Caractérisation de la stratégie de croissance du hêtre sous couvert



3.1. Avant-propos

Cette première partie de résultats concerne l'allocation de la croissance entre la hauteur et le diamètre des tiges et est présentée sous forme d'avant-projet d'article (Article 1). Seules les parties « matériel et méthodes » et « résultats » sont complètes. Les parties « introduction » et « discussion » sont des premières ébauches et seront sujet à des remaniements avant soumission. La contribution de chaque co-auteur à cet article est précisée dans le Tableau 3.1.

L'objectif de ce chapitre est d'estimer la relation entre la croissance axiale et radiale en statique et en temporelle. L'effet des ouvertures passées de la canopée sur cette relation est analysé et discuté.

Auteurs	Contribution à l'Article 1		
Estelle NOYER	Acquisition des données, analyse des résultats, principale rédactrice de l'article		
Catherine COLLET	Traitement statistique (modèle asymptotique et corrélation temporelle), contribution à la discussion et à la rédaction		
Jana DLOUHA Mériem FOURNIER	Contribution à la discussion et à la rédaction		
François NINGRE	Mise en place du site d'expérimentation du Grand Poiremont		

Tableau 3.1 : Contribution des co-auteurs à l'Article 1.

Canopy release influences allocation in height and diameter growth in understory beech trees. (In progress)

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3.2.1. Introduction

Forest is composed by several layers which correspond to a gradient of growth conditions (Rambo & North, 2009). Overstory trees, i.e. trees established at the canopy layer, form the forest cover. They have a better access to light, water (soil and rainfall) and nutrients resources (Bréda *et al.*, 1995; Aussenac, 2000) that favour an improved height and diameter growth rates than trees under the canopy (Nicolini *et al.*, 2001; Löf *et al.*, 2005; Petritan *et al.*, 2009). To maximise resource acquisition under the canopy, trees may adjust their growth allocation (Bloom *et al.*, 1985; Poorter *et al.*, 2011). It was reported that understory trees could favour the height growth and show slender stem to improve light interception in a high tree-competition context (King, 1990; Seki *et al.*, 2013; Sumida *et al.*, 2013; Trouvé *et al.*, 2015).

An improve height growth at the expense of the diameter growth might be an advantage in this context but the ratio between height and diameter growth could be limited to avoid hydraulic risks such as the disruption of the water transport (Ryan & Yoder, 1997; Becker *et al.*, 2000), and avoid mechanical damage as stem buckling (Niklas, 2002, 2007). Moreover, height and diameter growth rates are also related to water availability (Delagrange *et al.*, 2004; Trouvé *et al.*, 2015), leaf area and lateral growth (Coomes & Grubb, 1998; Sumida *et al.*, 2013). Though the ratio between the tree height and the stem diameter growth evaluate with the age or the tree size increasing (Genet *et al.*, 2011), ecological strategy of the tree species such as the adult stature (tall vs. short species) or the shade tolerance ability (King, 1991; Bohlman & O'Brien, 2006; Sendall *et al.*, 2015) are also determinant. Shade tolerant species are less plastic in term of growth allocation and more morphological plastic (Grime, 1977; Curt *et al.*, 2005), even if with the age individuals became less shade tolerant (Yagi, 2009; Sendall *et al.*, 2015).

In forest, understory trees experiment succession of canopy release and suppression events along their life (Rentch *et al.*, 2010; Trotsiuk *et al.*, 2012). Though these trees do not succeed to reach the canopy layer, they experiment fluctuations of their growth conditions. The strong sensitivity of the diameter growth rate with changes in growth conditions is commonly used by dendrochronology or dendroecology studies. An increase of diameter growth rate could be interpreted as a better past growth conditions (Dittmar *et al.*, 2003; Lebourgeois *et al.*, 2005) or a canopy release event (Rubino & McCarthy, 2004; Emborg, 2007). In the case of canopy release event, the amount of response depended of the species, the site or whether individual stem diameter (Plauborg, 2004; Skov *et al.*, 2004; Boncina *et al.*, 2007). At the contrary, the age of the tree when the event happen does not impact the intensity of the reaction of the diameter growth rate (Keyser & Brown, 2014).

As growth allocation varies with time, relationship between height and stem diameter at a given time could be not easy to interpret because of the influence of the fluctuant past growth conditions. To study relationship between height and diameter growth rates should provide more robust information but it is just recently studied (Sumida, 2015; Trouvé *et al.*, 2015).

The aim of this study is to evaluate the relationship between the height and diameter growth rates in understory trees. We chose the European beech (*Fagus sylvatica* L.), a shade-tolerant species because it can survive under a high level of inter-tree competition, and can rapidly respond to changes in canopy structure and local irradiance. Ours objectives are: (1) to analyse the growth trajectories of understory trees, (2) to evaluate the relationship between the height and the diameter growth, (3) to study the effect of the variations of diameter growth on the height growth, and (4) to determine the effect of the diameter growth of the past and current year on the height growth. We use retrospective measurements of the height and the diameter growth to reconstruct the growth allocation of along the life of the understory trees. We benefit of the past canopy release events to analyse the effect of a large range of diameter growth on the height growth. In addition to the growth trajectories, we used two approaches to respond to our objectives: a static approach and a temporal approach by the calculation of cross-correlations.

Two hypothesis were tested:

- (H1) Understory trees display asymptotic relationship between height and diameter growth;
- (H2) Canopy release influences the allocation of the growth and favours diameter growth in the first years.

3.2.2. Material and methods

Study site

The site was a 13-ha-stand in a managed forest in north-eastern France (47.9507°N, 6.3857°E, alt: 470m). The soil was a cambisol dystric to hyperdystric with a luvic layer between the A and S horizons (IUSS Working Group WRB, 2014). Meteorological data came from Aillevillers-et-Lyaumont (French National Climatic Network, Météo-France) 5 km from the stand. Mean annual temperature was 10.3°C and mean annual precipitation was 1218 mm.

The stand had been formerly managed as a coppice-with-standards. In 1955-1956, the stand was thinned and converted to a high forest. Management 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 2006, the stand was dominated by *Fagus sylvatica* L. (basal area: 21 m² ha⁻¹) with another 5.5 m² ha⁻¹ of *Quercus spp., Fraxinus excelsior* L., *Acer pseudoplatanus* L., *Carpinus betulus* L., *Betula spp., Abies alba* Mill, and *Picea abies* L. (H) Karst. Stand density was 513 stem ha⁻¹ and the mean height of the overstory trees was 31.6 m.

In fall of 2007, a sample of 42 understory beech trees distributed throughout the stand and at least 18 m from one another was selected for the study. The selected 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, had no visible injury, spiral grain, canker, or top dieback. The sample trees was then split into two subsamples with similar mean values for diameter. In winter 2007-2008, one subsample, the half of the total sample, was released by a thinning that removed the trees in competition in a 12 m radius around each target tree and the other subsample of trees, the another half, was left unreleased.

Diameter growth rate

Sample trees were felled in February-March 2014, six years after canopy opening. A 5-cmthick disk was collected at 1.30 m height from each tree, wrapped in plastic film and was stored at -20°C immediately after harvest. After disks were sanded, four perpendicular radii were imaged by digital camera on each disk. 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).

Height growth rate

For each tree, successive height annual increments on the main axis were accessed by measuring the length of the annual growth units (LGU, mm) from winter bud scars located on the bark. Each ten growth units, the number of years was checked by counting the number of rings from a disk sampled at the base of the corresponding stem segment. In case of discrepancy between the number of growth units and the number of rings, the stem length was divided in smaller sub-segments and the growth units and rings were counted on each sub-segment until the two estimations were found to be equal. Three trees were finally discarded from the analysis because it was not possible to identify without ambiguity each annual growth unit and each ring on the stem. This method allows to reach a rare precision in terms of dating and value robustness. Tree age was estimated as the number of growth units counted along the trunk.

Data analysis

For each tree, ring width and basal area increment (BAI, cm²) were estimated for each annual ring from the position data for ring boundaries, averaged over the four radii. BAI was estimated as follows:

$$BAI = \pi \left(r_1^2 - r_2^2 \right) \tag{3.1}$$

where r_1 and r_2 (cm) are the average of the radii from two successive years.

Detection of canopy release events

The dates of the successive canopy release events that occurred for each tree were unknown. Possible release events could be estimated for each tree by visual examination of its ring chronology. However, to standardise the identification of release events among the sample trees, a procedure to automatically detect and date release events was established. The procedure was calibrated against the events identified by visual examination and therefore may not be used as a standard for other studies. However, it may be used as a mean to homogenize the detection of release events among trees that had very different annual growth rates. A two-step-procedure was developed to identify the first year of past release events of the sample trees. The first step aimed at detecting release periods while the second step aimed at identifying the first year after release for each detected period.

In the first step, the percentage of growth change (PGC₁, %) for each year and on each tree is calculated as (Nowacki & Abrams, 1997):

$$PGC = \frac{M_2 - M_1}{M_1} \times 100 \tag{3.2}$$

where M_1 is the median of BAI for the preceding 8 years (excluding target year) and M_2 the median of BAI for the subsequent 4 years (including target year).

PGC₁ was then compared to a threshold value. All years where $PGC_1 > 25\%$ were identified, and time segments with at least 4 successive years above the threshold were considered as release periods. Black and Abrams (2003) used similar threshold values for shade tolerant species and understory trees and observed that it allowed to detect the creation of both large and partial canopy gaps. The minimal duration of the time segments was defined on the basis of a conservative criteria following Emborg (2007).

In the second step, the first year after gap creation was estimated for each release period. Nowacki and Abrams (1997) considered that the peak of PGC indicated the year of canopy disturbance. In our case, we observed important lags between years detected using this criteria and years identified by visual identification (\pm 4 years) and the approach was discarded. PGC₂ was then computed for each year using Eq. 3.2 with M₁ = 8 years and M₂ = 1 year. Within each previously detected time segments, the first year where PGC₂ > 25% was considered as the first year after canopy release.

The earliest release event that could be detected on each tree occurred at the age of 8. However, for each tree, the height that tree had reached at this date was examined, and events corresponding to a height less than 3 meters were discarded, to avoid trees potentially overtopped by neighbouring shrubs. Theoretically, the latest released event that could be detected on each tree occurred in 2009 (i.e. 4 years before the last year taken into account). In fact, the last release event (fall 2007) was not detected because the corresponding 4-year-release period (2008-2011) was not included in the interval taken into account. A total of 120 release events were detected in all trees, and the corresponding years ranged between 1934 and 2005 (Fig. 3.1). Release events appeared to be clustered.

Analysis of growth allocation trajectories

Relationship between tree height (H) and stem radius (R) was analysed using linear mixedeffects model, following:

$$H_{ij} = \beta_1 + \beta_2 \left(b_{ij} + R_{ij} \right) + \varepsilon_{ij} \tag{3.3}$$

where indices for trees (*i*) and year (*j*) were defined as i = 1, 2, ..., 39 and $j = 1, 2, ..., n_i$. β and b terms were parameters to be estimated. ε_{ij} was the model error term, randomly distributed such that $\varepsilon \sim N(0, \sigma_{\varepsilon}^2)$. β_1 is the intercept, β_2 is the slope. β terms were fixed effects and b term corresponded to a random tree effect which was assumed to be normally distributed, e.g., $b \sim N(0, \sigma_b^2)$, and independent between levels. The model was fitted on 2770 observations, collected on 39 trees.



Figure 3.1: Frequency of detected canopy release events per year between 1935 and 2005.

Analysis of growth allocation

Allocation between diameter and height growth was analysed using non-linear mixed-effects models. An asymptotic model was used to describe the relationship between annual ring width (RW) and annual growth unit length (LGU), following:

$$LGU_{ij} = \left(\beta_1 + b_{1,i}\right) \left(1 - e^{\left(-e^{\beta_2 \left(RW_{ij} - \beta_3\right)}\right)}\right) + \varepsilon_{ij}$$
(3.4)

where indices for trees (*i*) and year (*j*) were defined as i=1, 2, ..., 39 and $j=1, 2, ..., n_i$. β and b terms were parameters to be estimated. ε_{ij} was the model error term, randomly distributed such that $\varepsilon \sim N(0, \sigma_{\varepsilon}^2)$. ($\beta_1 + b_{I,i}$) was the asymptote, β_2 the logarithm of the rate constant, and β_3 the value of *RW* at which *LGU*=0 (Pinheiro & Bates, 2000). β terms corresponded to fixed effects and $b_{I,i}$ terms to a random tree effect which was assumed to be normally distributed, e.g., $b \sim N(0, \sigma_{b}^2)$, and independent between levels. The model was fitted on 2770 observations, collected on 39 trees.

In preliminary analyses, random effects (parameters $b_{2,i}$ and $b_{3,i}$) were added to β_2 and β_3 , but the parameter values associated to the 3 random effects were highly correlated, and $b_{2,i}$ and $b_{3,i}$ were therefore disregarded and only $b_{1,i}$ was kept in further analyses.

Auto-correlation plots for residuals indicated that the independence assumption was not met. Residual temporal correlation structures were incorporated in the model, using an autoregressive-moving-average ARMA(1,1) correlation structure (Zuur *et al.*, 2009). The incorporation of the ARMA correlation largely improved the AIC value (35 354 vs. 34 152) and residuals did not display any auto-correlation. However, distribution of model residuals was highly skewed for the model with ARMA correlation. The temporal correlation structure completely absorbed the random tree effect, and it was not possible to disentangle the individual tree effects from temporal autocorrelation effects. To facilitate interpretation of the results (Bellemare *et al.*, 2015), models without ARMA correlation were finally preferred. Models incorporating ARMA correlation will not presented.

Model residuals were visually checked to ascertain whether any remaining pattern with respect to potential covariates (tree diameter, height and age, number of years since the last canopy release) was to be found. No clear pattern was observed except for the duration since the last canopy release (DR, years).

To analyse the effect of the duration since the last canopy release on growth allometry, the mean of model residuals (MResid, mm) were computed for each DR value ranging between 0 and 25 years, and an asymptotic model was fitted according to:

$$MResid_{i} = \beta_{1} \left(1 - e^{\left(-e^{\beta_{2} \left(DR_{i} - \beta_{3} \right)} \right)} \right) + \varepsilon_{i}$$

$$(3.5)$$

where the index for year was defined as i=0, 2, ..., 25. β terms were parameters to be estimated, defined as in Eq. 3.4, and ε_i was the model error term, randomly distributed such that $\varepsilon \sim N(0, \sigma_{\varepsilon}^2)$.

To examine temporal correlation between diameter and height growth, cross-correlations (Venables & Ripley, 2002) between RW and LGU were computed for each tree, using Pearson correlation coefficient. A maximum lag of 10 years was set to compute the correlations. For each lag value (ranging between -10 and 10), a Wilcoxon test at 1% was performed to assess whether the median value of the correlation coefficients for all trees pooled differs from 0.

All calculation and statistical analyses were performed using R software (R Core Team, 2015) and asymptotic models were fitted using the nlme package (Pinheiro & Bates, 2000).





Trees were grouped into 3 classes according to their age in 2013: younger than 79-years-old (n=6), from 80 to 89-years-old (n=14), and older than 90-years-old (n=18). Mean \pm SE. The grey vertical dotted line shows the canopy release in winter 2007-08.

3.2.1. Results

Growth trajectories

Figure 3.2 presents tree growth trajectories over the study period. In 2013, mean tree height was 14.8, 19.0 and 18.9 m for young, intermediate and old trees, respectively (Fig. 3.2A). Tree height trajectories of intermediate and older trees were similar, except between 1945 and 1965. Mean tree height trajectory of younger trees was always below the trajectories of the 2 other age classes.

In 2013, trees from the 3 classes had no significant different mean stem diameters: 11.9, 14.2 and 13.8 cm for young, intermediate and old trees, respectively (Fig. 3.2B). As for height, intermediate trees showed the highest diameter values and young trees the lowest values.

In 2013, mean LGU was 22.6, 17.3 and 18.0 cm for young, intermediate and old trees, respectively (Fig. 3.2C). Among all years, the maximum value of LGU was 63.9 cm. LGU trajectories displayed large inter-annual variations regardless tree age. Mean RW was 1.8, 2.0 and 1.6 mm in 2013 for young, intermediate and old trees, respectively (Fig. 3.2D). As LGU, several peaks were observed and were synchronous between trees. Globally, Fig. 3.2C and 3.2D showed a succession of high and low growth periods. For high growth periods of 1960, 1968 and 2000, RW peaks seemed to precede LGU increasing.

Allocation between height and diameter growth

Tree height and stem radius are linearly and positively related (Fig. 3.3). The variability in the response variable (tree height) increased with the explanatory variable (stem radius). The slope superior than 1 (2.79 m cm⁻¹) indicated the preferential growth allocation to the height.

LGU and RW were positively related (Fig. 3.4, Table 3.2). Although a large variability was observed in the response variable, the asymptotic model fitted well the data. A negative β_3 indicated a non-null height growth (6.6 cm) when diameter growth is null. The asymptote (32.72 cm) was reached when annual ring width reached 2 mm. Above this width, height growth remained stable. All model parameters were significantly different from 0.



Figure 3.3: Relationship between the tree height (m) and stem radius (cm), for all trees and all years (n=2762).

The red line represents the linear mixed-effects model fitted on the data (Eq. 3.3)



Figure 3.4: Relationship between the length of growth unit (LGU, cm) and ring width (RW, mm), for all trees and all years (n=2762).

The red line represents the asymptotic model fitted on the data (Eq. 3.4, Table 3.2), with 95% confidence interval of the predictor adjusted by bootstrapping.

Model	Parameters	Estimate	SE	t value	p value
Eq. 3.4	B ₁	32.72	1.15	28.43	< 0.001
LGU vs RW	β_2	0.47	0.10	4.47	< 0.001
	B ₃	-0.14	0.04	-4.02	< 0.001
Eq. 3.5	B ₁	4.02	0.57	7.04	< 0.001
MResid vs DR	β_2	-1.85	0.21	-8.68	< 0.001
	B ₃	6.07	0.64	9.46	< 0.001

Table 3.2: Asymptotic model between annual height growth (LGU) and annual diameter growth (RW); and asymptotic model between the mean of model residuals and duration since the last canopy release (DR).



Figure 3.5: Relationship between the duration since the last canopy release (DR) and model residuals.

Year 0 is the year immediately after canopy release. A: model residuals. Blue line represents spline smoothing of the data. B: Mean of the residuals (MResid) \pm standard error, computed for each DR value between 0 and 25. Red line represents the asymptotic model fitted on the data (Eq. 3.5, Table 3.2). * Asterisks indicates MResid values that significantly differ from 0 (Wilcoxon-test, p<0.01).

Model residuals plotted against the duration after the last canopy release event showed a clear trend, with negative residuals for low DR values (Fig. 3.5A), indicating that trees allocate more diameter growth than to height growth during the first years after canopy release. The mean of model residuals, computed for each DR ranging between 0 and 25 years, showed an asymptotic fit (Fig. 3.5B, Table 3.2) and was significantly different from 0 the first 4 years (from year 0 to year 3). Residuals mean became positive in year 6. The asymptotic model indicated that growth allocation progressively switched from diameter to height following canopy release.

Temporal cross-correlation between RW and LGU were strong (Fig. 3.6). Height growth was positively correlated to diameter growth of the current year (correlation = 0.3) and to diameter growth of the ten previous years. Correlation with the diameter growth in the 5 previous years was higher than for the current year. The mean value of the correlation coefficient between height growth and previous diameter growth were significantly different from 0 for all lag values (ranging 0 and -10 years). Height growth was also positively correlated to diameter growth of the 4 next years but the correlations were smaller, and the mean values significantly differ from 0 only for lag value less than 4 years.



Figure 3.6: Correlation between ring width (RW) in year t+k and growth unit length (LGU) in year t, depending on the applied lag k.

Mean of the correlation coefficient computed on the 39 trees and standard deviation. Asterisks indicates median values that significantly differ from 0 (Wilcoxon test, p<0.01).

3.2.2. Discussion

Height and diameter growth rates relationship in understory beech trees The asymptotic relationship between height and diameter growth rate in understory trees was congruent with previous studies (Sumida *et al.*, 2013; Trouvé *et al.*, 2015). The negative β_3 parameter of the model of growth allocation suggested that height growth did not stop even if it was at the expense of the diameter growth (Table 3.2). This higher investment in height growth than diameter growth could be explained by the high tree competition for light (King, 1990) that resulting in slender trees as a survival strategy to the most limiting resource (Bloom *et al.*, 1985; Poorter *et al.*, 2011). Moreover, understory trees reached in average a height growth rate of 30 cm which corresponded to the range of values observed in overstory 98-year-old beech trees located at 300 km from our stand (Bontemps *et al.*, 2012; Latte *et al.*, 2016). This suggested that even if growth conditions were favourable to an improved growth (e.g. tree-competition), the height growth rate seemed to be driven by another additional important factors. The ecological strategy for a given species as shade tolerance or maximum adult stature (tall vs. short species) could explained by the behaviour of the height growth rate of beech species (Grime, 1977; Bohlman & O'Brien, 2006).

Allometric relationship after canopy release

Despite the asymptotic shape of the mean residuals (Fig 3.5B), canopy release did not significantly impact the growth allocation of understory trees, except for the first years. The overestimation of the height growth rate during the first years after canopy release could be explained by several hypotheses. The first is that the increase of wind movements after canopy release induced thigmomorphogenesis favouring the diameter growth and reducing or stopping the height growth (Pruyn et al., 2000; Telewski, 2006) to improve the biomechanical safety against disturbances. Secondly, in addition to the fact that height growth decreases with tree competition (King, 1990), we can suppose that the canopy release may enhance the development of the lateral growth, i.e. the crown, to improve the light interception and the lateral colonization which is not included in the present work. Moreover, it was demonstrated in seedling that height growth recovery was enhanced the second year after canopy release (Collet *et al.*, 2001). In our case, the delay of height growth recovery would be of 4 years but the response to canopy release at the individual scale could be delayed in term of diameter growth recovery (Hart et al., 2010) and it was possible that the same phenomena happened for the height growth. In addition, the method used to detect canopy release can be failed to detect some small possible canopy releases and induced a bias in the model. Nonetheless, our results suggested that the most important modifications of tree shape happened during the first 4 years after a canopy release regardless the developmental stage of the tree.

Temporal relationship

Our last objective focused on the temporal correlation between the height growth rate and the diameter growth rate. We found that the height growth rate was positively correlated to the previous years of diameter growth rate (Fig 3.6). As height growth happens at the beginning of the growing season while the diameter growth rate is spread among the growing season, to enhance height growth for a given year, the most important seemed to be the reserves of the past years. Moreover, beech species displayed a deep sapwood area (Granier *et al.*, 2000; Dalsgaard *et al.*, 2011) and the relationship between previous ring width and height growth rate could reflect a compromise between the functional rings and the potential water path length (i.e. height growth) increasing that sapwood area could sustain.

The diameter growth rate of current year impacted less the height growth rate than the diameter growth rate of the first 3 previous years. The height growth may depend mainly on the growing conditions of the previous year in some species (e.g. in conifers, Thornley 1999) whereas the diameter growth rate could depend on the sapwood area of the stem (e.g. in conifers too Galvan et al. 2012) and was mostly sensitive to the current climate (Lebourgeois *et al.*, 2005). In a time-scale, different factors acted on the two growth rates. If the past growth conditions were most decisive for the height growth rate, it was not trivial that the past diameter growth rate contributed too.

3.2.3. Conclusion

The high competition for light enhanced a continuous height growth although the maximum height growth rate seemed to be driven by the ecological strategy of the species. The canopy release impacted the growth allocation. As we suggested that a shade tolerant species as beech should prefer to develop a conservative strategy face to growth conditions changes, it will be interesting to orient the future investigations on the lateral growth or morphological and physiological possible modifications of understory trees to canopy release. Another perspective is to explore the individual trajectories of the relationship of height and diameter growth rates; this could be bringing some information about the dynamic of understory trees growth. Finally, we showed that the ten previous years of diameter growth rate positively impacted the height growth rate. It would be interesting to take account of the diameter growth increment of the previous years instead of the current stem diameter in predicted growth model.