

Height competition between *Quercus petraea* and *Fagus sylvatica* natural regeneration in mixed and uneven-aged stands

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Abstract

The mid-successional sessile oak (*Quercus petraea* (Matt.) Liebl.) and the late-successional European beech (*Fagus sylvatica* L.) are two major species of temperate forests. According to the literature, in mixed stands, large canopy openings should promote the growth of the light-demanding oak over the shade tolerant beech. Nevertheless, foresters who manage mixed oak and beech forests with continuous-cover silviculture in Western and Central Europe, face difficulties to promote the regeneration of oak. In the Belgian Ardennes, we monitored the mixed advanced regeneration of 7-13 year old oak and beech trees scattered across 23 sites to test the hypotheses regarding the relative advantage of the two species across the light gradient, the outcome of interspecific competition exerted by neighbouring saplings, the effect of direct and diffuse radiation and the site effect. We adjusted a set of mixed non-linear models of the height growth of saplings for the two species and selected the best model for the two species. In contrast to expectations, we found that beech saplings had the highest height growth rate at all light levels. Beech saplings reached an optimum growth at transmittance of 10%, whereas oak saplings needed more than 20%. The two species responded positively to soil richness but only oak saplings responded to direct radiation and micro-climatic variations. These results indicate that oak saplings are systematically outcompeted by beech saplings across the light gradient. Thus, the control of canopy opening is not sufficient to promote the natural regeneration of oak beneath a stand also containing beech in the Belgian Ardennes.

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1. Introduction

Close-to-nature forest management attempts to mimic natural processes and, in particular, promotes continuous-cover

forestry regimes with natural regeneration (Pommerening and Murphy, 2004). In the recent decades, the management of mixed stands has been increasingly promoted in order to improve forest biodiversity, resiliency, sustainability and ecosystem services (Schütz, 1997). However, this approach implies the coexistence of different forest species that can have contrasting shade tolerance. According to Kobe et al. (1995), light demanding species are characterised by fast growth allowing to outcompete neighbouring trees in high light environments, whereas shade-tolerant species are characterised by slow growth and low mortality allowing persistence in low light environments.

Sessile oak (*Quercus petraea* (Matt.) Liebl.) and European beech (*Fagus sylvatica* L.) are two major timber species of European temperate forests with contrasting shade tolerance. For historical reasons, the two species coexist in mixed stands, and forest managers attempt to perpetuate these stands. Indeed, the decline of beech trees (Jonard et al., 2010), a striking level of decay (Henin et al., 2003) and wind damage (Bock et al., 2005) are all factors highlighting the sensitivity of pure beech stands to climate change and pest hazards, reinforcing the need to promote the regeneration of admixed species. Consequently, maintaining sessile oak in beech forests is an important issue. However, foresters rarely succeed in promoting oak regeneration beneath stands that also contain beech in

Europe (von Lupke and Hauskeller-Bullerjahn, 1999).

The regeneration of oak and beech has been intensively studied in European forests. In particular, many studies have detailed the shade tolerance of both species (Table 1). Beech juveniles have greater abilities to survive and grow in shade than oak juveniles. They have a higher morphological plasticity, which can presumably enable them to maintain a positive carbon balance in low-light environments. Oak juveniles have therefore greater light requirements than beech juvenile (Collet et al., 1997; Emborg, 1998; Collet et al., 2001; Collet and Chenost, 2006; Stancioiu and O'Hara, 2006; Balandier et al., 2007; Petritan et al., 2007, 2009; Wagner et al., 2010). Nevertheless, accordingly to the definition of shade tolerance proposed by Kobe et al. (1995), under high light levels, the most light-demanding species, the oak, is expected to outgrow the beech (Dreyer et al., 2005).

Little information has been published concerning the in situ dynamic of the advanced and well-established natural regeneration of the two species in mixed stand. Indeed, both species have mostly been studied separately, at seedling stage, and in controlled conditions. Our understanding of the interspecific competition is therefore largely inferred by extrapolating information on the autoecology of the two species (Table 1). Moreover, there is an urgent need for scientific references in order to promote oak regeneration in the field and to provide a clear explanation for the difficulties faced by foresters in regenerating oak. These difficulties are particularly highlighted by the data of the Walloon Permanent Forest Resource Inventory that underlines a shortage of small oak trees (diameter lower than 25 cm) despite the opening of forest canopy by foresters and the decline of beech. At the opposite, the beech regeneration is abundant everywhere even in almost pure oak stands.

Additionally, growth modelling at the sapling stage raised two methodological issues. Firstly, it required to assess a relevant indicator of understory light conditions which depends on the interception of diffuse and direct rays by trees. The percentage of transmitted diffuse radiations has been often considered to represent accurately the percentage of total transmitted radiations (Petritan et al., 2007, 2009). Nevertheless, direct ray carries more energy than diffuse ray, but direct radiations transmitted under the canopy are limited in time and space (sunflecks) due to canopy irregularities and constant change of sunlight direction (Bonhomme, 1993). Secondly, due to the design of our in situ experiment, we could not control all the different factors that could influence sapling growth. The growth of beech and oak regeneration was expected to vary from site to site due to both biotic and abiotic factors. In particular, different herbaceous species are known to compete with the saplings for the supply of nutrient, water and light (Collet and Frochot, 1996; Coll et al., 2003, 2004; Wagner et al., 2010) or to produce allelochemicals (Timbal et al., 1990; Dolling, 1996; Jaderlund et al., 1996). Local variations in climate and soil (Turbang, 1954) are additional factors that could influence regeneration development even

though both species occupy a very large ecological niche (Piedallu et al., 2009) and are well adapted to the sampled ecological conditions.

In this context, we monitored mixed advanced regeneration in 242 square plots of 4 m² scattered across 23 sites in mixed stands of the Belgian Ardenne forests. Since the composition outcome greatly depends on specific ability to grow higher than the competing species to maintain a dominant position, and since mortality can be predicted as a function of growth and occurs mainly in suppressed saplings (Pacala et al., 1994; Kobe et al., 1995; Walters and Reich, 1996; Petritan et al., 2007), we focused in this study on height growth. We adjusted a set of non-linear mixed models for oak and beech saplings, and used the best fit to test that:

- the less shade-tolerant oak grow faster in high-light environment than the shade-tolerant beech;
- regeneration growth is reduced by the interspecific competition between saplings ;
- regeneration growth responds better to the availability of diffuse radiations than to the availability of direct radiations;
- regeneration growth vary from site to site and this “site effect” is correlated with the local climate and soil conditions.

Finally, we developed a set of practical recommendations for foresters that would like to promote the regeneration of oak in a continuous-cover forestry system.

2. Material and methods

2.1 Study sites

The study was conducted in mixed sessile oak (*Quercus petraea* (Matt.) Liebl.) and European beech (*Fagus sylvatica* L.) uneven-aged stands, in the Belgian Ardennes ecoregion (50°15' N, 5°40' E, supplementary material Fig. 1). The availability of nutrients and water was well representative of the medio-European acidophileous beech forests (CORINE classification 41.111) in the Ardennes. The mean annual rainfall varied between 931 and 1178 mm year⁻¹ and the mean annual temperature ranged between 8.4 and 9.4°C across the study sites. Dominant soils were well drained brown acidic soils (WRB soil classification) of variable depth (mean of 47 cm and standard deviation of 25 cm) that developed on hercynian oligotrophic schist and sandstone substrates. The dominant herbaceous species were *Luzula luzuloides* (Lam.) Dandy & Willm, *Vaccinium myrtillus* L., *Deschampsia flexuosa* (L.) Trin, *Dryopteris carthusiana* (Villar) H.P. Fuchs and *Pteridium aquilinum* (L.) Kuhn, typical of acid soils. Stands were selected in public forests managed with a continuous-cover forestry system. During the study period, there was no silvicultural intervention but a few beech windfalls did occur.

In spring 2007, we selected 23 sites with a well-established regeneration (10 to 300 cm high) in order to span a wide range of stand structure and composition. We fenced off the regeneration areas (100 to 6500 m²) to protect them from browsing by deer. Inside each fence, we sampled the saplings within 5

Table 1. Literature review of the shade tolerance of sessile oak and European beech

		Beech	Oak	References
Transmittance at light compensation point	1st-year seedling	very low	very low	Turbang (1954), Welander and Ottosson (1998), Chaar and Colin (1999), Nicolini et al. (2000)
	Young seedling	2-5%	10%	Madsen and Larsen (1997), Le Duc and Havill (1998), von Lupke and Hauskeller-Bullerjahn (1999), Emborg et al. (2000), Collet et al. (2001), Collet and Chenost (2006), Petritan et al. (2007)
Transmittance at saturating growth	young seedling	10%	20%	Dineur (1951), Emborg (1998), von Lupke (1998), Stancioiu and O'Hara (2006)
	old seedling (>10 y.o.)	20%	30%	Jarret (2004), Petritan et al. (2009)
Morphological plasticity to different light conditions		high	low	Farque et al. (2001), Collet and Frochot (1996), Stancioiu and O'Hara (2006), Wagner et al. (2010)
Sensitivity to ground vegetation competition		medium	low	Newbold et al. (1981), Collet and Frochot (1996), Coll et al. (2004), Lof and Welander (2004), Wagner et al. (2010)

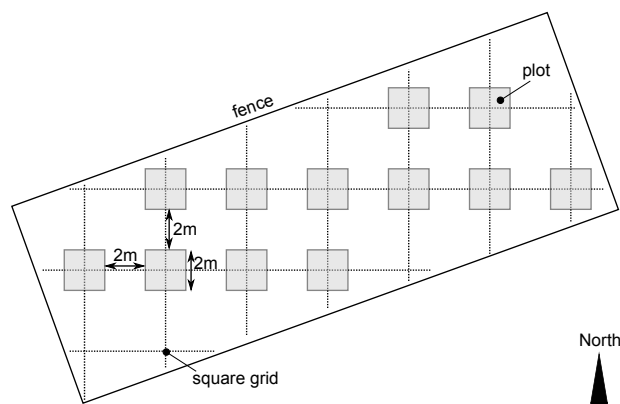


Figure 1. Plot layout in a site. Experimental plots were laid out following North-South and West-East transects inside a 2-m tall fence.

to 31 square plots of 4 m² (total of 242 plots). The plots were laid out every 4 m following a square grid (Fig. 1). Inside the fences and within 20 m outside the fences, we measured and mapped every tree with a diameter at breast height (dbh) greater than 6.4 cm. Hereafter, “sapling” and “tree” refers to a dbh smaller and greater than 6.4 cm, respectively.

We performed a soil and humus description (Jabiol et al., 1995) as well as floristic surveys (Braun-Blanquet method), in order to compute levels of the supply of nutrients and water at every site (Bartoli et al., 2000). Similarly to Ellenberg’s method every species indicates a range of nutrient and water conditions, and site values correspond to a weighted average

of the indexes of present species. The variation of soil richness between the sites appeared limited with index values ranging between 0.8 and 2 on a scale of 0 (very acid soils) to 6 (calcareous soil). The local variations of climate between sites were also assessed using a regional climate model and computing approximately 30 indexes of temperature, precipitation, and evapotranspiration (Tychon, 2000). They corresponded to averages, standard deviations, minimums, and maximums computed either per season or per year. Studied stands had complex vertical and horizontal structures and included a wide range of dbh and height classes. Stand composition was also diverse, varying from monospecific beech stands to stands almost completely dominated by oak (Table 2). Other species (mainly *Carpinus betulus* L., *Betula pendula* Roth and *Acer pseudoplatanus* L.) accounted for up to 20% of stand composition.

The percentage of above canopy light measured in the understorey (PACL) ranged between 1% and 61% for plots dominated by oak, and between 2% and 43% for plots dominated by beech. This encompassed a wide gradient ranging from a close canopy to a canopy with a gap size varying up to approximately 1200 m² (area without overtopping crown).

2.2 Regeneration height growth

In this study, we monitored sapling height growth between 2009 and 2011. In 2009 and 2011, we measured sapling height using a telescopic meter stick to the nearest centimetre of the 3 tallest saplings of oak and beech in each plot. Saplings measured in 2009 were not tagged and therefore the saplings measured in 2011 could have been different. The mean annual height increment in site *i* and plot *j* (iH_{ijs}) was computed for each species *s* (eq. 1).

Table 2. Characteristics of the study sites The structure and composition of the study stands is shown by the minimum and maximum tree diameter (dbh), the average basal area and the average proportion of oak. Regeneration is shown by the minimum and maximum height, age and total sapling density. The last column contains the minimum and maximum of the percentage of above canopy light (PACL). The table is sorted by average PACL.

Site	n plots	Overstory			Oak saplings		Beech saplings		All saplings	Light
		dbh cm	Basal area m ² ha ⁻¹	oak basal area %	height cm	age years	height cm	age years	density Trees m ⁻²	PACL %
17	6	9 - 74	25	80	26 - 39	4 - 8	49 - 127	4 - 12	10 - 36	6 - 10
22	18	12 - 78	16	74	105 - 209	7 - 12			6 - 13	3 - 14
25	20	13 - 81	22	0			28 - 248	5 - 16	3 - 110	2 - 25
12	10	13 - 81	22	68	16 - 171	5 - 12	39 - 220	5 - 10	12 - 39	5 - 23
15	31	6 - 72	23	80	18 - 58	3 - 6	29 - 145	5 - 13	3 - 25	1 - 26
19	12	8 - 84	15	0			176 - 252	9 - 14	4 - 52	2 - 13
26	6	7 - 80	14	6			133 - 265	7 - 12	4 - 14	2 - 43
3	7	7 - 66	18	17	23 - 80	3 - 6	42 - 210	4 - 21	21 - 94	10 - 19
2	6	6 - 74	17	25	73 - 186	6 - 17	155 - 245	10 - 15	5 - 19	8 - 23
10	9	6 - 60	23	85	123 - 249	12 - 13			10 - 29	10 - 22
29	15	7 - 67	20	51	25 - 204	4 - 12	105 - 264	6 - 17	10 - 43	10 - 21
8	11	6 - 63	19	89	76 - 243	1 - 13			6 - 69	9 - 27
20	5	7 - 92	19	37			159 - 231	11 - 18	14 - 19	10 - 27
4	7	6 - 74	25	73	168 - 255	13 - 18			4 - 95	13 - 20
14	7	7 - 73	20	41	74 - 134	7 - 17	174 - 274	10 - 19	5 - 30	16 - 22
24	11	6 - 55	11	93	166 - 273	10 - 15			17 - 75	10 - 34
28	18	14 - 65	10	6			122 - 246	9 - 12	6 - 15	14 - 32
23	15	6 - 77	21	58	80 - 245	7 - 13	196 - 277	7 - 11	4 - 28	7 - 29
13	2	7 - 73	14	51	21 - 111	7 - 14	203 - 248	12 - 17	8 - 45	12 - 13
1	3	6 - 67	11	28	13 - 43	3 - 5	99 - 152	4 - 11	25 - 67	20 - 26
18	5	6 - 80	7	19	47 - 234	8 - 14	208 - 272	9 - 14	3 - 12	4 - 35
11	9	7 - 68	14	91	165 - 236	11 - 17			7 - 13	42 - 45
9	8	7 - 50	11	95	175 - 240.3	12 - 13			3 - 53	14 - 61

$$iH_{ijs} = \frac{\overline{H11}_{ijs} - \overline{H09}_{ijs}}{2} \quad (1)$$

where $\overline{H09}_{ijs}$ and $\overline{H11}_{ijs}$ are, respectively, the average height of the three tallest saplings of species *s* in site *i* and plot *j* measured during year 2009 and 2011. iH_{ijs} therefore corresponds to the annual height growth of oak or beech saplings two years after the installation of fences. We counted the sapling in every 4 m² plot for every species in 2007 and 2012. In 2009, the sapling density was computed as the average of these two counts.

Up to five different species (beech, oak with mainly *Carpinus betulus* L., *Betula pendula* Roth, *Acer pseudoplatanus* L. and *Coryllus avellana* L.) were found to coexist in the plots. In order to take into account the effects of the potential competition between species, we identified the species dominance, i.e. whether $\overline{H09}_{ijs}$ was the greatest for the species *s* in plot *ij*.

In 2011, we selected five representative saplings of oak and beech within each site, inside the fences but outside the 4 m² plots, to determine sapling age. Sapling age was determined by counting the number of bud scars and growth rings (Collet et al., 1997). The rings were counted on stem sections at a height of 5 cm using a binocular microscope. The sections were carefully sanded beforehand with sandpaper with a grit designation of up to 2000.

2.3 Understory light conditions

To estimate light availability just above the saplings, hemispherical photographs were taken before sunrise during mid-summer 2010 above the regeneration at the centre of the plot. The photographs were used to compute three indexes of light availability for the whole growing season (from 1st April to 31st October): the percentage of total above canopy light (PACL), the percentage of diffuse above canopy light (DIFF) and the percentage of direct above canopy light (DIR). Photographs were thresholded with PfiPhotem software (Adam et al.) and light was calculated with GLA software (Frazer et al., 1999). Additional details are provided in the supplementary material.

We validated our PACL estimates by comparing them with measures of the Photosynthetically Active Radiation (PAR) carried out with sensors (Solem S.A., Palaiseau, France) in five sites during one day in July 2010. The relationship between the estimates and the measures was highly significant ($r = 0.91$, $P < 0.001$, $n = 70$) with a slope not significantly different from 1.

2.4 Statistical analyses

We modelled the height growth of saplings (iH) in relation to the initial dimensions corresponding of 2009 (H), understory light (PACL) and species dominance ($SDOM$). Similarly to other studies (Kunstler et al., 2005; Pacala et al., 1994; Petritan et al., 2007; Stancioiu and O'Hara, 2006; Wagner et al., 2010),

height growth of saplings (iH) was modelled with a non-linear saturated relationship with PACL, which meant that growth increased at an increasing rate with PACL up to a certain point (inflexion point) and then saturated progressively (asymptote). We attempted to add additional explanatory variables such as regeneration age and sapling density. Nevertheless, adding these latter variables did not improve significantly the models (Supplementary Figure 3). We used mixed models in order to take into account that the observed growth depends on a random site factor and a set of fixed factors (H , PACL and $SDOM$). Site characteristics were not included in the model as fixed factors because we did not sample the sites across a gradient of environmental conditions. The sites were thus considered as random repetitions of the experiment within the Belgian Ardennes. The mixed modelling approach enabled to quantify and explain the between-site variation. Based on Akaike's Information Criterion (AIC) and residual dispersal (further details are provided in the supplementary materials), we selected the logistic model among others. For beech (eq. 2), it was a function of both the initial height (H_{ij}) and the percentage of above canopy light (PACL). For oak, the selected model (eq. 3) took additionally into account the species dominance ($SDOM$).

$$iH_{ij} = (\alpha_j + b \sqrt{H_{ij}}) \frac{1}{1 + \exp\left(1 - \frac{PACL_{ij}}{c}\right)} + \varepsilon_{ij} \quad (2)$$

and

$$iH_{ij} = (\alpha_j + b \sqrt{H_{ij}}) \frac{1}{1 + \exp\left(1 - \frac{PACL_{ij}}{c_{SDOM}}\right)} + \varepsilon_{ij} \quad (3)$$

with

$$\begin{aligned} \alpha_j &\sim dN(0, \theta_{\alpha_j}) \\ \varepsilon_{ij} &\sim dN(0, \theta_{\varepsilon_{ij}}) \end{aligned}$$

We further tested whether adding the percentage of transmitted direct radiations improved significantly models containing the percentage of transmitted diffuse radiations. We replaced PACL in the model with a linear combination of the percentage of above direct (DIR) and diffuse light (DIFF): $eDIR + (1-e)DIFF$. The null hypothesis was that direct light would not influence height growth if the diffuse light was already taken into account, i.e. $e = 0$. According to the ratio between diffuse and direct radiation measured by the meteorological institute of Belgium, the mean annual proportion of direct radiation, e , equals 0.46 above canopy.

Finally, we computed the best linear unbiased estimates of the random factor α (BLUP $_{\alpha}$) and tested the Pearson's correlations between these estimates and indexes of nutrient and water supply as well as microclimatic indexes.

All of the statistical analyses were performed within the R environment (The R Development Core Team, 2012) with a

significance level of 0.05. Mixed models were adjusted with the nlme package (Pinheiro et al., 2011) using the restricted maximum of likelihood method.

3. Results

3.1 Regeneration characteristics

Details of the studied regeneration for every site are given in Table 2 and average characteristics are given in table 3. Regeneration density strongly varied across sites, from 0 to 110 saplings m^{-2} . Species composition also varied across sites. The proportion of other admixed species was large in some plots (max. 98%), but exceeded 50% in only 28 plots.

On average, beech saplings had higher initial height and height increment than oak saplings. Harvested saplings of the two species were 11 years old in average, but the studied regenerations were clearly uneven aged. Moreover, in plots with a mixture of beeches and oaks, oaks were on average 1.5 years younger (two-way mixed ANOVA, $F=5.8$, $p<0.001$).

Negative height increment occurred ($n=18$) because the three tallest measured saplings were not necessary the same for the two measurements. Saplings measured the first time were not tagged. Before the second measurement, some measured saplings could have died and be no longer among the three tallest saplings.

The Pearson's correlations between PACL and the initial height of oak and beech saplings were respectively 0.387 ($P<0.001$) and 0.042 ($P=0.608$). At the beginning of the study, high oak regenerations were thus mostly found in plots with higher light levels.

Overtopped and overtopping oak regenerations occurred in 104 and 70 plots, respectively. Overtopped and overtopping beech regenerations occurred in 120 and 29 plots, respectively. In half of the plots with overtopped oak regeneration, oak saplings represented the major proportion of the total sapling count. By contrast, overtopped regeneration of beech involved only a few individuals.

3.2 Height growth models

The modelling of height growth for the two species showed that beech saplings grew on average faster than oak saplings, whatever the light conditions (Fig. 2). For the two species, as PACL increased, growth increased following a sigmoid curve and then reached a horizontal asymptote. This asymptote increased with sapling initial height. For instance, in high light conditions, the height increment of small beech saplings ($H_{ij} = 50$ cm) was found to be approximately 20 cm, whereas the height increment of taller beech saplings ($H_{ij} = 300$ cm) was up to 50 cm. Between saplings of oak and beech of similar height, the beech saplings had a greater height increment than the oak saplings.

Moreover, beech saplings reached their asymptotic growth at lower light levels than oak saplings. Overtopping beeches, overtopping oaks, and overtopped oaks reached 90% of their asymptotic growth at, respectively, 12%, 20% and 29% of above canopy light. Indeed, the inflexion point of the models,

Table 3. Average (minimum and maximum) sapling characteristics for oak, beech and other species encountered in the plots.

Species	n	Height in 2009 (cm)	Height increment (cm)	Age in 2009 (years)	Proportion of subplots with dominant regenerations (%)
Beech	149	153 (23; 277)	26 (-9; 62)	10 (4; 21)	40
Oak	174	125 (13; 273)	16 (-10; 52)	10 (1; 19)	80
Other	93	118 (7; 285)	20 (-66; 84)	/	55

denoted by parameter c in equations 2 and 3, varied significantly between models (Table 4).

The good dispersal of residuals indicated no evidence of model bias. However, residual scatterplots indicated a substantial residual variation (Supplementary figures 2 and 3) that was greater in the model for beech ($\theta_{\epsilon_{ij}} = 10.5$ cm) than for oak ($\theta_{\epsilon_{ij}} = 6.8$ cm). The between-site variation, θ_{α_j} , was about 7 cm in both models.

3.3 Diffuse and direct radiation

We tested whether adding the percentage of transmitted direct radiations (DIR) into a model already including the percentage of transmitted diffuse radiations (DIFF) improved the prediction of height increment by replacing PACL in eq. 2 and 3 with $eDIR + (1 - e)DIFF$. The null hypothesis was accepted for beech ($e=0.300$, $P=0.640$) which means that DIR did not influence significantly the height growth of beech regeneration. At the opposite, the null hypothesis was rejected for oak ($e=1.001$, $P=0.005$). This indicated that the height growth of oak responded mainly to DIR. The same conclusion would have been obtained by adjusting models including only the overtopping saplings.

3.4 Analysing site effect

For the oak saplings, the “site effect”, estimated using $BLUP_{\alpha}$, was positively correlated with soil richness ($r=0.562$, $P=0.015$) and mean annual temperature ($r=0.638$, $P=0.004$). The site effect was negatively correlated with altitude ($r=-0.631$, $P=0.005$) and mean annual precipitation ($r=-0.689$, $P=0.002$). In addition, altitude was inversely correlated with mean temperature ($r=-0.522$, $P=0.026$) but not significantly with mean precipitation.

For beech saplings, the “site effect” was only positively correlated with soil richness ($r=0.553$, $P=0.001$).

4. Discussion

Our large in situ sampling of beech and oak saplings enabled us to adjust mixed non-linear models of height growth according to initial height, light availability and species dominance (eq. 2 and 3). We further used the adjusted models to ascertain (i) the height growth of the two studied species under different light conditions (ii) the effects of species dominance, (iii) the influence of direct radiation, (iv) the between-site variations, (v) and silvicultural implications.

4.1 Height growth ranking

The ecological theory of forest succession postulates that under high light levels, light demanding species outcompete

shade-tolerant species. According to Kobe et al. (1995), a high capacity to survive under low light levels is offset by lower growth rate under high-light levels. Light demanding species would thus allocate preferentially resources to height growth and hence risk dying from light starvation (Messier et al., 1999).

Our findings indicated well that oak saplings have greater light requirements than beech saplings. We found that the beech and oak saplings needed more than 10% and 20% of above canopy light (PACL), respectively, in order to exhibit more than 90% of the maximum height growth (Fig. 2). In accordance with previous studies (Farque et al., 2001; Petritan et al., 2007, 2009; Stancioiu and O’Hara, 2006), we found that under higher levels of PACL, any increase in PACL induced little variation in height growth (asymptote). Nevertheless, our findings indicated that oak saplings, the less shade-tolerant species, generally exhibited a lower height increment than beech saplings even under high light conditions ($PACL > 20\%$, Fig. 2). This observation is partly in contradiction with the definition of shade tolerance proposed by Kobe et al. (1995), but similar observations have already been reported with other species (Kunstler et al., 2005; Walters and Reich, 1996). It highlights the strong ability of beech to survive in deep shade (Wagner et al., 2010), and lead us to infer that oak saplings have an insignificant chance of survival under beech saplings. The lower height growth of oak means that in mixed clumps of oak and beech, oak saplings are naturally suppressed. Additionally, the height growth might be traded off with adaptations to low nutrient and water supply (Beaudet and Messier, 1998; Collet et al., 2001; Kobe et al., 1995; Wagner et al., 2010; Walters and Reich, 1996) or herbaceous competition (Coll et al., 2004, 2003; Walters and Reich, 1996).

In this study, we focused on the variations of saplings height growth with light availability and we admit that the response of diameter growth and mortality rate could have led to different conclusions. Nevertheless, height growth has been shown to be a good proxy for sapling mortality (Kobe et al., 1995; Kunstler et al., 2005; Petritan et al., 2007; Walters and Reich, 1996).

Beeches were on average taller and older at the beginning of the experiment, which gave them a competitive advantage over oaks. Due to their shade-tolerant nature and the higher frequency of seed production by adult trees, beech saplings often pre-exist in the understory before the canopy opening (Wagner et al., 2010). They maintain large seedling populations in the understory while waiting for more suitable light conditions. Consequently, beech saplings are often established before oak saplings. However, the small age differences be-

Table 4. Parameter estimates (confidence intervals with α level of 0.05) of the selected models presented in eq. 2 and 3. b is the parameters of the asymptotic height growth and c is the inflexion point. In the model for oak, there were two estimates for c : one for overtopping regeneration and one for overtopped regeneration. θ_{α_j} and $\theta_{\epsilon_{ij}}$ are, respectively, the standard deviation associated to the random factor (between-site variation) and the residual error (within-site variation).

Species	b	c (overtopping regeneration)	c (overtopped regeneration)	θ_{α_j}	$\theta_{\epsilon_{ij}}$
Oak	2.059 (1.642; 2.476)	6.058 (3.468; 8.648)	10.257 (6.469; 14.046)	7,255	6,759
Beech	2.431 (2.035; 2.828)	3.964 (2.378; 5.550)		7,261	10,491

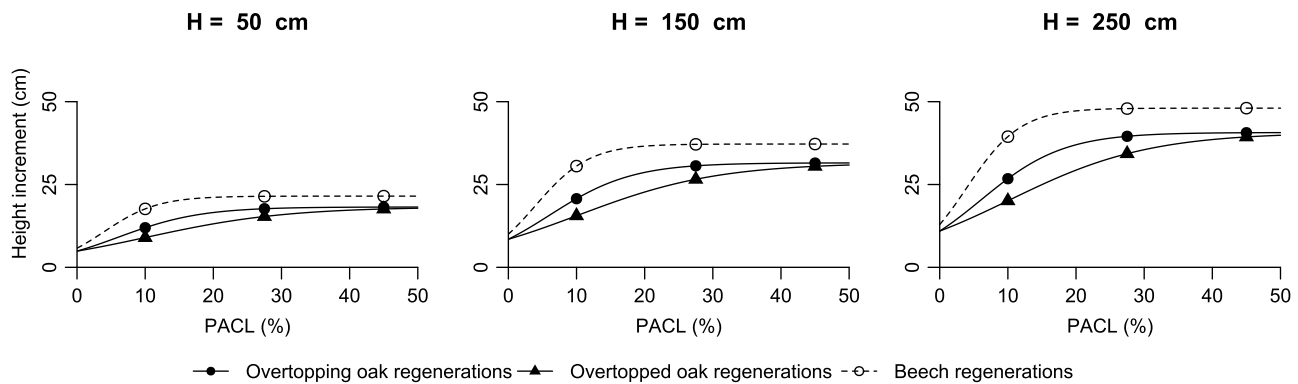


Figure 2. Simulation of height growth of oak and beech saplings in mixed forests in the Belgium Ardennes. Beech showed a higher growth rate under all light conditions. The presence of taller saplings of beech or hornbeam reduced the growth of the neighbouring oak saplings (overtopped oak saplings).

tween the oak and beech saplings in this study are unlikely to be responsible for the differences in height growth. Indeed, we found that sapling age did not appear as a significant explanatory variable in height growth models. This result is in agreement with the findings of Collet et al. (2001) and partly in agreement with those of Emborg (1998).

Growth ranking might depend on ontogeny, tree size (Balandier et al., 2007; Delagrangue et al., 2004; Niinemets, 2006) and availability of nutrient and water (Kobe et al., 1995; Walters and Reich, 1996). Our results might therefore be limited to the studied ontogenetic stage characterized by saplings with a height of less than 300 cm and within the conditions of the Belgian Ardennes.

4.2 Competition

Overtopping saplings of beech (and hornbeam) significantly reduced the height growth of overtopped oak saplings. This shifted leftward the inflexion point from 10 to 6% of above canopy light. Such a reduction was expected because PACL was measured above the regeneration and overtopped species receive only the PACL that was not intercepted by overtopping species.

Overtopped beeches were not significantly affected. The levels of transmitted radiations in plots with overtopped beeches was probably too high (average PACL of 15%) to model the effect of interspecific competition on the growth of beech

saplings. In such conditions (PACL > 10%), a small decrease in transmitted radiation does not really affect beech growth (Table 1 and Fig. 1). Moreover, diameter growth may be more affected by competition than height growth (Collet and Chenost, 2006; Prévosto and Balandier, 2007).

4.3 Direct radiation

We tested whether the height growth of oak and beech saplings was sensitive to direct radiations. Our results suggested that stem elongation of oak saplings was promoted by direct radiations in contrast with the height growth of beech saplings. This result confirmed the higher light requirement of oak saplings. In addition, beech growth was sensitive to light change when PACL was less than 10%. In these conditions, gaps are generally very small and the periods with transmitted direct radiations are very short (Chazdon and Pearcy, 1991). This stresses the importance of using total PAR radiations to model the growth of less shade-tolerant species. Diaci (2002) and Diaci et al. (2007) demonstrated the relative importance of diffuse and direct radiations on regeneration success of Norway spruce, beech and pedunculate oak in Slovenia. In particular, they reported the successful development of beech under diffuse canopy openings, something that is in accordance with our results. On the other hand, sites with higher levels of direct radiation might also be drier (Diaci et al., 2007). We studied solely the effect of light supply, while,

in another study, changes in light conditions were shown to induce changes in microclimatic and soil variables (Aussenac, 2000).

4.4 Between-site variation

In this study, we showed that between-site variations was substantial ($\theta_{\alpha_j} \approx 7.2$ cm) and in the same order of magnitude that the within-site error ($\theta_{\epsilon_{ij}} \approx 6.7$ and 10.5 cm for oak and beech, respectively). We attempted to explain this variation with both biotic and abiotic characteristics of the sites.

Soil richness was the only significantly correlated variable for both species. Indeed, both species are known to require similar levels of nutrient availability (Piedallu et al., 2009). Nevertheless, the investigated range of soil richness was small between the sites and it was computed from a floristic survey. These variations might hence denote complex interactions between canopy composition, canopy closure and ground vegetation.

In contrast with beech saplings, the height growth of oak saplings responded positively to mean annual temperature and negatively to mean annual precipitation. Oak has higher mean annual temperature requirements and its optimum temperature is about 11°C in Western Europe (Piedallu et al., 2009). Rainfall is abundant throughout the study area and should not affect negatively sapling growth in the absence of soil waterlogging. However, abundant rainfall implies greater cloud cover and precipitation that are negatively correlated with temperature. Sites with abundant rainfall could then be characterized by higher cloud cover and lower temperatures, which might negatively affect oak growth within the study area. Taken together, these climatic considerations underlined the submontane trend of the climate of the Ardennes which are less convenient for oak than for beech regeneration, even in high-light environments. Possible additional explanations for within- and between-site variations may lie in genetic variation, incidence of disease, canopy history, unmeasured soil and micro-climate conditions.

4.5 Silvicultural conclusions

We sampled in situ advanced regeneration within the whole range of conditions encountered in beech and oak forests managed with a continuous-cover forestry system in the Belgian Ardennes. Irradiance ranged from 1 to 60% under heterogeneous canopies. Irradiance below 3% is typical under closed canopy (Emborg, 1998), whereas, after canopy release, the level of irradiance might increase up to 15% (Collet et al., 2001), 30% (Pacala et al., 1994) or even beyond 60% according to our data.

We observed that beech saplings naturally outcompeted oak saplings. Beech saplings reached an optimum growth at 10% of above-canopy light whereas oak saplings needed twice as much light. In addition, our sapling age analysis highlighted that beech saplings were usually established before oak saplings. After canopy opening, these pre-existing beeches derived greater benefit from the increase of light availability than younger and smaller oaks. In these conditions, oaks

are rapidly suppressed and mixed stands of oak and beech evolve naturally toward pure beech stands. The two species have mainly coexisted because beech naturally regenerates under well-established oak stands where oak has previously been favoured by selective thinning, coppicing and plantations (Claessens et al., 2010). The reverse situation is unlikely to occur naturally without frequent disturbances (Messier et al., 1999).

As a result, foresters applying continuous-cover silviculture need to proceed in three phases. (1) Waiting for the emergence of oak seedlings, they must maintain a low light in the understory (PACL < 5%) in order to reduce the development of beech seedlings that continuously emerge under the canopy. Indeed, germination does not depend on light conditions (Chaar and Colin, 1999; Nicolini et al., 2000; Turbang, 1954; Welander and Ottosson, 1998), (2) Reducing overstorey stocking is essential to promote oak regeneration. This would mainly be achieved by creating gaps (PACL > 20%) and increasing the availability of direct radiations to oak seedlings. Higher light levels would only influence slightly the stem elongation of saplings. However, as saplings become taller, foresters need to open the gaps gradually in order to satisfy the increasing light requirements of older saplings (Messier et al., 1999). (3) Given the ecological conditions of the Belgian Ardennes, our analysis indicates that oak could not be promoted over beech only by managing overstorey. Foresters thus need to remove manually beech (and hornbeam) competitors that systematically overtop oak saplings (von Lupke, 1998), especially in the cases where beech seedlings were pre-existing. Moreover, we ensured strict protection of the studied saplings from herbivorous browsing. As deer prefer browsing oak over beech (Gill, 1992), an additional control of ungulate populations is one of the primary conditions for successfully regenerating oak in mixed beech and oak forests.

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