

# Light and competition gradients fail to explain the coexistence of shade-tolerant *Fagus sylvatica* and shade-intermediate *Quercus petraea* seedlings

Rosalinde Van Couwenberghe<sup>1,2,\*</sup>, Jean-Claude Gégout<sup>1,2</sup>, Eric Lacombe<sup>1,2</sup> and Catherine Collet<sup>1,2</sup>

<sup>1</sup>INRA, UMR1092, Laboratoire d'Etude des Ressources Forêt Bois, Centre de Nancy, 54280 Champenoux, France and  
<sup>2</sup>AgroParisTech, UMR1092, Laboratoire d'Etude des Ressources Forêt Bois, Centre de Nancy, 14 rue Girardet, CS 14216,  
54042 Nancy Cedex, France

\*For correspondence. E-mail [vancouwenberghe.rosalinde@yahoo.fr](mailto:vancouwenberghe.rosalinde@yahoo.fr)

Received: 28 May 2013 Returned for revision: 13 June 2013 Accepted: 18 July 2013 Published electronically: 12 September 2013

- **Background and Aims** The coexistence of forest tree species has often been linked to differences among species in terms of their response to light availability during the regeneration stage. From this perspective, species coexistence results from growth–growth or mortality–growth trade-offs along spatial light gradients. Experimental evidence of growth–growth trade-offs in natural conditions is sparse due to various confounding factors that potentially hinder the relationship. This study examined growth hierarchies along light gradients between two tree species with contrasting shade tolerance by controlling potential confounding factors such as seedling size, seedling status, seedling density and species composition.
- **Methods** Natural regenerated shade-tolerant *Fagus sylvatica* and shade-intermediate *Quercus petraea* seedlings were used, and growth rankings over a 4-year period were compared in 8- to 10-year-old tree seedlings.
- **Key results** No rank reversal occurs between the two species along the light gradient, or along the density, mixture or seedling size gradients. The shade-tolerant species was always the more competitive of the two. Pronounced effects of initial size on seedling growth were observed, whereas the effects of light and competition by neighbours were of secondary importance. The paramount effect of size, which results from the asymmetric nature of interseedling competition, gives a strong advantage to tall seedlings over the long term.
- **Conclusions** This study extends previous efforts to identify potential drivers of rank reversals in young tree mixtures. It does not support the classical assumption that spatial heterogeneity in canopy opening explains the coexistence of the two species studied. It suggests that spatial variation in local size hierarchies among seedlings that may be caused by seedling emergence time or seedling initial performance is the main driver of the dynamics of these mixed stands.

**Key words:** Rank reversal, seedling growth, density, mixture, niche differentiation, forest dynamics, succession, competition gradient, plant–plant interactions, *Fagus sylvatica*, *Quercus petraea*.

## INTRODUCTION

In temperate forests, light competition among trees is traditionally seen as a major process underlying stand dynamics (Oliver and Larson, 1996). On the basis of this assumption, differences in species response to light availability largely determine species coexistence and, eventually, forest community composition and structure (Denslow, 1987; Canham *et al.*, 1994; Silvertown, 2004). During the regeneration phase, these differences lead to distinct regeneration niches along spatial gradients of light availability (Grubb, 1977). According to this theory, canopy gaps play a key role in the maintenance of tree species diversity (Runkle, 1981), guaranteeing species establishment with different light requirements (Gravel *et al.*, 2010). Shade-tolerant species that experience high survival rates under low light and moderate growth response to canopy openings grow in closed canopy conditions. At the other extreme, shade-intolerant species with high mortality under low light and strong growth response to canopy openings dominate in open canopy conditions (Kobe *et al.*, 1995; Kobe, 1997). These contrasting strategies can lead to changes in growth hierarchies along a light gradient.

Two models of changes in growth hierarchies along light availability gradients have been proposed for young mixed forest stands

comprising tree species with contrasting shade tolerance (Sack and Grubb, 2001). According to the first model, light-demanding species grow faster than shade species at high light levels, whereas the opposite occurs at low light levels, inducing rank reversals in growth rates among species along the light gradient (Thomas and Bazzaz, 1999). Alternatively, other studies (Kitajima, 1994; Poorter, 1999; Rüger *et al.*, 2011) reported that light-demanding species grow faster than shade species at all light levels and did not observe any growth rate crossover along the light gradient. Beyond the idiosyncrasy of each plant community, such disparate results may be produced by variations in factors affecting inter-tree competition such as tree size, population density and specific composition (Sack and Grubb, 2001; Boyden *et al.*, 2009).

First, initial seedling size needs to be considered. Small differences in seedling size, whether they are caused by individual variability or by environmental microheterogeneity, are often magnified over time (Cannell *et al.*, 1984; D'amato and Puettmann, 2004). The non-linear relationship between growth rate and initial size commonly observed in many plant species provides an advantage for larger individuals compared with smaller individuals, even in the absence of competition (Schwinning and Weiner, 1998). Resource competition,

particularly for light, amplifies this growth advantage. Larger individuals are then able to pre-empt a disproportionate share of available resources and to outgrow smaller individuals rapidly (Sánchez-Gomez *et al.*, 2008; Caquet *et al.*, 2010; Gómez-Aparicio *et al.*, 2011). This framework implies that both absolute seedling size and relative size within the population (i.e. social status) should be taken into account when analysing the growth dynamics of seedlings competing for light (D'amato and Puettmann, 2004).

A second factor is local seedling competition. Local plot density and species composition determine the make-up of the competitive neighbourhood of individual seedlings. They are widely used as explanatory variables in studies of competitive interactions in young mixed tree populations (e.g. Boyden *et al.* 2009; Caquet *et al.*, 2010). Surprisingly, to our knowledge, no study has yet analysed the influence of local competition on the occurrence of rank reversals among tree seedlings along light gradients. Many studies involve isolated plants (Baraloto *et al.*, 2005; Baltzer and Thomas, 2007; Seiwa, 2007), and most other studies do not describe the competitive environment of measured seedlings (Poorter and Arets, 2003; Kunstler *et al.*, 2005; Beaudet *et al.*, 2007; Lilles and Astrup, 2012). As seedling density increases, competition becomes more intense and available light more depleted, leading to reduced average individual growth, increased size variability among seedlings and, eventually, magnified differences in species performances (Hara and Wyszomirski, 1994; Schwinning and Weiner, 1998; Boyden *et al.*, 2009). Boyden *et al.* (2009) showed that in full light conditions, shade-intolerant species, which achieve early size dominance, increase their advantage over more shade-tolerant species when plot density is higher, whereas at low plot density, their advantage over shade-tolerant species is reduced. In contrast, in low light conditions, shade-tolerant species may be expected to be less affected than intolerant species by neighbour competition due to the further reduced amount of available light. In such a scheme, crossover among species along light gradients should occur more frequently at higher density. Similarly, species composition within a mixture is known to affect relative species performances due to species-dependent resource capture strategies (Grime, 1979; Tilman, 1982, 1988). Changes in the nature of interspecific and intraspecific interactions along density gradients influence the overall production, and it is theorized that mixed stands might achieve greater overall productivity than monocultures of one species (Tilman, 1982). However, interactions between plant density, species composition and resource availability are of a complex nature, and little knowledge is presented in today's literature.

In the present study, we examined growth variations in young natural mixtures of oak (*Quercus petraea*) and beech (*Fagus sylvatica*) along light gradients and examined how they are affected by seedling size, seedling density and species composition. The two broadleaf species play critical roles in the mid and late succession dynamics of western and central European forests. They were chosen to represent contrasting growth strategies. Beech is classified as very shade tolerant, with growth approaching an asymptotic value at around 30 % light during the seedling stage (von Lüpke and Hauskeller-Bullerjahn, 2004; Petritan *et al.*, 2007). Oak has a low shade tolerance and experiences maximal growth in full light conditions (Landolt, 1977; Ellenberg *et al.*, 1992). Contradictory results have been reported on the relative performance of the two species along light gradients. In a greenhouse pot

experiment, Dreyer *et al.* (2005) showed that 2-year-old oak seedlings had superior growth over beech seedlings at all light levels along a wide gradient of light availability. In a plantation experiment, von Lüpke and Hauskeller-Bullerjahn (2004) observed rank reversals in height growth between the two species at relative light intensity levels around 40 %, with beech being more competitive below the threshold light values and oak being more competitive above the thresholds. In different contexts, silvicultural field experiments extended the superior competitive performance of beech seedlings towards oak among all the light gradient (e.g. *Quercus robur* and *Quercus petraea*) (von Lüpke, 1998; Kunstler *et al.*, 2005; Wagner *et al.*, 2010). The conflict among these observations may arise from a variety of factors, including tree developmental stage and population structure (density, composition and dominance), a series of factors that are usually found to be highly correlated in natural conditions. The main objective of the present study is to analyse how these factors may influence potential rank reversals along light gradients between oak and beech seedlings.

Throughout western and central Europe, oak regenerates with difficulty when mixed with beech in both managed and unmanaged forests (von Lüpke, 1998). For conservation and for production purposes, forest managers often attempt to maintain or even to favour oak over beech (Gebler *et al.*, 2007) and require silvicultural methods to enhance the performance of oak seedlings. A secondary objective of this study is to identify the factors (light availability, seedling population structure) on which silvicultural operations should focus during the regeneration stage in order to favour oak over beech.

The following hypotheses were tested: (1) oak and beech show growth rank reversal along light gradients found in semi-natural forests, beech being superior to oak at low light levels and inferior at high light levels; (2) when density increases, differences in species performances increase and potential rank reversals become more pronounced; (3) seedling size strongly affects seedling growth and must be taken into account to test the first two hypotheses; and (4) beech seedlings are stronger competitors than oak seedlings for neighbouring oak seedlings at all light levels. Finally, since the explanatory variables chosen correspond to factors that are dealt with through standard silvicultural operations (canopy opening, tending operations, control of species composition), practical recommendations to manage mixed oak and beech regenerations will be proposed.

In a mixed oak and beech stand undergoing natural regeneration, we selected plots along gradients of light availability, local competition and seedling size. We quantified these factors along with recent seedling radial and axial growth history. These variables were then used to model relative species performances. A stronger focus was placed on oak in order to identify which factors should be emphasized to enhance oak performance.

## MATERIALS AND METHODS

### Site description

The study area is located in the community forest of Epinal in the Lorraine region of France. The climate is characterized as continental with oceanic influences, with a mean annual winter temperature of 1 °C and a mean annual summer temperature of 17 °C. Precipitation is evenly distributed throughout the year,

with a mean of 96 cm (Bénichou and Le Breton, 1987). The study site is located at 6.5 °E and 48.18 °N, on a plateau with an elevation of 415 m a.s.l. Soils are uniform within the study area and consist of a hemimoder humus on top (Baize *et al.*, 2009) and two main horizons on a sandstone substrate: the first horizon is 4 cm deep with a loamy–clayey texture ( $\text{pH}_{\text{water}} = 4.5$  and  $\text{C/N} = 18$ ), and the second horizon is 50 cm deep with a loamy–clayey texture. Hydromorphic traces appear at a soil depth of 47 cm.

The site was a 17 ha managed uneven-aged mixed oak–beech stand (*Quercus petraea*–*Fagus sylvatica*), with 90- to 170-year-old overstorey trees. In December 1999, the storms, Lothar and Martin, which caused widespread damage in the region, created gaps of different sizes – many small gaps (approx. 0.1 ha) and three large gaps (59, 155 and 255 ha). Fallen logs were harvested immediately after the storms and no other silvicultural operation was performed in the stand in the following years. In 2005, the basal area of overstorey trees (oak and beech) was  $24 \text{ m}^2 \text{ ha}^{-1}$ . In autumn 1999, mast seeding occurred for beech and oak, producing a large crop the following year that added to the number of previously established seedlings.

### Study design

In July 2008, natural regeneration was abundant and ranged between 0.3 and 6 m high. Regeneration was dominated by beech and oak. A total of 169 circular plots of  $2 \text{ m}^2$ , centred on an oak seedling (the target seedling), were established.

In order to reduce potential correlation among explanatory variables in the analysis, a stratified sampling procedure to select the study plots was established as follows. Three main gradients were considered, each one divided into three classes: (1) canopy closure intensity above the plot, which was visually estimated and classified as closed (i.e. outside gaps), intermediate (i.e. in small gaps or at the edge of large gaps) and open (i.e. in large gaps); (2) regeneration mixture in the plot, which was classified as an oak-dominated mixture (more oak than beech seedlings), oak–beech equivalent mixture or beech-dominated mixture (more beech than oak seedlings); and (3) status of the central target oak seedling within the plot, which was estimated from the oak seedling height relative to the height of all the neighbours within the plot and expressed as dominant, co-dominant or dominated. The three gradients were crossed, creating a  $3 \times 3 \times 3$  contingency table (see Supplementary Data Table S1), and the objective was to establish approximately six plots in each of the nine cells of the contingency table in order to obtain a balanced sampling design. However, some combinations were difficult to find (e.g. dominant seedling in a beech-dominated mixture in closed canopy conditions), and the number of plots sampled in each of the nine cells finally ranged between zero and nine, with an average of 6.2 plots per cell. The stratification into  $3 \times 3 \times 3$  levels was used only for selecting the study plots and, in further analyses, quantitative variables reflecting the three gradients were used instead of the initial classes established for sampling. This approach made it possible to sample very wide gradients ranging between extreme values and largely encompassing values usually found in oak–beech natural regeneration. Crossing the three gradients made it possible to control

the correlation among the explanatory variables and, therefore, to perform an independent evaluation of their impact on seedling growth.

Plots were only selected if they had high seedling density, no species presence other than beech and oak, no herbaceous vegetation, no adult trees (diameter at breast height:  $>7 \text{ cm}$ ) and no visible damage (browsing, frost, fungi, etc.) of any tree seedling. A minimum distance of 2 m between neighbouring plots was established. All selected plots were located on a site map. The target seedling of each plot was labelled.

### Data collection

After the plots had been selected, the relative light intensity above each plot was estimated using hemispherical photography. A Nikon Coolpix 5000 digital camera with a FC-E8 Fisheye Converter Lens was used. The camera was positioned 2 m above the ground at the centre of each plot, except for eight plots where regeneration was higher than 2 m and where pictures were taken at 4 m above the ground. Photographs were captured under uniform cloud cover conditions during the day in July and August 2008, on a ‘high speed’ setting to increase the distinction between sky and foliage. Photographs were manually thresholded to black and white, and the relative light intensity (percentage total radiation – direct and diffuse – penetrating through the canopy) was calculated for each photograph using HemIMAGE software (Brunner, 1998). In the plots studied, relative light intensity ranged between 0.1 and 88 % (Table 1).

All seedlings within the plots were assessed in autumn 2008: species (oak or beech), basal diameter (5 cm above ground), total height (stretched length) and distance to the target oak were measured for each seedling, except for seedlings smaller than 30 cm. Measurements on small seedlings ( $<30 \text{ cm}$  height) included only the number of seedlings per species.

One or two stems were collected in each plot for detailed growth measurements. In each plot, the target oak seedling was selected and, in plots containing beech taller than the target oak, the tallest beech was also selected. The 169 collected target oaks and the 105 tallest beech seedlings were brought to the lab for annual height and radial growth measurements. In all seedlings, the last four annual height growth units (2005–2008) were identified by examining the scars left by the winter buds, and the length (cm) of each growth unit was measured. A section was cut at the seedling base, and seedling age was estimated based on annual ring counts. The width of all annual rings was estimated from the measurement of ring width on four opposite radii with a microscope (precision of 1/100 mm). The detailed measurements were classified into three groups for further analysis: the 169 target oak seedlings; the 93 tallest oak seedlings corresponding to a sub-group of target oaks with a dominating and co-dominating status; and the 105 tallest beech seedlings.

### Analytical approach

Models were used to analyse the combined effects of light availability, initial seedling size and competition from



TABLE 1. Individual plot characteristics (a total of 169 plots)

Year	Variable	Dec <sub>10</sub>	Median	Dec <sub>90</sub>
2008	Relative light intensity: diffuse light (%)	5	16	34
	Relative light intensity: direct light (%)	3	20	59
	Seedling density: total (no. of stems per 2 m <sup>2</sup> plot)	26	74	150
	Large (H > 30 cm) seedlings (no. of stems per 2 m <sup>2</sup> plot)	22	49	87
	Percentage of oak, among large (H > 30 cm) seedlings (%)	13	40	74
	Mean seedling height (cm)	50	85	170
2004	Target oak seedling			
	Age (years)	3	5	10
	Initial height (cm)	19	34	98
	Initial diameter (cm)	26	52	94
	Tallest oak seedling			
	Age (years)	3	5	6
	Initial height (cm)	21	35	102
	Initial diameter (cm)	3.1	6.3	12.1
	Tallest beech seedling			
	Age (years)	5	7	9
	Initial height (cm)	56	102	180
	Initial diameter (cm)	9.3	14.3	23.6

For each variable estimated in 2004 or in 2008, the first decile (Dec<sub>10</sub>), median (Median) and last decile (Dec<sub>90</sub>) are indicated.

neighbours on seedling height and radial growth for oak and beech seedlings. The following general model was withheld:

$$\text{Growth} = \text{Light} + \text{Size} + \text{Competition} \quad (1)$$

where *Growth* refers to height or radial growth, expressed as the increment over the last four growing seasons (2005–2008) of the target seedling (oak) or of the dominant seedling (beech or oak) of each plot, *Size* is initial seedling size, and *Light* and *Competition* are calculated from individual plot conditions.

*Explanatory variables.* Light was expressed by three relative light intensity variables: diffuse light, direct light and total light, estimated from the 2008 measurements. Different growth–light functions to describe the relationship between seedling growth and its light environment were tested: logistic with two parameters, potency and inverse exponential; logistic with three parameters; Gompertz and cubic functions (Lebreton and Millier, 1982; Brown and Rothery, 1993).

Initial seedling size was either stem diameter or stem height at the beginning of the growth period (i.e. end of 2004) and was computed for each individual as seedling size measured in 2008 minus the increment over the last 4 years.

Intra- and interspecific competition from neighbouring seedlings in the plot was described with two alternative approaches: (1) competition was expressed in the model by three different factors classically used in forestry: density per plot (either the total number of seedlings in the plot or the number of seedlings higher than 30 cm in the plot, divided by plot surface area), mixture (proportion of oak seedlings in the plot among seedlings higher than 30 cm), and the status of the individual seedling (dominant, co-dominant or dominated); or (2) competition was expressed using competition indices accounting for the species (oak or beech), the absolute or relative size of each neighbouring seedling in the plot and its distance to the target seedling (Silander and Pacala, 1985; Collet and Chenost, 2006). Different models were tested for each approach and their

performances compared. Finally, the best approach was then chosen, as explained below.

Disparities among variables according to the date at which they were estimated could be observed. The response variable was based on growth over the 2005–2008 period, and initial size was estimated at the end of 2004. Plot characteristics (competition and light) were estimated from 2008 measurements. However, successive estimations of light or seedling competition in natural regeneration are usually highly correlated over short periods (4 years) and the 2008 values may be considered as good estimates of the factors over the growth period considered.

*Model development.* Model development involved two successive steps. The first step included the identification of the best set of variables explaining the growth of the target oak seedlings. The second step included the analysis of the growth response of the tallest oak and beech seedlings, using the variables selected in the first step.

Step 1. The best set of explanatory variables and equations to explain height and diameter growth was identified using the target oak seedlings from the 169 plots. Different growth models containing initial size, one expression of light and one expression of competition were fitted. The choice of best model was made according to: (1) the Akaike information criterion (AIC) where models with higher AIC were penalized; (2) correlation among explanatory variables where models with the lowest correlation were preferable; and (3) residual analysis where models with trended residual distribution or heterogeneous variance were eliminated. Once the best set of explanatory variables and functions had been selected, a stepwise backward selection procedure was applied to test the significance of each selected variable and their interactions using analysis of variance (ANOVA) tests and excluding all variables with a *P*-value > 0.05. In both models (e.g. diameter growth model and height growth model), first-order interactions were never significant and were therefore

excluded. Finally, the following non-linear model was selected and used in all subsequent analyses on target oak seedlings:

$$\begin{aligned} \text{Growth} = & a_0/[1 + \exp(-a_1 \text{Light})] \\ & + b\text{Size} + c\text{Density} + d\text{Mixture} + e_i\text{Status} \end{aligned} \quad (2)$$

where *Growth* refers to individual seedling height or diameter increment over 4 years (cm), *Light* to diffuse radiation percentage (%), *Size* to initial seedling height or diameter (cm), *Density* to the number of seedlings higher than 30 cm within the plot, *Mixture* to the percentage of oak seedlings higher than 30 cm within the plot (%), *Status* to seedling status within the plot, and  $a_0, a_1, b, c, d$  and  $e_i$  to the model coefficients. The *Status* variable is the only categorical variable within the model, presenting three levels ( $i = 0$ , seedling is dominated;  $i = 1$ , seedling is co-dominant; or  $i = 2$ , seedling is dominant).

None of the three components of competition (*Density*, *Mixture*, *Status*) showed significant correlation with *Light* or with *Size*, except for *Size* × *Status* correlation when considering diameter growth. In contrast, *Light* and *Size* were highly correlated (Spearman rank coefficient approx. 0.5), a correlation that was taken into account when interpreting the results.

The fitted model was used to quantify the importance of the effects of the different explanatory variables on seedling growth. For each variable, a response range was computed: predicted values of seedling growth were computed by setting the variable to the first and to the ninth decile (10 and 90 %) of its gradient and by setting all other variables to their median value. The response range was then estimated as the difference between the two predicted values. These response ranges were computed for each explanatory variable and were used to compare the quantitative effects of the different variables.

Step 2. The model established in Step 1 was adapted, to compare the effects of light, initial size and competition on the diameter and height growth of the tallest oak and beech seedlings. For oak, 93 target seedlings that were classified as dominant or co-dominant were used. For beech, the 105 tallest seedlings were considered. Since only dominant and

co-dominant seedlings were used in the analysis, seedling status was removed from the model eqn (2). The following non-linear model was selected and used in all subsequent analyses on the tallest oak and the tallest beech seedlings:

$$\begin{aligned} \text{Growth} = & a_0/[1 + \exp(-a_1 \text{Light})] \\ & + b\text{Size} + c\text{Density} + d\text{Mixture} \end{aligned} \quad (3)$$

where *Growth* refers to individual seedling height or diameter increment over 4 years (cm), *Light* to diffuse radiation percentage (%), *Size* to initial seedling height or diameter (cm), *Density* to the number of seedlings higher than 30 cm within the plot, *Mixture* to the percentage of oak seedlings higher than 30 cm within the plot (%) and  $a_0, a_1, b, c$  and  $d$  to the model coefficients.

Separate models were fitted for each species and for each growth type (diameter and height), which resulted in four models. A stepwise backward selection procedure was applied to test parameter significance for each model.

All models were fitted using the non-linear least squares statistics of the R open source software, version 2.14.0 (R Development Core Team, 2011).

## RESULTS

### Plot regeneration

A total of 13 784 seedlings were counted in all 169 plots. The minimum and maximum number of seedlings per plot were four and 248 seedlings (i.e. two and 123 seedlings per m<sup>2</sup>), respectively (Table 1). Half the plots contained >37 seedlings, with >24 seedlings higher than 30 cm. The average seedling height per plot was 100 cm (83 and 123 cm for oak and beech seedlings, respectively). In the plots studied, the proportion of oak within the plot ranged between 1 and 99 % (Table 1).

### Effects of competition, size and light on tallest oak growth

The height growth of the tallest oak seedlings was significantly affected by *Light*, *Size* and *Mixture* (Table 2, Model 1). *Density*

TABLE 2. Effects of diffuse radiation percentage (*Light*), initial seedling size (*Size*), number of seedlings in the plot (*Density*), percentage of oak seedlings in the plot (*Mixture*) and seedling status (*Status*:  $e_0$  = dominated,  $e_1$  = co-dominant and  $e_2$  = dominant) on seedling growth [calculated as  $\text{Growth} = a_0/[1 + \exp(-a_1 \text{Light})]/ + b\text{Size} + c\text{Density} + d\text{Mixture} + e_i\text{Status}$  [eqn (2)] for the target oak seedlings and  $\text{Growth} = a_0/[1 + \exp(-a_1 \text{Light})]/ + b\text{Size} + c\text{Density} + d\text{Mixture}$  [eqn (3) for the tallest seedlings], for height and diameter growth and for different types of seedlings: model number, seedling type, number of observations ( $n$ ), response variable (height or diameter increment:  $D\text{growth}$  or  $H\text{growth}$ ), parameter coefficient estimate and associated P-value.

Model	Seedling type	$n$	Response	Light		Size, $b$	Density, $c$	Mixture, $d$	Status		
				$a_0$	$a_1$				$e_0$	$e_1$	$e_2$
1	Tallest oak	93	Hgrowth	105.72***	3.54**	0.71***		-0.45**	n.i.	n.i.	n.i.
2	Tallest oak	93	Dgrowth	173.59***	0.23	0.10***	-0.79**		n.i.	n.i.	n.i.
3	Tallest beech	105	Hgrowth	85.49***	0.14	0.68***		0.53**	n.i.	n.i.	n.i.
4	Tallest beech	105	Dgrowth	272.15**	0.13	0.08**	-1.49**	1.71**	n.i.	n.i.	n.i.
5	Target oak	169	Hgrowth	122.87***	0.24**	0.53***			-75.02*	-59.78*	-29.16
6	Target oak	169	Dgrowth	126.33	0.25	0.13***	-0.49**				

No coefficient was indicated for parameters that were not significant in the corresponding model.  
 n.i., parameter not included in the model.  
 \* $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

had no significant effect. *Size* showed the greatest impact, followed by *Light* and *Mixture*, corresponding to a response range of 58, 41 and 28 cm, respectively. The model fitted on the tallest oak (Table 2, Model 1) showed one parameter difference with the model fitted on the target oak (Table 2, Model 5), due to *Mixture* substituting *Status* when using co-dominant and dominant seedlings.

The diameter growth of the tallest oaks was significantly affected by *Light*, *Size* and *Density* (Table 2, Model 2). *Mixture* had no significant effect. The different variables had a similar impact, with a response range of 68, 57 and 57 mm for *Size*, *Light* and *Density*, respectively. As for height, the diameter model, fitted on the tallest oak seedlings attributed slightly more importance to *Light* and less to *Size* than the model fitted on diameter growth of the target oaks.

#### Effects of competition, size and light on tallest beech growth

The height growth of the tallest beeches (Table 2, Model 3) included the same significant factors as the model fitted on the tallest oaks (Table 2, Model 1). *Size* showed a major effect, followed by *Light* and *Mixture* (corresponding to a response range of 95, 23 and 27 cm, respectively). For beech, a higher percentage of oak seedlings in the plot was positively correlated with increased seedling growth, in contrast to oak seedlings which showed less growth in oak-dominated mixtures. Light was less important for the tallest beech than for the tallest oak seedlings, as shown by smaller regression coefficients (Table 2).

The diameter growth of beech was significantly affected by all variables: *Light*, *Size*, *Density* and *Mixture* (Table 2, Model 4). The parameters were of similar importance and corresponded to a response range of 79, 119, 87 and 82 mm, respectively. In comparison with the model fitted on oak, *Mixture* had a significant effect.

Figures 1 and 2 show the simulated growth, using *Size*, *Light*, *Mixture*, *Density* and *Status* as input values that correspond to the range of growth values observed for each of the two species. They

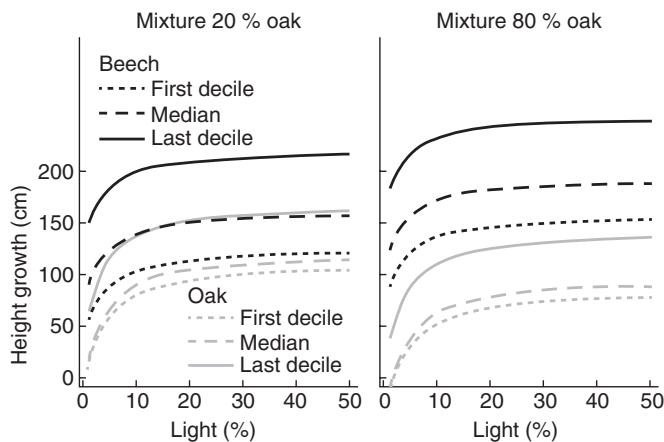


FIG. 1. Simulated 4-year height growth (cm) of the tallest oak and tallest beech seedlings as a function of diffuse radiation percentage (*Light*), according to Models 3 and 5 from Table 2. In each graph, simulated height growth values are drawn for three *Size* values, with initial height fixed at the observed first decile, median and last decile values: 21, 35 and 102 cm, respectively, for oak (grey); -56, 102 and 180 cm, respectively, for beech (black), with *Mixture* set to 20 % oak or 80 % oak.

illustrate the differences in growth between the tallest oak and the tallest beech seedlings. Beech seedlings showed superior growth across all conditions, irrespective of light availability, neighbourhood competition and species composition, for both diameter and height growth. The larger growth observed for beech resulted from a higher growth rate in given conditions of light, mixture and density, but also from larger initial seedling size for beech compared with oak. Finally, although the impact of light availability on seedling growth is stronger for oak than for beech (Table 2, Models 1–4, Figs 1 and 2), oak always has a lower growth rate than beech (even at high light levels).

#### Rank reversals

Potential growth differences between the tallest oak and the tallest beech seedlings for pairs of seedlings were simulated using Models 1–3 (Fig. 3). Simulation was performed using the same initial size, light and competition conditions for both species. Light and competition conditions were set to the median observed values. For initial size, a median value computed on the two species pooled was used, as different median values were observed for the two species.

In the beech-dominated mixture, a reversal in average height growth occurred at 10 % diffuse radiation, but the growth responses of the two species do not differ significantly. In oak-dominated mixtures, beech always showed greater height growth than oak. Diameter growth was always greater for beech in all mixture conditions.

#### Effects of competition, size and light on target oak growth

The height growth of target oak seedlings was significantly affected by *Light*, *Size* and *Status* (Table 2, Model 5). *Mixture* and *Density* had no significant effect. *Status* and *Size* played a major role compared with *Light* and *Mixture* (Fig. 4). This result showed the capital importance of both absolute seedling size and social status, particularly the dominated status, within the population when analysing the growth dynamics. All parameters were positively correlated with height growth, except *Status*, for which the dominant and co-dominant status significant corresponded to lower seedling growth. The dominant level showed the most important negative impact on growth relative to the other *Status* levels.

The diameter growth of target oaks was significantly affected by *Light*, *Size* and *Density* (Table 2, Model 6). Larger annual rings were achieved with increasing light conditions, and the initial size and decreasing number of neighbouring seedlings. The response ranges were 39, 74 and 35 mm for the three variables, respectively. As opposed to height growth, annual ring width was not affected by the proportion of oak seedlings in the plot or by seedling status.

## DISCUSSION

Characteristics of individual seedlings (initial size, status), plot (density, species composition) and local environment (light) appear to be main factors controlling the growth of oak and beech seedlings, two species known for their contrasted growth strategy. These factors should be considered as major drivers of species coexistence in young mixed oak–beech stands.

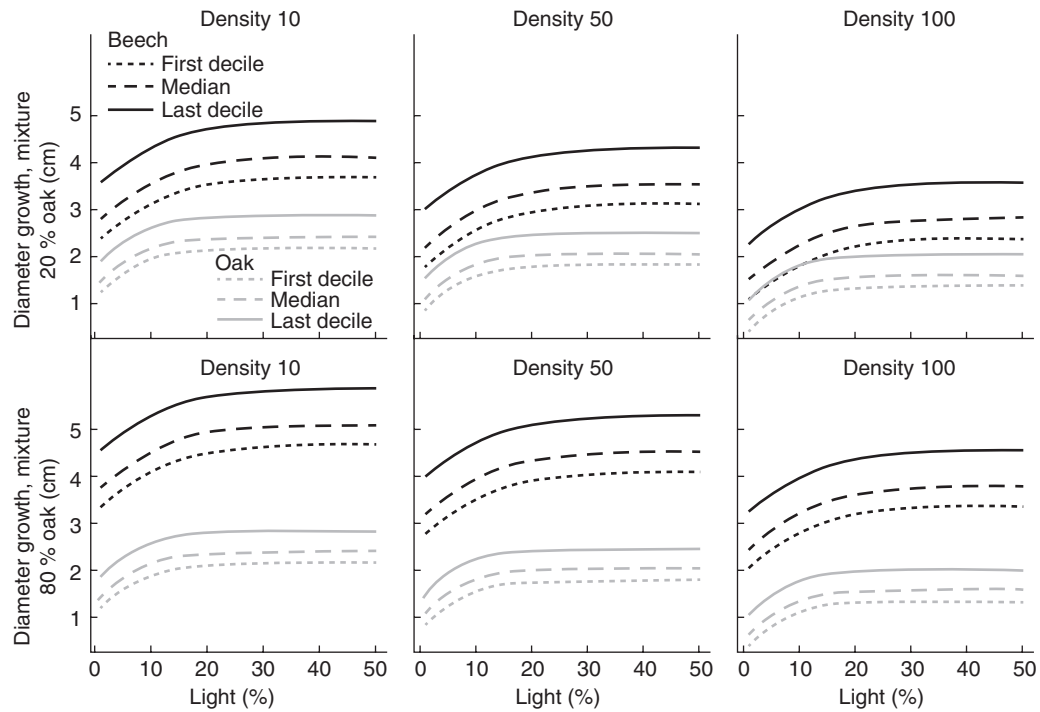


FIG. 2. Simulated 4-year basal diameter growth (cm) of the tallest oak and tallest beech seedlings as a function of diffuse radiation percentage (*Light*), according to Models 4 and 6 in Table 2. In each graph, simulated height growth values are drawn for three values of *Size*, with initial diameter fixed at the observed first decile, median and last decile values (3.1, 6.3 and 12.1 cm, respectively, for oak; 9.3, 14.3 and 23.6 cm, respectively, for beech) and with *Density* set to 10, 50 or 100 seedlings per plot (2 m<sup>2</sup>) and *Mixture* set to 20 % oak (upper graphs) or 80 % oak (lower graphs).

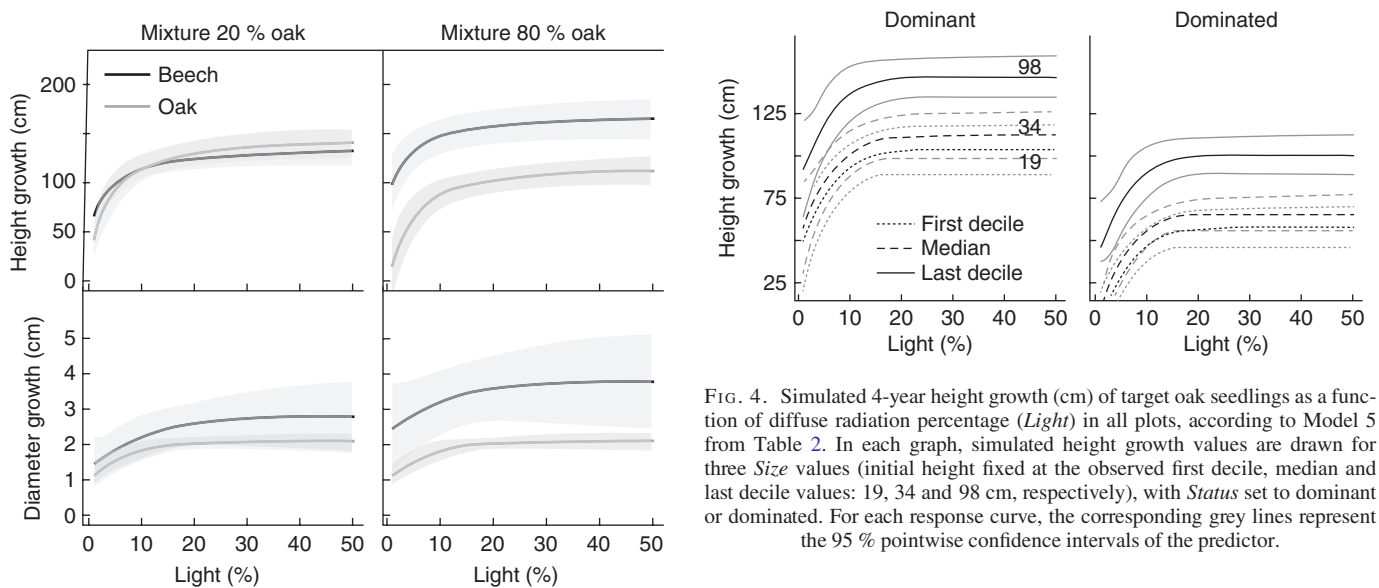


FIG. 3. Simulated 4-year height and diameter growth (cm) of the tallest oak and tallest beech seedlings as a function of diffuse radiation percentage (*Light*), at *Mixture* set to 20 % oak or 80 % oak, according to Models 3–6 from Table 2. In each graph, simulated height growth values are drawn for a fixed *Size* value (initial height, 70 cm for oak and beech; initial diameter, 9 cm for oak and beech) and *Density* fixed to 49 seedlings per plot (2 m<sup>2</sup>). For each response curve, shading lines represent the 95 % pointwise confidence intervals of the predictor.

*Absence of rank reversal*

In this study, no rank reversal occurred between the two species along the different gradients, although large gradients were investigated. First, the investigated light range encompassed the threshold values at which rank reversals might possibly occur (relative light intensity 30–40 %) considering the growth response to



light of the two species (von Lüpke, 1998; von Lüpke and Hauskeller-Bullerjahn, 2004). Secondly, the range of seedling density that was investigated amply bounded density values observed in natural regeneration patches in oak and beech forests but did not contain very low values of density such as those that prevailed in field plantations or in pot experiments. Low densities are not observed in natural conditions under the studied light levels (situations with low tree seedling density may occur, but they are characterized by the presence of an abundant neighbouring vegetation that also competes with the tree seedlings). Thirdly, the range of species composition examined was large and made it possible to analyse the effects of this factor fully. Finally, we focused on a 4-year growth period, a period of time that seems adequate to detect potential rank reversals in 8- to 10-year-old tree seedlings (Sack and Grubb, 2001).

No inversion of species performance occurred along the light gradient, and the shade-tolerant species was always the most competitive species. Potential confounding effects such as seedling size or local competition were taken into account in the analysis. Actually, the introduction of these effects would reinforce the competitive superiority of beech over oak. The lack of rank reversals implies an absence of growth–growth trade-off between the two species along light gradients. In addition, as a strongly shade-tolerant species, beech has a high survival rate under low light levels, in contrast to oak (Hansen *et al.*, 2002; von Lüpke and Hauskeller-Bullerjahn, 2004; Wagner *et al.*, 2010). The lower mortality rate under low light levels combined with higher growth under high light levels of beech compared with oak implies that there is also an absence of mortality–growth trade-off along the light gradient for the two species. Spatial variations in light availability in young forest stands and niche differentiation along this gradient, due either to a growth–growth or to a mortality–growth trade-off, have often been cited as a mechanism enabling the coexistence of shade-tolerant European beech seedlings and shade-intermediate sessile oak seedlings (von Lüpke, 1998; Wagner *et al.*, 2010). The results obtained in the present study do not support this hypothesis. Other mechanisms must be invoked to explain the coexistence of these species, such as differential species response to temporal light availability, potential rank reversals along soil resource or temperature gradients, or potential trade-offs involving other processes (colonization strategy, capacity for vegetative reproduction). In addition to these potential deterministic trade-offs, stochasticity may also contribute to species coexistence. In the present study, all of the models revealed a high degree of individual variability in growth in response to the different factors, as indicated by large overlaps in the confidence intervals of the coefficient estimates of the two species. Wide variability among individuals in relation to the difference between species mean values has been shown to promote species coexistence (Gravel *et al.*, 2006; Clark *et al.*, 2007).

#### *Growth response affected by species composition*

For both species, admixture of the other species had positive effects on seedling growth, and, quantitatively, these effects were of the same order of magnitude as those of light availability. The existence, the sign (positive or negative) and the magnitude of the effects of species mixture on individual tree growth have been shown to be strongly dependent on species identity (Bartelink,

2000; Pretzsch and Schuetze, 2009), and careful control of local tree density and vertical tree stratification is usually needed to test and quantify these effects. The present study made it possible to disentangle the effects of these factors and to show that as long as the seedlings within the mixed population have similar sizes, the mixture is favourable to height growth increment for both species.

Although both species react positively to admixture relative to monoculture, admixture will have opposite long-term effects for the two species. This is a direct consequence of the higher growth rate of beech seedlings, compared with oak. Oak seedlings grow faster in height when they are surrounded by beech seedlings of the same size than when they are surrounded by other oak seedlings. However, oaks surrounded by beech show significantly less diameter growth than their beech neighbours and rapidly important size differences might appear, leading to growth reduction in the future. As a result, although admixture in itself has a positive effect on oak seedlings, the higher growth rate of beech seedlings counteracts this effect, leading to a long-term negative effect of admixture on oak seedling growth. The picture is significantly different for beech. Beech seedlings grow faster in height and in diameter when they are surrounded by oak seedlings of the same size, compared with beech seedlings growing in monospecific plots. This tendency adds to the positive impact of the other factors, and leads to a strong positive long-term global effect of admixture on beech growth.

The opposite long-term effects of admixture on oak and beech development might be explained in relation to different species growth strategies. Beech is considered as a strong competitor (Peters *et al.*, 1992; von Lüpke, 1998). In the present experiment, it shows improved height and diameter growth when surrounded by oak, a less competitive species. Its better growth in mixed plots can be directly related to a higher degree of competitiveness, compared with oak. In contrast, in mixed plots, oak seedlings show greater height growth but unchanged diameter growth, and their response is better explained by an escape strategy. Oak seedlings try to escape lateral competition from their neighbours rapidly by increasing their height growth at the expense of diameter growth (Henry and Aarssen, 1997). Oak seedlings that are not able to escape the competition from neighbouring beech seedlings will most probably not survive more than a few years.

#### *Growth response affected by density*

Negative density-dependent effects on seedling growth occurred for both species. Diameter growth responded to the number of neighbours while height growth was not affected, following the general observation that diameter growth is more sensitive to density than height growth (Lanner, 1985; Collet and Chenost, 2006).

Density had a greater effect on beech than on oak seedlings, leading to reduced height growth differences between the two species. However, even at higher densities, beech was always the more competitive of the two species, and density did not lead to any reversal in their performances, in contradiction to the second hypothesis that was tested.

#### *Growth response affected by initial size and status*

For both species, initial size was the primary factor explaining variations in individual seedling growth, before light and



competition from neighbours, in agreement with the third hypothesis of this study. Social status was of secondary importance. Other studies have recognized the necessity of accounting for initial size and social status of the target tree when predicting growth (D'amato and Puettmann, 2004; Collet and Le Moguedec, 2007; Caquet *et al.*, 2010). Seedling growth was positively related to initial size and dominance status, indicating that small size constitutes a strong handicap. The paramount effect of size and status directly arises as a result of competition in which the tallest individuals obtain a larger amount of the available resources and suppress the growth of smaller individuals (Schwinning and Weiner, 1998).

The pre-eminent effect of initial seedling size, irrespective of the value of the other factors, means that existing intra- and inter-specific size hierarchies among seedlings are rapidly amplified in all conditions. As a result, the growth advantage of beech over oak is strongly reinforced.

Differences in initial size among seedlings in natural conditions may originate from many sources. In the present study, emergence time was probably a first source, as shown by seedling age that varied between 4 and 12 years. All seedlings aged  $\geq 9$  years germinated before the storm opened the canopy gaps, and most of them were beech seedlings. Another potential source of size hierarchies is the difference in early seedling growth between the two species. Due to its large seed size, oak grows rapidly during the first year, even in unfavourable conditions, which may give it an advantage over seedlings from other species that germinate in the same year. However, in the present study, difference in seed size or in initial growth was probably of second order compared with differences in emergence time when explaining differences in initial size among seedlings at the beginning of the study. At the age of 10 (average age in the study), seedlings had the opportunity to overcome these differences.

#### *Conclusions: dynamics of oak–beech regeneration*

Beech was always superior to oak in terms of growth, and no rank reversal occurred along the density and the light gradients. Our results suggest that the spatial variability in light conditions prevailing in regenerating stands does not promote the coexistence of oak and beech.

Pronounced effects of initial size on seedling growth were observed, as in many other studies that model seedling growth. Locally dominant seedlings may maintain their dominance for several years, irrespective of species. Spatial variation in local size hierarchies among seedlings within a mixed stand, with the juxtaposition of patches dominated by oak and patches dominated by beech (Gazol and Ibanez, 2010), should lead to the coexistence of the two species. Local stand history, species life history traits and individual seedling performances are primary causes of the occurrence of size hierarchies among seedlings in regeneration patches (Maltez-Mouro *et al.*, 2009). Identifying and quantifying the relative importance of these different sources of variation would be useful to model the dynamics of mixed regenerating stands and to identify the factors that determine species coexistence during the early stages of stand development.

The management objectives in many mixed oak and beech forests of western and central Europe are to maintain or to

restore oak dominance over beech. It has been recognized that silvicultural operations to favour oak should begin in the early stages of stand development (von Lüpke, 1998). In the present study, oak and beech seedlings were abundant 9 years after canopy disturbance along the whole light gradient, in agreement with previous studies performed in the same biogeographical zone (Degen, 2006; Van Couwenberghe *et al.*, 2010). However, oak was clearly threatened by beech, which appeared to be very competitive. If the silvicultural objective is to maintain oak, beech needs to be controlled in all patches where both species grow in intimate mixture. Regulation of canopy closure and seedling density have been proposed as tools to control the balance between oak and beech seedlings (von Lüpke, 1998; Wagner *et al.*, 2010). Our results do not support this hypothesis since beech always grows better than oak at all light and all density levels. The present study suggests that the only method to control beech in mixed regeneration patches is to remove all dominant and co-dominant beech seedlings. Mixed oak and beech regenerating stands are characterized by high spatial heterogeneity in local seedling composition and local species dominance, and monospecific regeneration patches or patches where oak seedlings are highly dominant may provide future young oak trees without the need for major silvicultural operations.

#### SUPPLEMENTARY DATA

Supplementary data are available online at [www.aob.oxfordjournals.org](http://www.aob.oxfordjournals.org) and consist of Table S1: the  $3 \times 3 \times 3$  contingency table of the sample design.

#### ACKNOWLEDGEMENTS

We would like to thank all of the people who were involved in the establishment and measurement of the sites, as well as data gathering in the laboratory, with special thanks to Frédéric Bordat, René Canta, Fatiha Fifel, Bruno Garnier, Gilles Grisard, Guy Maréchal, Arnaud Metais, Michel Pitsch and Damien Salgues. We thank François Morneau for his programming advice. R.V.C. was funded by a PhD grant from the Lorraine Region and the Office National des Forêts, registered under no. 533-2007.

#### LITERATURE CITED

- Baize D, Girard M-C, Association française pour l'étude du sol. 2009. *Référentiel pédologique 2008*. Versailles: Éditions Quae.
- Baltzer JL, Thomas SC. 2007. Determinants of whole-plant light requirements in Bornean rain forest tree saplings. *Journal of Ecology* **95**: 1208–1221.
- Baraloto C, Goldberg DE, Bonal D. 2005. Performance trade-offs among tropical tree seedlings in contrasting microhabitats. *Ecology* **86**: 2461–2472.
- Bartelink H. 2000. A growth model for mixed forest stands. *Forest Ecology and Management* **134**: 29–43.
- Beaudet M, Brisson J, Gravel D, Messier C. 2007. Effect of a major canopy disturbance on the coexistence of *Acer saccharum* and *Fagus grandifolia* in the understorey of an old-growth forest. *Journal of Ecology* **95**: 458–467.
- Benichou P, Le Breton O. 1987. Prise en compte de la topographie pour la cartographie des champs pluviométriques statistiques. *La Météorologie* **7**: 23–35.
- Boyden SB, Reich PB, Puettmann KJ, Baker TR. 2009. Effects of density and ontogeny on size and growth ranks of three competing tree species. *Journal of Ecology* **97**: 277–288.
- Brown D, Rothery P. 1993. *Models in biology: mathematics, statistics and computing*. Chichester, UK: John Wiley & Sons Ltd.

- Brunner A.** 1998. A light model for spatially explicit forest stand models. *Forest Ecology and Management* **107**: 19–46.
- Canham CD, Finzi A, Pacala S, Burbank D.** 1994. Causes and consequences of resource heterogeneity in forests – interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **24**: 337–349.
- Cannell M, Rothery P, Ford E.** 1984. Competition within stands of *Picea sitchensis* and *Pinus contorta*. *Annals of Botany* **53**: 349–362.
- Caquet B, Montpied P, Dreyer E, Epron D, Collet C.** 2010. Response to canopy opening does not act as a filter to *Fagus sylvatica* and *Acer* sp advance regeneration in a mixed temperate forest. *Annals of Forest Science* **67**: 105
- Clark JS, Dietze M, Chakraborty S, et al.** 2007. Resolving the biodiversity paradox. *Ecology Letters* **10**: 647–659.
- Collet C, Chenost C.** 2006. Using competition and light estimates to predict diameter and height growth of naturally regenerated beech seedlings growing under changing canopy conditions. *Forestry* **79**: 489–502.
- Collet C, Le Moguedec G.** 2007. Individual seedling mortality as a function of size, growth and competition in naturally regenerated beech seedlings. *Forestry* **80**: 359–370.
- D'amato AW, Puettmann KJ.** 2004. The relative dominance hypothesis explains interaction dynamics in mixed species *Alnus rubra*/*Pseudotsuga menziesii* stands. *Journal of Ecology* **92**: 450–463.
- Degen T.** 2006. *Dynamique initiale de la végétation herbacée et de la régénération ligneuse dans le cas de trouées, au sein d'une hêtraie (Luzulo-Fagetum). Quels enseignements tirer de la tempête de décembre 1999 dans les Vosges du Nord?* PhD Thesis, Université Catholique de Louvain, France.
- Denslow J.** 1987. Tropical rain-forest gaps and tree species-diversity. *Annual Review of Ecology and Systematics* **18**: 431–451.
- Dreyer E, Collet C, Montpied P, Sinoquet H.** 2005. Caractérisation de la tolérance à l'ombrage des jeunes semis de hêtre et comparaison avec les espèces associées. *Revue Forestière Française* **57**: 175–188.
- Ellenberg H, Weber H, Düll R, Wirth V, Werner V, Paulsen D.** 1992. Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica* **18**: 1–248.
- Gazol A, Ibanez R.** 2010. Scale-specific determinants of a mixed beech and oak seedling – sapling bank under different environmental and biotic conditions. *Plant Ecology* **211**: 37–48.
- Geßler A, Keitel C, Kreuzwieser J, Matussek R, Seiler W, Rennenberg H.** 2007. Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. *Trees-Structure and Function* **21**: 1–11.
- Gómez-Aparicio L, García-Valdés R, Ruiz-Benito P, Zavala MA.** 2011. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: implications for forest management under global change. *Global Change Biology* **17**: 2400–2414.
- Gravel D, Canham CD, Beaudet M, Messier C.** 2006. Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters* **9**: 399–409.
- Gravel D, Canham CD, Beaudet M, Messier C.** 2010. Shade tolerance, canopy gaps and mechanisms of coexistence of forest trees. *Oikos* **119**: 475–484.
- Grime JP.** 1979. *Plant strategies and vegetation processes*. Chichester, UK: John Wiley & Sons.
- Grubb PJ.** 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Reviews* **52**: 107–145.
- Hansen U, Fiedler B, Rank B.** 2002. Variation of pigment composition and antioxidative systems along the canopy light gradient in a mixed beech/oak forest: a comparative study on deciduous tree species differing in shade tolerance. *Trees-Structure and Function* **16**: 354–364.
- Hara T, Wyszomirski T.** 1994. Competitive asymmetry reduces spatial effects on size – structure dynamics. *Annals of Botany* **73**: 285–297.
- Henry HAL, Aarssen LW.** 1997. On the relationship between shade tolerance and shade avoidance strategies in woodland plants. *Oikos* **80**: 575–582.
- Kitajima K.** 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* **98**: 419–428.
- Kobe RK.** 1997. Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship and growth. *Oikos* **80**: 226–233.
- Kobe RK, Pacala S, Silander J, Canham CD.** 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications* **5**: 517–532.
- Kunstler G, Curt T, Bouchaud M, Lepart J.** 2005. Growth, mortality, and morphological response of European beech and downy oak along a light gradient in sub-Mediterranean forest. *Canadian Journal of Forest Research* **35**: 1657–1668.
- Landolt E.** 1977. Ökologische Zeigerwerte zur Schweizer Flora. *Veröffentlichungen des geobotanischen Institutes der ETH, Stiftung Rübel* **64**: 5–208.
- Lanner R.** 1985. On the insensitivity of height growth to spacing. *Forest Ecology and Management* **13**: 143–148.
- Lebreton JD, Millier C.** 1982. *Modèles dynamiques déterministes en biologie*. Paris: Masson.
- Lilles EB, Astrup R.** 2012. Multiple resource limitation and ontogeny combined: a growth rate comparison of three co-occurring conifers. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **42**: 99–110.
- von Lüpke B.** 1998. Silvicultural methods of oak regeneration with special respect to shade tolerant mixed species. *Forest Ecology and Management* **106**: 19–26.
- von Lüpke B, Hauskeller-Bullerjahn K.** 2004. Beitrag zur Modellierung der Jungwuchsentwicklung am Beispiel von Traubeneichen-Buchen-Mischverjüngungen. *Allgemeine Forst und Jagdzeitung* **175**: 61–69.
- Maltez-Mouro S, García L, Freitas H.** 2009. Influence of forest structure and environmental variables on recruit survival and performance of two Mediterranean tree species (*Quercus faginea* L. and *Q. suber* Lam.). *European Journal of Forest Research* **128**: 27–36.
- Oliver C, Larson BC.** 1996. *Forest stand dynamics*. New York: John Wiley & Sons.
- Peters R, Nakashizuka T, Ohkubo T.** 1992. Regeneration and development in beech dwarf bamboo forest in Japan. *Forest Ecology and Management* **55**: 35–50.
- Petritan AM, von Lüpke B, Petritan IC.** 2007. Effects of shade on growth and mortality of maple (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*) saplings. *Forestry* **80**: 397–412.
- Poorter L.** 1999. Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional Ecology* **13**: 396–410.
- Poorter L, Arets E.** 2003. Light environment and tree strategies in a Bolivian tropical moist forest: an evaluation of the light partitioning hypothesis. *Plant Ecology* **166**: 295–306.
- Pretzsch H, Schuetz G.** 2009. Transgressive overyielding in mixed compared with pure stands of Norway spruce and European beech in Central Europe: evidence on stand level and explanation on individual tree level. *European Journal of Forest Research* **128**: 183–204.
- R Development Core Team.** 2011. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. [www.r-project.org](http://www.r-project.org).
- Rüger N, Berger U, Hubbell SP, Vieilledent G, Condit R.** 2011. Growth strategies of tropical tree species: disentangling light and size effects. *PLoS One* **6**: e25330.
- Runkle J.** 1981. Gap regeneration in some old-growth forests of the Eastern-United-States. *Ecology* **62**: 1041–1051.
- Sack L, Grubb PJ.** 2001. Why do species of woody seedlings change rank in relative growth rate between low and high irradiance? *Functional Ecology* **15**: 145–154.
- Sánchez-Gomez D, Zavala M, Van Schalkwijk D, Urbieto I, Valladares F.** 2008. Rank reversals in tree growth along tree size, competition and climatic gradients for four forest canopy dominant species in Central Spain. *Annals of Forest Science* **65**: 605–605.
- Schwinning S, Weiner J.** 1998. Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* **113**: 447–455.
- Seiwa K.** 2007. Trade-offs between seedling growth and survival in deciduous broadleaved trees in a temperate forest. *Annals of Botany* **99**: 537–544.
- Silander J, Pacala S.** 1985. Neighborhood predictors of plant performance. *Oecologia* **66**: 256–263.
- Silvertown J.** 2004. Plant coexistence and the niche. *Trends in Ecology and Evolution* **19**: 605–611.
- Thomas SC, Bazzaz FA.** 1999. Asymptotic height as a predictor of photosynthetic characteristics in Malaysian rain forest trees. *Ecology* **80**: 1607–1622.
- Tilman D.** 1982. *Resource competition and community structure*. Princeton, NJ: Princeton University Press.
- Tilman D.** 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton, NJ: Princeton University Press.
- Van Couwenberghe R, Collet C, Lacombe E, Pierrat J-C, Gégout J-C.** 2010. Gap partitioning among temperate tree species across a regional soil gradient in windstorm-disturbed forests. *Forest Ecology and Management* **260**: 146–154.
- Wagner S, Collet C, Madsen P, Nakashizuka T, Nyland RD, Sagheb-Talebi K.** 2010. Beech regeneration research: from ecological to silvicultural aspects. *Forest Ecology and Management* **259**: 2172–2182.