les perches dominées présentent de très faibles accroissements radiaux. La profondeur des trous réalisés contient, en moyenne, 15 cernes pour les arbres non libérés et 3 cernes pour les arbres libérés. Par ailleurs, les résultats de Purba *et al.* (2015) démontrent que les ICC à 1m30 ne sont pas modifiés suite à l'ouverture de la canopée. Les valeurs d'ICC mesurées sont donc utilisées comme une valeur moyenne de l'état de tension du bois durant les 13 années étudiées par la suite. 4.3. Article 2 : How trees maintain an erect habit in real managed forests: a theoretical and experimental biomechanical analysis in beech poles (*Fagus sylvatica* L.). (In progress)

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Abstract

Context To maintain an erected habit is a vital need for tree regardless its growth condition. Limited access to light may induce a tortuous or tilted habit however once the competition is released, this habit has no more functionality.

Aims In this study, we examined whether beech poles growing in understory with limited access to light exhibit a risk of sagging and if they are able to restore their verticality after a sudden competition release.

Methods To assess the posture control at the tree level, we need to pool together many traits measured at different scales. Stem curvature and lean were measured by TLS (Terrestrial LiDAR Scanner) scans before the release and 6 years after. Tree biomass distribution and taper were determined during tree harvest. Height and radial increment were retrospectively estimated. Concerning wood properties, GSI (growth stress indicator) and wood density were measured. From these traits, theoretical tropic curvature rate and change in lean angle were computed and compared to the lean change estimated from TLS scans.

Results Even under highly constrained environment, two thirds of beech poles were able to counterbalance gravitational curvature and avoid sagging. After release, beech poles with high initial lean angle were up-righting while beech poles with lean angle lower than 6° did not move much. The theoretical tropic curvature rate increased after release to slow down after two years likely due to the stem diameter increase. Theoretical model overestimated lean correction. Technical obstacles likely responsible for this overestimation, are discussed.

Keywords

Posture control; Fagus sylvatica; competition release

4.3.2. Introduction

Gravitropism is the capacity of plant to reorient their stem and control their posture during the growth phase. As stated by Darwin (Darwin & Darwin, 1880), movement is a basic necessity of plant life (Whippo & Hangarter, 2009; Moulia & Fournier, 2009). Actually, without gravitropism that allows plants to counteract gravitational forces, growth, which represents an increasing of both the self-weight and the height of the centre of mass, would be mechanically unstable (Moulia *et al.*, 2006). Among plants, trees, which are high, extremely slender and long living, could not maintain their erected habit, with a dramatically increasing of trunk lean during tree life (Fournier *et al.*, 2013).

Biomechanics and mechanobiology study how plants sense signals associated to gravity (Telewski, 2006) or their own shape (Hamant & Moulia, 2016) to right themselves smartly. As tree stems are mainly made of lignified, dead, and stiff wood, biomechanics pays also attention to how growth and cell differentiation at the stem periphery can produce enough energy to reorient so rigid bodies. Differentiation of the secondary cell wall in wood, associated to polymerization shrinkage, can generate forces of high enough magnitude (Archer, 1987; Moulia & Fournier, 2009). When the force between the two sides of the stem is asymmetric, due to reaction wood formation, it can provoke upward bending, i.e. a gravitropic curvature opposed to the gravitational one, which lead to downward bending and increasing lean (Wilson & Archer, 1979; Moulia & Fournier, 2009).

Then, the challenge of erected tree stem habit is figured out as a balance between gravitational and gravitropic curvatures. The ratio of the gravitropic curvature to the gravitational one represents the performance of the gravitropic process i.e. its ability to change significantly the stem habit (Fournier *et al.*, 2013). Going further in biomechanical modelling, the effects of several variables that influence the gravitropic movement can be disentangled (Alméras *et al.*, 2005a; Alméras & Fournier, 2009): the gravitropic curvature has been modelled as a curvature rate per unit of radial growth. It varies as a function of both section size (diameter) and independent to tree size variables (wood maturation strain asymmetry or eccentricity of radial growth). The gravitropic curvature per unit of radial growth represents the efficiency of the gravitropic process in respect to the investment in radial growth.

This theoretical framework removes some obstacles for studying the ecological relevance of gravitropic processes. First, it formalizes how gravitropic processes (i.e. the energy production to counteract gravity) are always and necessarily stimulated in the field, even in the lack of movement, when gravitropic energy just compensates gravitational downward bending. For example, Huang *et al.* (2010) use biomechanical models of gravitropic curvature

to discuss how branches can maintain their habit over time. Secondly, it proposes key traits, related to tree morphology or to wood tissue mechanical properties, involved in gravitropic efficiency and performance, that can compensate themselves with formalized trade-offs. For example, Dassot et al. (2012) examined in several silvicultural conditions whether radial growth and reaction wood properties can compensate the great constraint of increasing thickness, since the model states that gravitropic efficiency scales as the inverse of the square of the stem diameter (Dassot et al., 2012). Investigating why advanced regeneration of Fagus sylvatica is more efficient than the seed bank to insure forest resilience and regrowth after a strong gap opening, Collet et al. (2011) demonstrated that beech saplings restore efficiently and quickly a vertical trunk, useful in light foraging in open conditions, after having survived several decades with an oblique trunk and tree shape, typical of shade tolerance, and efficient in the previous poor light conditions. Lastly, the biomechanical traits involved in gravitropic efficiency and performance formalize a capacity of movement, quite independently of peculiar experimental conditions. Therefore, observations of gravitropic movements in greenhouse tilting experiments can be used to assess more generically the gravitropic performance of a population of trees. For instance, Alméras et al. (2009) discussed the functional diversity of gravitropic performance among a set of tropical species, although they observed movements in peculiar conditions of gravitropic stimulus or available resources. In the same vein, Sierra-de-Grado et al. (2008) proposed to use the gravitropic efficiency estimated from tilting experiments, rather than the trunk straightness itself, which is too variable and linked to too many processes, in breeding programs of maritime pine.

The validation of models faces three technical obstacles. Firstly, the movements expected by models are usually quite slow (excepted in tilting experiments in young small stems). Moreover, the relevant variable of movement is the rate of curvature with growth, i.e. the time derivative of the spatial derivative of lean along the stem (Moulia & Fournier, 2009). Therefore, very accurate measurements of stem longitudinal shape over time are required, which are cumbersome in the field and on tall trees over long periods. Secondly, the observed movement is the superimposition of both gravitropic and gravitational bending, and the validation of both theoretical models of curvature involves a lot of parameters (e.g. Alméras *et al.*, 2009; Huang *et al.*, 2010). For instance, modelling gravitational curvature involves generally unknown data about how both the total mass and the centre of mass height vary during growth. Thirdly, models involve wood properties as maturation strains or modulus of elasticity, and geometrical properties (eccentricity of radial growth) that cannot be assessed without destructive experiments in wood science labs.

For these three reasons, experimental studies which have used the biomechanical models to link wood or stem morphological properties to observed stem movements have concerned mainly on one hand, small and young stems easy to manipulate and of fast movements, and on the second hand, artificially tilted stems, where gravitropism is strongly stimulated, so that the gravitropic curvature is much greater than the gravitational one, which can then be neglected (e.g. Coutand *et al.*, 2007; Sierra-de-Grado *et al.*, 2008) or roughly assessed (Alméras *et al.*, 2009). Due to the great number of tedious to measure parameters, authors usually inversed the model to estimate unmeasured traits of the gravitropic performance or efficiency.

In this study, we will study gravitropic efficiency and performance of beech trees in field conditions. Gravitropic reactions are assumed to be stimulated by thinning after a long period of growth in dense high forests. This assumption is supported by results of Collet *et al.* (2011), although the tree ages will be older, and environmental conditions quite different, representative of a silvicultural disturbance rather than large gaps.

Thanks to the terrestrial laser scanner (TLS) technology, it is the first study that monitors accurately stem movements in tall and big trees on the field, and can then compare these observed movements to the model prediction from parameters measured independently on wood after tree harvesting.

The questions addressed are therefore the following:

- (Q1) Is very low radial growth before thinning compensated by other traits of gravitropic performance to maintain the capacity of the tree to control habit? Or can we suspect that unthinned trees could become mechanically unstable?
- (Q2) Do trees move upright after thinning? If yes, what is the main drivers of these movements, higher radial growth alone or a more complex synergy with traits related to wood properties.
- (Q3) Is the biomechanical model, previously used for the prediction of the capacity of movement of big stems (e.g. Dassot *et al.*, 2012), and mainly validated by movements observed in young tilted stems (e.g. Alméras *et al.*, 2009), definitely able to capture the reality of stem movement of big old trees in the field?

4.3.3. Material and Methods

Study sites and plant material

The site was a broadleaved 13-ha-stand in north-eastern France (47.9507°N, 6.3857°E, alt: 470m) formerly managed as a coppice-with-standards. In 1955-1956, stand was thinned, converting it to a high forest. Records show it was further thinned between 1956 and 1995, but the years of thinning were not recorded. After 1995, there was no further thinning.

In fall of 2007, a sample of 42 understory beech trees distributed throughout the stand and at least 18 m from one another were selected for study. The trees originated from seeds and grew up under closed canopy or in small gaps. Sample trees met the following criteria: breast height trunk diameter was 7.5 to 17.5 cm, stems were unforked, leaned < 11°, had fewer than 25 epicormic branches (sensu Colin *et al.*, 2012) along the lowest 4 m of stem, and had no visible injury, spiral grain, canker, or top dieback. The sample trees were then split into two subsamples with similar mean values for diameter, height and relative vertical crown length (see Noyer *et al.*, 2017 for more details). In winter 2007-2008, one subsample was released by a thinning that removed the trees within competition in a 12-m radius around each target tree (hereafter referred to as "thinned" trees) and the other subsample of trees was left unreleased ("control" trees) (Ningre *et al.*, 2011). Two trees that exhibited an abrupt increase in lean angle and two trees with errors in TLS images were excluded from the study so that 18 control and 20 thinned trees were investigated. Six years after thinning in winter 2013-2014, all trees were harvested.

TLS scans and characterisation of tree shape and lean

Tree morphology was recorded using a terrestrial laser scanner (TLS). From December 2007 to March 2008 and from December 2013 to January 2014, one scan per tree was performed using a phase-shift FARO Photon 120 scanner (FARO, USA) mounted on a tripod at a distance of 6 m of the tree. For each tree, the location (distance and azimuth) of the TLS was identical for the scans performed in 2007-08 just before the thinning and in 2013-14. On each scan, the target tree was isolated by using FARO Scene 4.5 software as primary clean step, and Polyworks software (PolyWorks, InnovMetric Software Inc.) to isolate more precisely crowns of understory trees from neighbour trees.

Computree (computree.onf.fr) was then used to describe stem morphology. Horizontal circles were adjusted every 10 cm along the stem, and the neutral line of the stem was defined as the line passing through the centres of the successive circles. Lean angle at different heights was computed from the coordinates of the neutral line points. To compute the lean angle at a given height, three successive points at the base of the tree and at a given height were used.

Osculating circles, or curvature circles, were calculated for each horizontal circle from its centre by best taking account of the five above and below horizontal circles alignment, i.e. 50-cm-length on both side of the trunk shape. The inverse of the osculating circle radius was the local curvature of the trunk at this point. For the horizontal circles, recorded data were the radius, the x, y and z coordinates of the centre circles. For the osculating circles, the x, y and z coordinates, the curve abscissa was given.

Growth stress measurement

Before tree harvesting peripheral growth stress indicators (GSI, μm) were measured at breast height of the stem by the single-hole method (Fournier et al., 1994) using CIRAD's sensor. This method consists in measuring the relative displacement of two pins inserted in wood after drilling a hole between them and so releasing the longitudinal growth stresses in the outmost layer of wood. Eight measurements equally distributed along the stem circumference were performed, the first being located on the upper side of maximal local lean angle. After bark removal, two nails separated by 45 mm in the longitudinal direction were tapped at each location. Each value was then converted in deformation by the calibration done by Fournier et al. (1994), where $GSI(\varepsilon) = GSI(\mu m) \ge 15.8 \ 10^{-6}$. Due to very narrow growth rings in our trees (0.4 mm for control trees and 3.1 mm in thinned trees), attempts to use image analysis based on photographs under a particular light incidence that makes the TW shiny (Barbacci et al., 2008) to access retrospectively the amount of TW generated each year were not conclusive. As the GSI measurement by the single hole-method encounters cca 8 mm outmost wood layer of wood (Sassus, 1998) which corresponds to cca 15 growth ring in control and 3 growth rings in thinned trees and as nor average GSI value nor the TW intensity were affected by thinning (Purba et al., 2015), measured values were considered as average values for all years examined in the retrospective analysis of biomechanical traits.

Biomass distribution and stem taper

After harvest, tree stems were divided into six successive segments. The basal segment measured 2m; other five segments were of equal length. To increase accuracy of log-log models of taper (n) and biomass distribution along the height (m) according to Jaouen *et al.* (2007), the two distal segments were cut again in two segments of equal length. For each segment, we measured the length, the two perpendicular basal cross-section diameters and segment and branches weight. These data together with the coordinates of neutral line were also used to compute the height of the centre of mass (H_{CG}). For the computation of PC trait (Postural Control), H_{CG} of the distal part where the GSI are measured were used while for

comparison between modelled lean change and lean change measured by TLS scanner, $H_{\rm CG}$ of the whole tree more representative of the global lean of a tree was used.

$Retrospective\ analysis\ of\ tree\ axial\ and\ radial\ growth\ and\ wood\ density$

For each tree, successive height annual increments along the stem were estimated through measurements of the length of the successive growth units (LGU, mm) based on the bud scars observed on the bark. The age of the growth units was checked by counting the annual ring on disks sampled every 10 GUs and, in case of observed discrepancy between GU age and the number of rings, GU and rings were measured again.

Five-cm-thick disks were collected at 1.35m-height just above the GSI measurement from each tree for micro-density measurements. The disks were wrapped in plastic film and were stored at -20°C immediately after harvest. After disks have been sanded, four perpendicular radii were identified in regard to GSI values. The radius corresponding to the highest GSI values observed on the tree was designated as tension wood (TW) radius, the opposite one as opposite wood (OW) radius while the last two perpendicular radii as normal wood (NW) radii. On each radius, the width of each tree-ring (RW, mm) from pith to bark was measured to a precision of 0.01 mm, by image analysis using TSAP-Win (Rinntech, Germany) for last 13 years to allow for growth analysis 6 years before and 6 years after the thinning. From ring width, disk diameter between TW and OW radii was used for the calculation of growth asymmetry (parameter k_m). After ring width measurements, a NW radius without knots or visible damage was selected. A radial strip (2.5 x 5 cm², T x L) was cut in the selected radius and conditioned for one month at 12% relative humidity at ambient temperature. Then, a radial slice (1.0 x 0.2 cm², T x L) was cut for X-ray micro-densitometry measurements with a microfocus X-ray source (Hamamatsu L9181-02 130 kV) and a digital X-ray detector (Varian PaxScan 4030R). The Crad and Cerd software suite was used to compute radial wood density (WD, kg m⁻³) profiles (Mothe *et al.*, 1998). Wood density was used to estimate elastic modulus according to Guitard and Fournier (1994).

Biomechanical traits

Integrative approach proposed by Fournier et al. (2013) was used to estimate the motricity traits at the whole tree level combining data measured at different scales. Measured data allow for retrospective analysis of both traits in view to compare predicted lean angle change with measured lean angle change.

The tropic motion velocity (MV) defined as the theoretical curvature rate of the stem tropic movement was calculated as:

$$MV = -4 \ \frac{F_m \,\Delta\alpha}{D^2} \frac{dD}{dt} \tag{4.1}$$

where F_m is the radial growth asymmetry motor, $\Delta \alpha$ is the GSI asymmetry (µdef), D is stem diameter at breast height (m), dD/dt is the annual radial growth increment (m).

 F_m represents interaction between maturation strains and radial growth asymmetry and is defined from Alméras et al. (2005) as:

$$F_m = 1 + 2.k_m \cdot \frac{\overline{\alpha}}{\Delta \alpha} \tag{4.2}$$

where k_m is the asymmetry of radial growth and $\bar{\alpha}$ the average of GSI values (µdef).

The posture control (PC) is the ratio of active up-righting curvature and gravitational curvature due to an increase in biomass. As growth stresses generating the active up-righting curvature were measured at breast height, only the distal part of a tree above the breast height was considered for the computation of PC:

$$PC = \frac{-dC_m}{dC_g} = \frac{E\Delta\alpha}{4(1+b)\rho_T g \sin\varphi} \frac{F_m}{F_g} \frac{D}{H^2}$$
(4.3)

where *E* is Young's modulus (N m⁻²), *b* is the ratio of axial (*d*H/H) to radial (*d*D/D) increment, ρ_{T} is total fresh biomass supported, including leaves, trunk, and branches, per unit of trunk volume (kg m⁻³), *g* is gravity acceleration (N kg⁻¹), ϕ is the lean angle (°), H is the height of the distal part of the tree (m) and F_g is the growing weight form factor calculated as:

$$F_g = \frac{2}{(m+1)(2n+1)} \tag{4.4}$$

where m is the biomass distribution and n is taper.

PC higher than unity means that the tree is up-righting i.e. the curvature rate generated by the maturation strains of the growing stem per unit of growth (dC_{mat}/dD) is higher than the curvature rate due to gravity (dC_g/dD) . Active up-righting curvature rate and gravitational curvature rate are computed as follows:

$$\frac{dC_{mat}}{dD} = -4 \frac{F_m \Delta \alpha}{D^2} \tag{4.5}$$

$$\frac{dC_g}{dD} = 16(1+b) F_g \sin \varphi \, \frac{\rho_T \, g}{E} \frac{H^2}{D^3} \tag{4.6}$$

To allow retrospective analysis, the relative height of the centre of mass of the distal part was determined for 2013 and used to compute the position of H_{CG} in previous in previous years based on the height of a given year. Further, the lean angle of previous year was corrected for the change in lean angle generated according to the PC during a given year.

Variance decomposition

The variance decomposition was realized for MV. We analysed the relative contribution of each parameter: dimensions (diameter D), growth (dD/dt), material properties (magnitude

of GSI $\Delta \alpha$) and shape (F_m). After a log-transformation of the equation 1, we estimated the variability due to the treatment (Var_{treat}) and due to inter- tree variability inside the treatment (Var_{tree/treat}) as:

$$Var(\ln MV) = Var_{\frac{tree}{treat}}(-2\ln D) + Var_{\frac{tree}{treat}}\left(\ln\frac{dD}{dt}\right) + Var_{\frac{tree}{treat}}(\ln\Delta\alpha) + Var_{\frac{tree}{treat}}(\ln F_m) + Var_{treat}(-2\ln D) + Var_{treat}\left(\ln\frac{dD}{dt}\right) + Var_{treat}(\ln\Delta\alpha) + Var_{treat}(\ln F_m)$$
(4.7)

Statistical analysis

Linear regressions were adjusted by the ordinary least-squares to obtain the adjusted-R². P-values were obtained by t-test.

To test the effect of the release on the lean changes, a linear model was built with the initial lean (i.e. 2007) as explanatory co-variable. Due to the precision of the lean measurement from TLS, the significant threshold was 0.1.

For MV, and for each year, treatment levels were compared using a Kruskal-Wallis test with a significant threshold where P < 0.05. All statistical analyses were performed using R software version 3.2.3 (R Core Team 2015).

4.3.4. Results

Measured changes in stem lean at 2-m height and at the height of centre of mass of the tree

Relationships between the stem lean angle in 2007 and 2013 at 2-m height and HG are displayed in Fig. 4.4. For both group of trees, linear regressions were significant (P < 0.001) what is the height analysed. Ten trees (4 thinned and 6 controls) were above the sagging line. At 2-m height and for both years, lean angle of control trees was not significantly different than the lean angle of thinned trees (5.82° and 5.48° in control trees and 5.17° and 4.70° in thinned trees, in 2007 and 2013 respectively, Table 4.2). At H_{CG}, only 4 trees had an inclination superior than 8° in 2007. Most of trees had an inclination inferior than 7° for both years (Fig. 4.4). Mean lean angle for control trees were significantly different than those of thinned trees (4.13° and 3.98° for control trees and 4.03° and 3.50° for thinned trees, in 2007 and 2013 respectively. Table 4.2) and 3.50° for thinned trees, in 2007 and 2013 respectively. Table 4.03° and 3.50° for thinned trees, in 2007 and 2013 respectively. Table 4.03° and 3.50° for thinned trees, in 2007 and 2013 respectively. Table 4.20° for thinned trees, in 2007 and 2013 respectively. Table 4.20° for thinned trees, in 2007 and 2013 respectively. Table 4.20° for control trees, slope of linear regression was lower at 2 m (0.91) than at H_{CG} (0.97). For thinned trees, it was the opposite: slope was higher at 2 m (0.89) than at H_{CG} (0.8, Fig. 4.4).

The lean changes between 2007 and 2013 were not significantly correlated to the initial lean in 2007 for both treatments at 2-m height (Fig. 4.5). At H_{CG}, the correlation was significant only for thinned trees ($R^2 = 0.24$, P = 0.0162, Fig. 4.5) and its slope was negative (slope = -

0.20). After 6 years of treatment, thinned trees may change their lean angle until 3.38° at 2m height and 2.41° at H_{CG}. When we compare the mean lean changes of both treatments, a significant difference was found for H_{CG} but not for 2-m height (Table 4.2).



Figure 4.4: Relationship between the stem lean (°) deduced from TLS scans at 2-m height (left) and at the height of the centre of mass (right) in 2007 and 2013 of control and thinned poles.

Grey circles correspond to control poles and orange triangles to thinned poles. Black dotted line represents sagging line. Linear regressions for both groups of trees and for the two heights are significant (P < 0.001).



Figure 4.5: Relationship between the change in lean angle (°) between 2007 and 2013 and the initial lean angle in 2007 at 2-m height (left) and at the height of the centre of mass of the tree (right).

Grey circles correspond to control poles and orange triangles to thinning poles. No significant relationship was found for control trees at the two height tested. Significant relationship was found for thinned at the height of the centre of mass of the tree (P < 0.001).

Table 4.2: Mean ± standard error (SE) of stem lean angle, relative and absolute lean angle changes between 2007 and 2013 measured with TLS scans, and stem lean angle changes predicted with model.

Usich+	Treatment	Stem lear	n angle (°)	% of change	Δ Lean angle	Δ Lean angle	
neight	Treatment	2007	2013	and 2013	TLS (°)	predicted (°)	
9 m hoight	Control	5.82 ± 0.55	5.48 ± 0.55	-5.84 %	-0.34 ± 0.24	-0.17 ± 0.04	
2-m-neight	Thinned	5.17 ± 0.61	4.70 ± 0.59	-9.09 %	-0.47 ± 0.26	-1.47 ± 0.23	
	Control	4.13 ± 0.6	3.98 ± 0.6	-3.63 %	-0.15 ± 0.11 a	-0.51 ± 0.12	
HCG	Thinned	4.03 ± 0.49	3.50 ± 0.42	-13.15 %	-0.53 ± 0.18 b	-4.22 ± 0.58	

Different letters indicate a significant difference at 0.1 between control and thinned trees for a same height.

Table 4.3: Variance decomposition of parameter groups (S: shape, G: growth, D: dimensions, M: material) between trees inside a same treatment (Tree) and between treatments (Treatment) of MV trait in 2013.

		Vari	ance			Covariance								
-	\mathbf{S}	G	D	М	S,G	S,D	S,M	G,D	G,M	D,M	_ 10tai			
Tree	1.76%	31.55%	8.17%	29.53%	4.13%	-0.33%	-6.49%	-2.03%	-8.52%	2.04%	59.8%			
Treatment	0.00%	76.41%	3.02%	0.46%	-0.06%	0.31%	-0.02%	-30.37%	-11.92%	2.37%	40.2%			
Total	1.76%	107.96%	11.19%	30.00%	4.07%	-0.02%	-6.51%	-32.41%	-20.43%	4.41%	100.0%			





Data and images came from TLS scans. The height of the centre of mass of the tree (H_{CG}) are indicated by blue and red dotted line in 2007 and 2013, respectively. Black dotted line indicated 1.3–m-height, i.e. the location of material properties measurements.

Complexity of stem lean and stem shape

Despite significant relationship between lean angle at 2-m-height and H_{CG}, the coefficient of correlation was low ($R^2 = 0.49$, Fig. 4.7) showing that an extrapolation of stem lean angle at 2-m-height to taller in the tree is difficult and no general pattern could be established as illustrated by the Fig. 4.6. The 2 selected thinned trees presented complex shape with high variation in local curvatures. For the first tree (Fig. 4.6A), we noted the tilted branches and main axis reflecting a possible asymmetric crown. The maximal curvature is located around 5.8-m-height. For the second tree (Fig. 4.6B), stem presented 2 mains curvatures at 2.5-m-height and at 3.5-m-height.



Figure 4.7: Relationship between lean angle (°) at HCG and 2-m-height in 2007. In black, the linear regression is significant (P < 0.001).

Theoretical stem motricity

Up-righting curvature rate

Thinned beech poles increased strongly and significantly their theoretical MV values the two first year after thinning to reach $3.07 \ 10^{-3}$ against $0.32 \ 10^{-3} \ m^{-1}$ year⁻¹ for control poles in 2009 (Fig. 4.8). After 2009, MV of thinned poles decreased until 1.66 $10^{-3} \ m^{-1}$ year⁻¹ in 2013. For this year, the MV variability in thinned poles was mainly due to the growth improvement (76.4 %, Table 4.3). Material properties contributed only inside a same radial growth interval (29.5%), where value was close to growth contribution (31.6%). The total covariance between growth and material properties was of -20.43% (-8.52% between trees inside treatment, and -11.92% between treatments). The variability due to trees was higher than this to treatment (59.8% and 40.2% respectively).

The ratio between the geometrical up-righting motor (dD) and brake (D^2) reflects how far growth increment is efficient in counteracting the inertia of the diameter. The Fig. 4.9

showed a positive and significant relationship between MV and the geometrical factor dD/D^2 (R² = 0.49, P < 0.001).



Figure 4.8: Evolution of tropic motion velocity (MV) of control poles (grey, dotted line) and thinned poles (orange, solid line) from 2001 to 2013 (mean ± SE). Vertical dotted line represented the date of thinning. Symbol * indicated a significant difference

Vertical dotted line represented the date of thinning. Symbol * indicated a significant difference between control and thinned poles (Kruskal-Wallis test, P < 0.05).



Figure 4.9: Link between tropic motion velocity MV and geometrical brake dD/D^2 (diameter increment on the trunk diameter squared) in 2013. In black, the linear regression is significant (P < 0.001).

Relationship between gravitropic and gravitational curvatures

The relationship in 2013 between the gravitropic curvature (dC_{mat}) and the gravitational curvature (dC_g) is significant ($R^2 = 0.42$, P < 0.001, Fig. 4.10), the slope is different than the unity (-9.4) and the intercept is not significantly different to zero (-0.01). Contrary to the Fig. 4.4, no trees are above the sagging threshold. Then, trees close or on the sagging threshold presented low dC_g values. Surprisingly, trees with high lean angle did not enhance high dC_{mat} values and trees with lean angle superior than 6°, except one, generated high C_g .



Figure 4.10: Relationship between gravitropic curvature (dC_{mat}) and gravitational curvature (dC_g) in regard to lean angle at HCG of the stem in 2013.

Lean angle inferior than 2° (black diamonds), between 2 and 4° (yellow triangles), 4 and 6° (blue inverse triangles), 6 and 8° (grey squares), superior than 8° (red circles). Black dotted line represents sagging line. In black, the linear regression is significant (P < 0.001).

Comparison between predicted and observed stem lean change

The Fig. 4.11 shows the relationship between stem lean changes at H_{CG} predicted by PC model and deduced from the TLS data. Linear regression is significant (P < 0.05) however the coefficient of determination is relatively low (0.10), the slope higher than unity (1.39) and intercept relatively far from zero (-1.97) showing that predicted lean change is largely overestimated as summarized in Table 4.2.



 Δ lean TLS scans

Figure 4.11: Link between lean angle changes (°) predicted by computation of the model from the H_{CG} to the ground and measured from TLS scans. In black, the linear regression is significant (P < 0.05).

4.3.5. Discussion

Control of stem lean in different growth conditions

When we compare the lean change in control and thinned trees, we can see that at 2 mheight both groups of trees move with similar magnitude (Table 4.2) and this movement is independent of initial lean (Fig. 4.5). On the contrary at CG-height, which may be understood from the biomechanical viewpoint as a simplified proxy of the tree global lean, thinned trees move more than control trees (Fig. 4.5, Table 4.2). One third of control trees is above sagging threshold and trees with relatively high lean of the stem (>8°) struggle to maintain a fixed lean angle (Fig. 4.5). However, we do not expect control trees to upright their stem in a significant way as they are constrained by the presence of light gaps to access the light (i.e. phototropism). It is interesting to note that despite their very low radial growth (0.36 mm in average), two thirds of control trees remain able to avoid sagging which means that posture control is one of the priorities even in very constrained growth condition. After the release of competition from neighbours, trees clearly try to up-right their stems (Fig. 4.5, Table 4.2) and trees with high lean in 2007 invest more in the stem lean correction than trees with low lean in 2007. Is it reasonable to expect that thinned trees will achieve completely vertical stems? Some reports mention that for light capture, it may be beneficial to keep lean angle different from the vertical (Ishii & Higashi, 1997) which may be interesting for trees after thinning whose foliage needs to acclimate to the new environment. The only report we found with experimental data of tree lean change after competition release in big trees was the work done by Constant et al. (2006). In this study, no global behaviour of trees after release could be identified and measured reactions were very small and complex.

Tropic curvature rate after release is increased ten times mainly due to the growth rate increase

Theoretical MV values of control poles were close to previous results obtained in beech poles with similar stem diameter (Dassot *et al.*, 2012). After the thinning however, MV increased up to 10-fold despite the increase in stem diameter which represents a geometrical break in up-righting process (Eq. 4.1). Increase in stem diameter may however explain the slowdown of the theoretical tropic curvature rate after the second year after thinning (Fig. 4.8). As we can see from Fig. 4.9, considering the growth increment and diameter explains already 49% of the MV variability. As average value of GSI as well as the intensity of TW were not affected by thinning (Purba *et al.*, 2015), the difference in MV due to the thinning results mainly from the increase in growth rate. Nevertheless, inside the same treatment, contribution of GSI intensity is of the same order as the growth increment when decomposition of MV variance is performed (Table 4.3).

Why simple biomechanical model of up-righting process does not work well for big trees and how can we improve it?

In biomechanical model of tree posture control, lean angle used in the computation is the lean angle of the distal part in respect to the height of GSI measurement. However, when we look at the complexity of tree curvature and lean variation along the height in big trees (Fig. 4.6, 4.7), one may wonder how representative this proxy is of the global or local loading at a given height of the stem. Moreover, it is interesting to see how dC_{mat} and dC_g are related because it shows if dC_{mat} is used to counterbalance the bending moment we expect it to counterbalance. Sagged trees observed in experimental measurements at CG-height (Fig. 4.4) did not appear when we computed curvatures at the base of the distal part (Fig. 4.10). The applied hypothesis beside the estimation of the gravitropic curvature is that all TW detected in the section at the base of the segment allows for the distal segment up-righting. In this way, high dC_{mat} values should (i) correspond to high loading and (ii) be related to the presence of TW (Eq. 4.5). In our case, the absence of the detection of sagged trees such as the overestimation of the gravitropic curvature could be explained by the high quantity of TW in the section at 1.30-m-height. As in beech saplings, only one-third of the up-righting is induced by the stem basal part movements (Collet *et al.*, 2011), a part of produced TW might not contribute to up-righting process and be involved at a more local level. Moreover, the azimuth of the stem curvature was not included in the calculation. The computed gravitropic curvature might be not in the same azimuth that the GSI and growth asymmetry causing bias in calculation.

In saplings, lean angle is in general very high (58°) as well as its change (18°) thanks to small stem inertia (Collet *et al.*, 2011). Further, the variation of curvature along the sapling's height presents in general at maximum one peak corresponding to a change in lean angle (Almeras *et al.* 2009). In big trees that evolved in constrained condition, the lean angle does not exceed 10° at CG-height, the change in lean angle is of 0.53° in average and the stem curvature variation along the tree height is complex (Fig. 4.6). Moreover, the lean angle significantly varies along the tree height from the lean 2-m-height) (Fig. 4.5). Another problem with big trees is that they may generate a torsion moment due to for example the rotation of a crown especially after thinning where the light access become suddenly homogeneous (Constant *et al.*, 2006) and crown, often asymmetric, is free to evolve in a symmetric way again while in saplings, the up-righting process is generally contained in one vertical plane even if it can be also helped by establishment of relay axes as it was for example observed for *Acer pseudoplatanus* saplings (Collet *et al.*, 2011). Crown movements could explain the low dC_{mat} coupled to high dC_g in Fig. 4.10. Unfortunately, in big trees,

crown data are complicated to access contrary to saplings. Several TLS scans per trees will be necessary. This technology limits the description of tree architecture to the winter period without leaves on branches.

Considering the data used for the computation of active curvature, GSI and ring width measurements including the growth eccentricity, which are the main factors driving the active up-righting curvature change (Almeras, Thibaut & Gril 2005), are very local. To see what happens higher in the tree or, for example at the height where the achieved change in curvature is maximal, one should measure GSI and ring widths at this location. Such measurements may help to better understand how the tree lean and curvature change is controlled along the tree height. Another option, unfortunately not investigated in this study, is to separate maturation stresses and "spring-back" strain (strains due to the load) which allows to characterize the gravitational moment due to the lean or asymmetric growth as done for example in Hung *et al.* (2016). This will allow for characterization of the load locally "sensed" by the stem and give a clue for the choice of the best geometrical descriptor of the tree shape to determine the loading inducing the gravitational curvature but also used as an input to correct by active curvature. Finally, this method will also permit the characterisation of crown asymmetry.

4.3.6. Conclusion

This work showed that posture control is one of the priorities for trees even under high growth constraints. For big trees, the up-righting movements were enhanced at CG-height at the contrary of small trees from the literature where movements were detected at the stem base. In addition, the intensity of the up-righting movements increased with the initial stem lean for thinned trees. From theoretical tropic curvature rate calculation, we stated that this increase was due to the boosted radial growth rate which was also the cause of the observed slowdown by the increase of the stem diameter. The application of existing model to predict retrospectively the stem lean overestimated the gravitropic curvature. Because of the complexity of tree shape, we suggested that the tension wood included in the calculation of the model more acted at the local level and might not fully participate to the up-righting process of the distal part. Moreover, crown movements could be also involved in the up-righting process or in the loading of the basal part. As perspectives, we proposed (i) to include the azimuth of the stem curvature and the GSI, (ii) to realise several TLS scans per trees, (iii) to measure GSI and ring widths at the location of maximal curvature changes and (iv) to measure "spring-back" strains.

4.4. Article 3 : Safety against self-buckling and against wind-break in beech poles after competition release. (In progress)

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4.4.1. Introduction

In understory trees or saplings growing under a dense forest cover the risk of self-buckling may be high. In such environment, trees may partially rely on their neighbours for mechanical support, they are sheltered from wind forces and foraging for light is the main environmental constraint. To access the light, trees allocate their biomass preferentially to height growth instead of radial growth achieving very slender structures. In some cases, they can become nonself-supporting as described by Jaouen et al. (2007) in saplings from tropical forest understorey. While the tree size has the greatest effect on self-buckling risk, form factor including the taper and biomass distribution along the stem height needs also to be considered.

Once an understory tree is released from its neighbours' competition, wind penetrates more easily to the tree and mechanical loading due to the wind becomes more important. Moreover, access to light and to other nutriments allows for the crown development which increases the sailing area exposed to the wind. From thigmomorphogenetic studies we know that when a plant is submitted to longitudinal bending, axial growth is stopped and radial growth is boosted (Coutand, 2010). Bonnesoeur *et al.* (internal report, 2016) observed an increase of radial growth of 44% to 67% in young beech poles after the release depending on the meteorological condition of the year. This explains why decrease in slenderness is observed in trees after the competition release (Mitchell, 2000) and also why trees from windy habitats evolve typically short and thick stems with reduced crown area such as a flag tree (Telewski, 2012). Increase in diameter is essential to resist the wind forces because the stem resistance in bending scales with the third power of diameter while the effect of height acting as an arm level is only proportional (Peltola, 2006).

In the present study, we examine the change in biomechanical safety traits, namely safety against self-buckling and against wind-break on a sample of beech understorey trees submitted to a long compression period and released in 2007. In winter 2009, fifteen of released beech trees were broken by the wind. Final sample consists therefore of 21 control trees, 21 released trees unharmed in 2009 and 15 released trees broken in 2009. The aim is to examine how trees acclimated to an increased mechanical loading in terms of shape

change (slenderness, taper, biomass distribution) and material properties change. Further, the relevance of safety against wind-break trait based solely on allometric comparison will be discussed. Two other samples were used to discuss the variability of biomechanical safety traits in beech in function of growth condition: canopy trees from a regular stand and standard trees from a coppice with standards site.

4.4.2. Material and methods

Study sites

Two distinc sites were used in this study.

Site 1 was a broadleaved 13-ha-stand in north-eastern France (47.9507°N, 6.3857°E, alt: 470m) formerly managed as a coppice-with-standards. In 1955-1956, stand was thinned, converting it to a high forest. Records show it was further thinned between 1956 and 1995, but the years of thinning were not recorded. After 1995, there was no further thinning. In fall of 2007, a sample of 72 understory beech trees distributed throughout the stand and at least 18 m from one another were selected for study. The trees originated from seeds and grew up under closed canopy or in small gaps. Sample trees met the following criteria: breast height trunk diameter was 7.5 to 17.5 cm, stems were unforked, leaned $< 11^{\circ}$, had fewer than 25 epicormic branches (sensu Colin et al., 2012) along the lowest 4 m of stem, and had no visible injury, spiral grain, canker, or top dieback. The sample trees were then split into two subsamples with similar mean values for diameter, height and relative vertical crown length. In winter 2007-2008, one subsample was released by a thinning that removed the trees within competition in a 12-m radius around each target tree (hereafter referred to as "released" trees) and the other subsample of trees was left unreleased ("control" trees) (Ningre et al., 2011). From thirty-six released understorey trees, fifteen were broken by the wind in winter 2009 and twenty-one remained unharmed. For wind-broken released trees, we have only the initial measurement of tree morphology while released trees were followed until harvested in winter of 2013-2014.

Site 2 was situated in Montiers-sur-Saulx in north-eastern France (48.538 N, 5.305 E). On this site, two stands were used for sampling. The first stand was a regular mixed *F. sylvatica* and *A. pseudoplatanus* even-aged high forest and the second one a coppice-with-standards stand. Thirty-two trees *F. sylvatica* canopy trees from the regular stand and three standard trees from the coppice-with-standards stand were sampled in 2009 and 2010 during an experimental campaign of ANR EMERGE project which aimed to evaluate the available forest biomass in France (p37-46, Gamblin, 2013).

Tree measurements

For understorey beech trees from site 1, retrospective analysis of radial and axial growths as well as the determination of biomass distribution parameter and taper parameter was performed according to the procedure detailed in §4.3.3 Further, horizontal crown projections were measured for all trees at 2007, 2010 and 2013 by a four-radii method.

For beech trees from site 2, only values measured during the tree harvesting were available. Taper parameter was fitted at the same manner as for site 1. During EMERGE project, biomass distribution along the trunk was measured for all branches with diameter higher than 7cm while smaller axes were weighted all together. To obtain biomass distribution parameter m, weights of sections smaller than 7cm were distributed along the stem proportionally to the weight of branches with higher diameter. For some trees, branch data was not of a good quality so that only twenty-one canopy tree and three standard trees were used for the study. Crown projections are missing for site 2. Therefore, we used diameters of branches at insertion to predict the length of branches according to Constant & Morisset (2015). Length was converted into projected length using average angle at insertion according to Kint et al. (2010) and average of at least three branches was used as an average crown radius. When less than three branches was recorded on the tree, crown radius was not computed which reduced the number of trees for which we could estimated the crown radius to 9 canopy trees and 3 standard trees. Basic morphological characteristics by tree type are summarized in Table 4.4.

Biomechanical integrative traits

Biomechanical safety traits were computed according to Fournier *et al.* (2013). Safety against self-buckling was estimated as follows:

$$SB = 0.836H^{-3/4}D^{1/2}E^{1/4}(\rho_T g)^{-1/4}(2n+1)^{-1/4}F_b^{1/2}$$
(4.8)

where H is the tree height, D is the basal diameter, E is the wood elastic modulus, ρ_T is the ratio of total fresh biomass including branches to the volume of the stem, g is the gravitational acceleration, n is the taper parameter and F_b is the shape factor which is computed as follows:

$$F_b = 0.1785(|m - 4n + 2|) \cdot (2n + 1) \cdot J_{\frac{4n-1}{m-4n+2}}^{-1}$$
(4.9)

where m is the biomass distribution coefficient and $J_{\frac{4n-1}{m-4n+2}}^{-1}$ is the first root of Bessel function that can be solved using linear regressions fitted by Jaouen et al. (2007).

Safety against the wind-break was estimated as:

$$SW = \frac{\pi \sigma D^3}{16A_c H k_w} \tag{4.10}$$

where σ is the wood strength, D is the tree diameter at breast height, A_c is the crown area and Hk_w is the height of the centre of pressure *i.e.* the centre of mass that we can obtain from the biomass distribution along the trunk.

As for beech trees from site 2 we did not have data about the wood properties and the center of the pressure, simplified version of SW was computed without these parameters designated in the following as SW1 using horizontal projection as a crown area. Bonnesoeur *et al.* (2013) suggested to compute the bending moment applied on the tree crown assumed to have a diamond shape as R_cH^2 where R_c is the crown radius and H is the tree height. Using this expression of the bending moment, SW can be also calculated as follows:

$$SW2 = D^3 / (R_c H^2). ag{4.11}$$

Variance decomposition

In order to estimate the weight of each parameter on the total variance of SB trait, we did the variance decomposition. First, Eq. 4.8 was log-transformed and parameters were grouped according to their nature as follows:

$$Log SB = \log 0.836 + \log (H/D)^{-3/4} + \log \left(D^{-\frac{1}{4}}\right) + \log \left(E^{\frac{1}{4}}\right) + \log (\rho_T g)^{-1/4} + \log \left((2n+1)^{-1/4} + F_b^{1/2}\right)$$

$$(4.12)$$

where $S = slenderness = log(H/D)^{.3/4}$

$$D = diameter = \log (D^{1/4})$$

 $E = elastic modulus = log (E^{1/4})$

- L = load ratio by biomass = log ($\rho_T \cdot g$)^{-1/4}
- $F = shape = log ((2n+1)^{-1/4} \cdot F_b^{1/2})$

Variance of the linearized form of SB trait (Eq. 4.12) was decomposed to obtain the contribution of each parameter and to separate the variance due to the treatment and variance due to individual trees inside each treatment.

Statistical analysis

Statistical analyses were performed with the Origin software. A Student's t-test at specified level of significance was used to assess the difference between treatments.

Table 4.4: Morphological of	characteristics of F. sylvatica	trees from different growth	conditions in 2013.
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 H/D_{130} and H/D_{basal} are the tree slenderness ratios taking the diameter at breast height (D_{130}) and the tree basal diameter (D_{basal}) respectively, as a reference value for diameter.

	Nb Age (yrs)		Height (m)		D _{basal} (m)		D ₁₃₀ (m)		H/D_{basal}		H/D ₁₃₀		Crown area (m²)	
		Mean	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Control	21	86.0	18.3	3.34	0.16	0.04	0.13	0.03	113.8	11.9	144.6	12.7	30.7	14.0
Released	21	84.8	18.4	3.32	0.19	0.03	0.15	0.03	96.9	17.6	121.0	18.0	35.5	13.4
Canopy trees	21	52.4	22.2	2.06	0.36	0.09	0.30	0.08	66.6	17.0	78.3	19.9	341.4	147.5
Standards	3	140	26.3	0.93	0.84	0.12	0.71	0.05	31.6	3.8	37.3	1.6	432.5	243.5

Table 4.5: Biomechanical traits of *F. sylvatica* trees from different growth conditions.

 ρ_{T} is the load factor, n is the taper, m is the distribution of biomass factor, Fb is the shape factor, SB is the safety against self-buckling, SW_1 is the safety against wind break according to Fournier *et al.* (2013) and SW_2 is the safety against wind break according to Bonnesoeur *et al.* (2011).

-	рт (kg m ⁻³)		n		m	m		$\mathbf{F}_{\mathbf{b}}$		SB		SW_1		SW_2	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	
Control	1285	175	0.97	0.11	2.72	0.28	3.01	0.32	1.68	0.11	9.2E-06	5.9E-06	4.1E-06	1.5E-06	
Released	1357	119	0.98	0.12	2.75	0.26	3.06	0.27	1.82	0.24	1.2E-05	4.4E-06	6.6E-06	3.1E-06	
Canopy trees	1475	186	0.95	0.14	3.15	0.32	3.63	0.40	2.08	0.25	8.2E-06	4.7E-06	1.1E-05	6.0E-06	
Standards	2038	217	1.17	0.10	3.76	0.30	4.42	0.43	2.90	0.13	5.9E-05	2.2 E- 05	7.7E-05	2.0 E- 05	



Figure 4.12: Change in slenderness ratio (H/D₁₃₀) in control and released beech poles from 2001 to 2013.

Stars designate positive result of t-test at 0.001 (***), 0.01 (**) or 0.05 (*) level of significance.



Figure 4.13: Slenderness ratio (H/D₁₃₀), safety against self-buckling (SB) and safety against wind-break (SW) in beech trees from different growth conditions.

4.4.3. Results

Morphology changes of beech understorey trees after the release

We found that beech trees evolving during their whole life in the forest undrestorey exhibited very high slenderness ratio. During the six years after the release, slenderness ratio has been continously decreasing (Fig. 4.12) and no stabilisation was reached. The slenderness ratio of released poles in 2013 was in average 16.3% lower when compared to control poles (Table 4.4, slenderness ratio with the diameter at breast height is taken as a reference). Increase in crown area was not significant six years after the release.

Morphology of beech trees from different growth conditions

Canopy trees exhibited significantly lower slenderness (*p*-value < 0.001) and larger crowns (*p*-value < 0.001) than understorey trees of similar height. Biomass distribution factor was higher (Table 4.5, *p*-value < 0.01) while taper factor did not significantly differ between canopy and understorey trees. Standard trees from the coppice-with-standards site growing without competition for light but submitted to wind loads exhibited very thick stems, low slenderness ratio (Fig. 4.13) and large crown areas.

Biomechanical traits in beech trees from different growth conditions

We found that safety against self-buckling was low in understorey trees (1.68) and significantly increased after the release (Table 4.5, Fig. 4.13, *p-value* < 0.05). This increase was mainly driven by changes in slenderness and in diameter; the weight of other factors on SB change after the release was lower than 0.3% (Table 4.6). It is interesting to note that inter-tree variance was very high between undrestorey trees (Table 4.6). When comparing understorey trees with canopy and standard trees, we can note significant increase in SB trait (2.08 and 2.90 for canopy and standard trees respectively, Fig. 4.13). While slenderness and diameter factors are again the main drivers of observed difference in SB traits for different growth conditions, shape factor variance becomes more important than for the release change. Shape factor variation is mainly due to change in biomass distribution (parameter m, Table 4.5) while surprisingly, taper factor seems to be less affected by growth conditions.

Table 4.6: Variance decomposition of SB trait.

S stands for slenderness, D for diameter, E for elastic modulus, L for load and F for shape factor.

First part of the table represents variance decomposition of SB trait in understorey trees after release for all factors separating the variance due to individuals in the same group (tree) and due to the release (treatment) while second part of the table represents variance decompositin of SB trait in different growth conditions (status = understorey, canopy or standard tree).

		\mathbf{S}	D	\mathbf{E}	\mathbf{L}	\mathbf{F}	Total
Release	Tree	56.4%	11.3%	1.5%	3.3%	6.0%	78%
	Treatment	18.9%	2.3%	0.1%	0.2%	0.0%	22%
	Total	75.3%	13.6%	1.6%	3.5%	6.1%	100%
Status	Tree	15.4%	3.0%	0.2%	0.7%	1.2%	21%
	Status	63.3%	12.4%	0.5%	0.7%	2.4%	79%
	Total	78.8%	15.5%	0.7%	1.5%	3.6%	100%

Table 4.7: Morphological characteristics and safety against wind of released *F. sylvatica* understorey trees.

 D_{130} is the tree diameter at breast height, H/D_{130} is the tree slenderness ratio, SW1 is the safety against wind break according to Fournier *et al.* (2013) and SW2 is the safety against wind break according to Bonnesoeur *et al.* (2011).

	Nb	Height (m)		D ₁₃₀ (m)		H/D ₁₃₀		Crown area (m ²)		SW1		SW2	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Unharmed	21	16.5	3.6	0.12	0.03	144.2	21.6	27.9	12.8	4.3E-06	2.3E-06	2.4E-06	7.6E-07
Wind-break	15	17.6	2.4	0.13	0.02	136.3	19.5	40.0	16.1	3.9E-06	1.1E-06	2.5E-06	6.7E-07

Safety against wind-break was found to significantly increase in understorey trees after the release when computed according to Fournier *et al.* (2013) (SW1, Table 4.7, *p-value* < 0.01) but the difference was not significant if SW2 was considered. Safety against wind-break was high in standard trees but when comparing understorey released and canopy trees, it depended on the method used for SW determination. From the comparison of the morphology of released understorey trees broken by the wind in winter 2009 and unharmed released trees we can see that broken trees exhibited higher crown area (*p-value* < 0.05) and thicker stems (*p-value* < 0.1) but slenderness ratio was not significantly different. Estimation of the safety against wind-break based on allometric parameters did not allow for discrimination of broken trees.

4.4.4. Discussion

The safety against self-buckling in understorey trees was comparable to saplings from the tropical forest where Jaouen *et al.* (2007) observed an average value of 1.56 ± 0.23 . It shows that self-buckling risk is present not only for small saplings but also for relatively large understorey trees, the main factor being the density of forest cover. From allocation of tree biomass after the release, we can see that beech understorey trees allocated more biomass to radial growth. This allowed for reduction of slenderness (Fig. 4.12) which was identified as the main driver of the safety against self-buckling change after the release (Table 4.6). Jaouen *et al.* (2007) reported that shape factor was the second most important factor of intraspecific variance (7.6%) of the safety against self-buckling. In this study, the shape factor accounted for 6% of total variance mainly due to the intertree variance but was not significantly affected by the release, likely because it is difficult to significantly modify the taper or biomass distribution in relatively large established trees.

More surprisingly when compared beech trees from different growth conditions, the shape factor, exhibiting the result of long-term acclimation to different wind and light regimes, accounted only for 2.4% of the total SB variance (Table 4.6). While distribution of biomass was significantly affected by the growth conditions, taper factor did not differ between canopy and understorey trees (Table 4.5). If thinning is known to affect the stem taper (Baldwin Jr *et al.* 2000), Makinen & Isomäki (2004) reported that in case of late thinning this effect is not significant. This only confirms that small saplings can rapidly change their geometry by an increase in diameter growth while this is more difficult for large trees: Collet *et al.* (2011) reported that beech saplings doubled their diameter in four years after the release while in our study we observed an increase in diameter of 18.8% in six years.

Slenderness ratio is also often used as a proxy of wind firmness (Mitchell 2000). Slenderness significantly decreased after the release and was still not stabilized six years after the

release. Safety against the wind-break (SW1) increased after the release in understorey trees however high variability was observed among trees in comparison for example with the SB trait (Table 4.5). This likely comes from the difficulty to properly asses the crown surface exposed to the wind. The crown surface used in this study was the horizontal projection of the crown. We also tried to compute vertical projection which is more appropriate in the case of wind loading however considering the very diverse crown shapes of understorey trees, it was not really possible to describe them in a simple geometric way. Unfortunately, we did not have an operational routine to treat TLS scans to obtain better information about the crown profile. From the comparison of released understorey trees broken by the wind (no windthrow was observed) and unharmed released understorey trees (Table 4.7), it is clear that estimate SW based solely on allometric comparison is not satisfactory because it does not allow to discriminate trees exposed to higher risk. To assess properly the risk of windbreak, it seems necessary to take into account the local topology that can largely affect the wind flow and thus the wind load applied on an individual tree.