

Advance *Fagus sylvatica* and *Acer pseudoplatanus* seedlings dominate tree regeneration in a mixed broadleaved former coppice-with-standards forest

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Summary

This study assessed the species composition and the development of regeneration plots in gaps created by a windstorm in a mixed-species broadleaved stand. The stand was a former coppice-with-standards characterized by a high broadleaved tree species diversity. Thirteen years after gap creation, all gaps were fully stocked and the regeneration was almost exclusively dominated by *Fagus sylvatica* and *Acer pseudoplatanus* seedlings, two species characterized by a high shade tolerance in their early stages. All other species (*Quercus* sp., *Fraxinus excelsior*, *Carpinus betulus*, *Acer campestre*, *Acer platanoides*, *Sorbus torminalis*, *Tilia* sp.) were either absent from the regeneration or completely over-topped by the two dominant species. These features were ascribed to a regime of periodic natural or anthropic disturbance of intermediate intensity, where small gaps are regularly created in the canopy. This regime results in a succession of short, open and closed canopy episodes that eventually promote shade-tolerant species. During this regime, the shade-tolerant species are able to build a strong advance regeneration that is ready to outgrow the other species when gaps are created. If the management objective is to maintain species diversity during the regeneration process, the development of this advance regeneration will have to be strictly controlled.

Introduction

Increasing pressure to maintain or restore mixed-species stands has raised new questions about the management and silviculture of forest stands, especially in the early stages of stand development (Kirby and Patterson, 1992; Puettmann

and Ammer, 2007). Regeneration and establishment are critical stages during which considerable losses in species diversity often occur (Peet and Christensen, 1987; Clark *et al.*, 1999). These stages are usually characterized by a large initial seedling bank that is favoured by a high proportion of unoccupied growing space and a diversity

of microsite characteristics. As the plants increase in size and fill in the available space, competition among plants becomes more intense and the growing conditions become more homogeneous. The initial seedling bank progressively declines, and species diversity may dramatically decrease as the less competitive species are eliminated. One of the major silvicultural challenges when regenerating mixed-species stands is to fully exploit the initial existing species diversity and to ensure that all desired species are kept throughout the regeneration phase.

Gap dynamics theory predicts that gap formation enables species coexistence by producing the necessary abiotic and biotic heterogeneity (Shugart, 1984; Pacala *et al.*, 1996; Laska, 2001). The importance of the gradients in environmental factors induced by gaps varies with their size, their shape and their distribution within the stand. By opening gaps with different structures, foresters may create a wide range of environmental conditions that will favour species coexistence and maintain high species diversity. According to the gap theory, pioneer shade-intolerant species will dominate in large gaps or in the center of intermediate-sized gaps, whereas intermediate and shade-tolerant species will be most successful in small gaps or at the periphery of intermediate gaps (Kneeshaw and Bergeron, 1999; Huth and Wagner, 2006).

The limestone plateaux of northeastern France are dominated by broadleaved stands that were historically managed according to the coppice-with-standards system and began to be converted into high forests some decades ago. These stands are distinguished by a high broadleaved tree species diversity, with many economically valuable species (Decocq *et al.*, 2005). Most of these stands, which are presently reaching maturity, will be regenerated in the next decades, and the main objective is to ensure full site stocking with valuable broadleaves while maintaining the existing species diversity.

These former coppice-with-standard stands typically include a diverse mixture of shade-tolerant (*Fagus sylvatica* L., *Acer pseudoplatanus* L., *Carpinus betulus* L., *Tilia cordata* Mill. and *Tilia platyphyllos* Scop.), intermediate (*Acer platanoides* L. and *Acer campestre* L.) and shade-intolerant species (*Quercus petraea* (Mattus.) Liebl., *Quercus robur* L., *Fraxinus excelsior* L., *Prunus avium* L., *Sorbus torminalis* (L.) Crantz. and *Sorbus aria*

(L.) Crantz.). The regeneration of some of these species has been widely investigated. *Fagus* and *A. pseudoplatanus* seedlings have been shown to be well adapted to shaded or intermediate light conditions (Gardère, 1995; Szwagrzyk *et al.*, 2001; Mountford *et al.*, 2006; Stancioiu and O'Hara, 2006) and to develop an abundant advance regeneration under canopy cover, which is able to rapidly recover active growth after canopy opening (Collet *et al.*, 2001; Wohlgemuth *et al.*, 2002; Nagel *et al.*, 2006). During the early phase of stand development, these two species are known to be very competitive towards most other broadleaved species (von Lüpke, 1998), especially under intermediate light conditions (per cent of above canopy light, PACL, < 30 per cent). *Fraxinus* is also considered as very competitive towards other tree species due to its rapid height growth. However, the development of *Fraxinus* is strongly reduced at lower light levels (Emborg, 1998; Marigo *et al.*, 2000), and its competitive advantage appears only under intermediate or open canopy conditions (PACL > 20 per cent). On the contrary, *Quercus* seedlings have been shown to be poor competitors towards seedlings from other tree species such as *Fraxinus*, *Fagus* or *Carpinus*, as well as to the neighbouring vegetation (Humphrey and Swaine, 1997; Le Duc and Havill, 1998; von Lüpke, 1998; Harmer *et al.*, 2005). In addition to their low competitiveness, *Quercus* seedlings have high light requirements that greatly limit their survival and growth in closed stands (Vera, 2000). The natural regeneration of the other tree species found in these type of stands has not been studied as intensively, and the establishment and growth dynamics of these species and their response to changes in environmental conditions are not precisely documented.

The general objective of the present study is to assess whether the creation of gaps of different sizes will produce the necessary diversity of environmental conditions to successfully regenerate the various species present in the mature stand of a typical former coppice-with-standards stand, without requiring any other silvicultural operations. We selected a mature forest with high species diversity, where gaps of a wide range of sizes had been created by a storm in 1990 and where no silvicultural operations have been performed since the storm occurred. In 2003, 13 years after the storm, an analysis of the regeneration under various canopy closure conditions was

made in order to address two specific questions: (1) does the existing gradient of canopy closure conditions allow the different species to regenerate? and (2) which species dominate along the gradient of canopy closure conditions?

Materials and methods

Study site

The study site was located in the Graouilly forest (49° 04' N, 06° 01' E), ~15 km SW of Metz, in the Lorraine region (northeastern France). The forest was located on a limestone plateau, 300 m.a.s.l. Annual average temperature was 10.1°C and average annual precipitation was 745 mm.

The stand was a former coppice-with-standards broadleaved stand that was managed for timber and firewood production. The last coppice cuts were performed in the 1960s. At that date, the dominant species in the standards were *Fagus* and *Quercus* sp. The stand was subsequently converted into a mixed-species even-aged forest, and coppice cuts were no longer performed. Very few thinning operations on the former reserves had been carried out since the 1960s, and the

basal area had progressively increased. A storm occurred in February, 1990, and created many gaps of various sizes. The stand was not thinned between 1990 and 2003, and no silvicultural operations were performed on the regeneration.

The present study was part of a larger study where we also analysed the relationship between canopy structure and light availability (Piboule *et al.*, 2005). For this study, it was necessary to find a wide range of canopy conditions (closed canopy, small and large gaps) on a small surface area with reduced buffered zones. In 2003, two study plots were established in order to obtain the smallest surface area encompassing the different canopy conditions. The first study plot (1.1 ha) contained small gaps (<200 m²) in a matrix of undisturbed closed stand, and the second study plot (0.15 ha) contained the northern edge of a large gap (0.5 ha) and an undisturbed part of the stand (Figure 1). The distance between the centres of the two study plots was 270 m. Light conditions under the canopy showed important spatial variation, and the percent of above canopy light (PACL defined below) ranged from <1 per cent under the closed canopy to up to 75 per cent in the largest gaps.

In 2003, the total basal area calculated over the two study plots (including the gaps) was 25.6

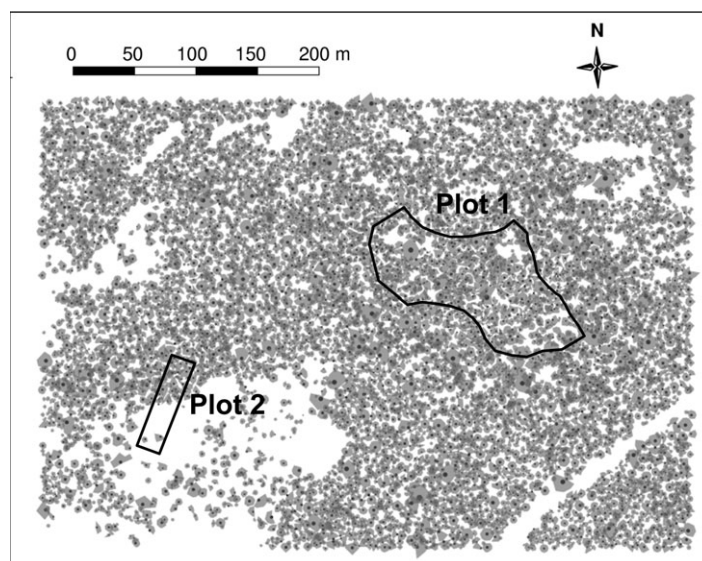


Figure 1. Map of the study area and the two study plots. Study plot 1 contains a closed stand with many small gaps, and study plot 2 is located at the edge of a large gap. On the map, each polygon represents the vertical crown projection of an adult tree.

$\text{m}^2 \text{ha}^{-1}$ and the total density was 550 stems ha^{-1} . Dominant trees (former standards) were mainly beech (*Fagus sylvatica* L., basal area: $3.4 \text{ m}^2 \text{ha}^{-1}$), oak (*Quercus petraea* (Mattus.) Liebl. and *Quercus robur* L., $3.5 \text{ m}^2 \text{ha}^{-1}$), sycamore (*A. pseudoplatanus* L., $1.5 \text{ m}^2 \text{ha}^{-1}$), Norway maple (*Acer platanoides* L., $0.8 \text{ m}^2 \text{ha}^{-1}$) and some scattered wild service trees (*S. torminalis* (L.) Crantz., $0.3 \text{ m}^2 \text{ha}^{-1}$). Due to the high basal area and the high level of competition within the stand, *Quercus* trees were of low vigour and often showed large crown die-back. Coppice was mainly composed of hornbeams (*C. betulus* L., $12.1 \text{ m}^2 \text{ha}^{-1}$) and some field maples (*A. campestre* L., $1.6 \text{ m}^2 \text{ha}^{-1}$), limes (*Tilia cordata* Mill. and *Tilia platyphyllos* Scop., $1.4 \text{ m}^2 \text{ha}^{-1}$) and white beams (*S. aria* (L.) Crantz., $0.7 \text{ m}^2 \text{ha}^{-1}$). Although no *F. excelsior* L. were present in the study plots, several large *Fraxinus* trees were found in the other part of the stand, in close proximity to the study plots (<100 m away).

Regeneration inventory

A regeneration inventory was performed on two series of $2 \times 2 \text{ m}$ quadrat plots:

- A first series of 94 quadrats was established in study plot 1 on a $20 \times 20 \text{ m}$ grid, oriented SSW–NNE. This systematic sampling was established in order to analyse overall regeneration density in the stand, and was representative of the light regime prevailing in the stand. Seventy-six per cent of the quadrats were located under closed canopy conditions (PACL < 5 per cent), and this series of quadrats was not adequate to analyse the effects of light availability on regeneration development because of an insufficient number of quadrats located under intermediate or open canopy conditions (only seven quadrats with PACL > 10 per cent).
- A second series of 245 quadrats was established along transects across several gaps in study plot 1 (183 quadrats) and study plot 2 (62 quadrats) and was used to analyse the effects of understory light availability on regeneration development. In study plot 1, six gaps were selected and three line transects were placed in each gap: the first transect was always oriented SSW–NNE, the second transect, perpendicu-

lar to the first transect, was always oriented WNW–ESE and the third transect, bisecting the first and second transects, was randomly oriented NNW–SSE or ENE–WSW. The line transects crossed the gaps and extended into the surrounding closed stand on both sides. The transect length depended on the geometry of the gap and ranged between 24 and 60 m. In study plot 2, four 60 to 64-m-long parallel transects oriented SSW–NNE (perpendicular to the edge of the gap) were placed from the closed stand into the centre of the gap. In study plots 1 and 2, sampling quadrats were located at 4-m intervals on each of the line transects.

The total number of quadrats was 277 and 62 for study plot 1 and 2, respectively, and 339 for the whole study. The data from the grid and transect plots were pooled, except for the analysis of mean seedling density and mean seedling height across the site, for which only the data from the grid plots were used.

The choice of the quadrat size resulted from observations made during a rapid preliminary inventory in the stand. The preliminary inventory showed that seedling height ranged from <0.05 m to >8 m, and local seedling density from 0 to >100 seedlings m^{-2} . High density values were always found in regeneration patches containing small seedlings. According to standard sampling recommendations, sampling plot size should be large enough to include a minimum number of seedlings and small enough so as not to require excessive measurement time, leading to smaller plots for small trees and/or for dense stands (Spurr, 1952). These observations led to two opposite constraints: (1) restriction of the size of the sampling quadrats in order to avoid sampling a high number of small seedlings over a large surface area, which would considerably increase the time necessary to perform the inventory, and (2) enlargement of the quadrat size, in order to adequately describe the regeneration patches containing tall seedlings.

To allow for these two constraints, we used concentric quadrat plots of two different sizes. At each sampling point, a small inner $1 \times 1 \text{ m}$ quadrat and a big outer $2 \times 2 \text{ m}$ quadrat were established (Figure 2). In the small quadrat, all seedlings were inventoried, regardless of their height. In the remaining 3 m^2 of the full quadrat

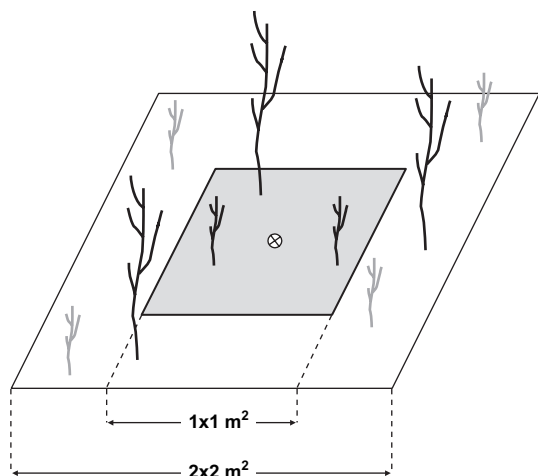


Figure 2. Sampling strategy in the inventory quadrats: in the outer quadrat (4 m²), large seedlings (height ≥ 1.5 m, drawn in black) are measured and small seedlings (height < 1.5 m, drawn in grey) are not taken into account. In the inner quadrat (1 m²), all seedlings are measured, regardless of their height (drawn in black).

(a 50-cm-wide strip around the inner quadrat), only the large seedlings (height ≥ 1.5 m) were inventoried and small seedlings (height < 1.5 m) were not taken into account.

Within each quadrat, and for each selected seedling, the following data were recorded: species, total height (stretched length) and basal diameter (5 cm above the ground). All measurements were performed in May 2003 (13 years after the 1990 storm).

Retrospective analysis of seedling growth

In order to evaluate the age of the seedlings in the regeneration patches, 96 seedlings of the two main species (57 *Fagus* seedlings and 39 *A. pseudoplatanus* seedlings) were harvested in June 2003 and analysed. In order to span a wide range of understory variation in light availability and seedling size, additional line transects across the gaps and extending into the surrounding closed stand were established. In study plot 1, a transect oriented either NNW–SSE or ENE–WSW was placed in four gaps and, in study plot

2, a line transect oriented SSW–NNE (perpendicular to the edge of the gap) was placed between the transect used for the inventory quadrats. The length of each transect depended on the geometry of the gap.

Sample points were placed every 4 m on each transect, and a 1.5-m-radius circular plot was established around each sample point. In each circular plot, the two tallest seedlings (*Fagus* and/or *A. pseudoplatanus*, depending on local species composition) were selected and harvested. The age of each harvested seedling was estimated by combining a ring count at the stem base and an annual shoot count along the stem. This method is well adapted to seedlings that have undergone both periods of active growth and periods of reduced growth in response to changes in environmental conditions (Collet *et al.*, 2002).

A 1-cm-long stem section was cut at the base of each seedling to count the rings. The samples were embedded in carbowax, and a 15- μ m-thick section was cut using a sliding microtome and observed under a microscope. In seedlings showing active growth and well-formed rings, rings were counted on two opposite radii. In seedlings with reduced growth, for which annual rings might be partly or completely missing, rings were examined and counted on the entire section. In seedlings with reduced growth, ring counting led to an underestimation of seedling age.

We tried to identify and count the successive annual growth units along the stem on each seedling. On the apical part of the stems, the scars separating two successive annual growth units were clearly visible. However, on the lower part of the stem, these scars were difficult to identify and led to an underestimation of seedling age.

Seedling age was then estimated for each seedling as the highest value of its ring count and its annual growth unit count.

Characterization of understory light conditions

Understory light conditions prevailing at each inventory quadrat and each retrospective analysis sampling plot were estimated using a light transmission model (Brunner, 1998) supplied with data measured in 2003 in the stand. The model provided an estimation of the PACL (defined as the proportion of photosynthetically active radiation

reaching the top of the canopy that is transmitted by the canopy), calculated 3 m above the ground for each of the various sampling points. The model was supplied only with data representing the adult trees (spatial coordinates and description of the crown extension of each tree) and, therefore, did not take light interception by regeneration or any other understory plants into account. The model was calibrated against PACL values measured using light sensors in the same forest and on plots where no understory plants were present [see Piboule *et al.* (2005), for details about the calibration of the light model in the Graouilly forest].

Light availability was only evaluated in 2003 and was considered to be correlated with the light conditions prevailing in the 13 years following the 1990 storm. Gap closure by the adjacent adult trees probably rapidly began after the storm and induced a progressive reduction in the available understory light. On the basis of a stump inventory made in 2003 in the stand, we could see that all the gaps created in 1990 still existed in 2003. Although it was impossible to quantify the magnitude of the differences between PACL values measured in 2003 and PACL prevailing during the 1990–2003 period, it could be assumed that large values in 2003 corresponded to large gaps created in 1990, small values to small gaps and extremely low values to parts of the stand that remained closed.

Data analyses

The probability of the presence of the main species was related to other characteristics recorded in the inventory quadrats (PACL, seedling density, seedling height) using logistic regression models (Collett, 1991). The logistic model can be written as:

$$\text{logit}(p_i) = \log\left(\frac{p_i}{1-p_i}\right) = \beta_0 + \beta_1 X_i,$$

where p_i is the probability of the presence of the selected species in quadrat i , X_i is the explanatory variable for quadrat i , and β_0 and β_1 are the coefficients of the model. These coefficients are estimated using maximum likelihood. The significance of the predictors was estimated by an analysis of deviance comparing the full model (with the predictor) with the null model (with only the

intercept). Models with different predictors were compared by comparing their deviances (models were established on a common subset of data with no missing value for all predictors).

All calculations, statistical analyses and graphs were performed using the R environment (R Development Core Team, 2007).

Results

Species composition, seedling size

Average seedling density in study plot 1 (calculated using the grid plots) was 59 000 seedlings ha⁻¹. In both study plots 1 and 2 (all 339 quadrats), 11 quadrats contained no seedlings at all and only half of the plots had more than five seedlings. *Fagus* and *A. pseudoplatanus* were the main species: they represented 2/3 of the total number of seedlings (Table 1) and each of them was found in ~60 per cent of the quadrat plots. *Fagus* was the tallest species, with a mean seedling height of 1.7 m, with relatively few small seedlings compared with other species (Figure 3). Mean height for *A. pseudoplatanus* seedlings was 0.7 m, and most *A. pseudoplatanus* seedlings were <0.5 m high.

Carpinus, *A. campestre* and *Acer platanoides* were the next most abundant species, with a density of between 5000 and 10 000 seedlings ha⁻¹. However, these three species were small, and almost no seedlings of *Carpinus*, *A. campestre* or *A. platanoides* reached or exceeded 0.5 m in height. The other tree species found were *S. torminalis*, *Fraxinus excelsior* L., *Sorbus aria* (L.) Crantz, *Tilia* sp., *Quercus* sp., *Ulmus minor* Mill. and *Prunus avium* L. Their density was always below 500 seedlings ha⁻¹ and they were found in <4 per cent of the inventory quadrats.

Seedling age

Estimated age varied between 2 and 35 years for *Fagus* and for *A. pseudoplatanus* seedlings. For both species, ~85 and 15 per cent of the seedlings had germinated before and after the storm, respectively. A loose relationship existed between estimated seedling age and seedling basal diameter (Figure 4), which was similar for *Fagus* and for *A. pseudoplatanus*. This relationship did not

Table 1: Total number of plots where at least one seedling of the species was present, out of 339 measured grid and transect plots; total number of seedlings present, counted over 339 grid and transect plots; mean seedling density calculated over 94 grid plots; mean seedling height (calculated as the mean across the 94 grid plots of the plot-mean seedling height), for each of the 12 species found in the site

Species	Number of plots	Number of seedlings	Density, seedlings ha ⁻¹	Mean height, m
<i>Fagus sylvatica</i>	251	1190	16037	1.68
<i>Acer pseudoplatanus</i>	240	1160	19495	0.72
<i>Carpinus betulus</i>	117	879	10027	0.26
<i>Acer campestre</i>	135	220	7261	0.24
<i>Acer platanoides</i>	82	171	4468	0.15
<i>Sorbus torminalis</i>	13	23	452	0.96
<i>Fraxinus excelsior</i>	19	20	133	4.48
<i>Sorbus aria</i>	15	17	372	1.00
<i>Tilia</i> sp.	12	15	27	1.65
<i>Quercus</i> sp.	12	14	426	0.15
<i>Ulmus minor</i>	4	4	106	0.76
<i>Prunus avium</i>	1	1	106	0.34

make it possible to estimate seedling age from basal diameter measurements. A similar relationship also existed between seedling age and seedling height (data not shown).

Regeneration structure, relationships with PACL

PACL values estimated at 3 m above the ground in the centre of the inventory plots ranged between 0.5 and 75 per cent. The distribution was uneven, and we had no inventory plots with an associated PACL value between 32 and 54 per cent (Figure 5). PACL values >54 per cent were all found in study plot 2.

The number of tree species found in the plots ranged between 0 and 7 species per plot, with a median value of 3 (Figure 5). No clear relationship was observed between PACL and the number of tree species per plot; the number of species remained stable around 3, regardless of the light level. Seedling density ranged between extreme values of 0 and 87 seedlings m⁻², and 90 per cent of the plots had a density between 1 and 16 seedlings m⁻². There was no specific variation trend of seedling density with PACL.

Seedling total basal area showed a considerable variability among plots (Figure 5). It varied between extreme values of 0 and 43 cm² m⁻², with 90 per cent of the plots between 0.1 and 14.2 cm² m⁻². Variability in basal area was considerable at

all PACL values, but a trend of increasing basal area with increasing PACL was observed: for plots with PACL values <10 per cent, the mean basal area value was 3 cm² m⁻², and for plots with PACL values >50 per cent, the mean basal area value was 14.2 cm² m⁻².

Maximum seedling height (height of the tallest seedling in the plot) also varied considerably among plots, regardless of light availability (Figure 5). It varied between extreme values of 0.06 and 9.2 m, with a median value of 2.1 m. When PACL increased between 1 and 80 per cent, maximum height showed a trend toward an optimal value of 6 m for a PACL value of 32 per cent. Plots with PACL values <10 per cent had an average maximum height value of 2 m, and plots with PACL values >50 per cent had an average maximum height value of 3.4 m. Maximum seedling height per plot was poorly related to the number of tree species per plot or to total seedling density per plot (Figure 6).

Species dominance

For the five main species of the regeneration (*Fagus*, *A. pseudoplatanus*, *Carpinus*, *A. campestre* and *A. platanoides*), species dominance was characterized using the species presence (or absence) in the inventory plots and its height relative to the height of the other tree species.

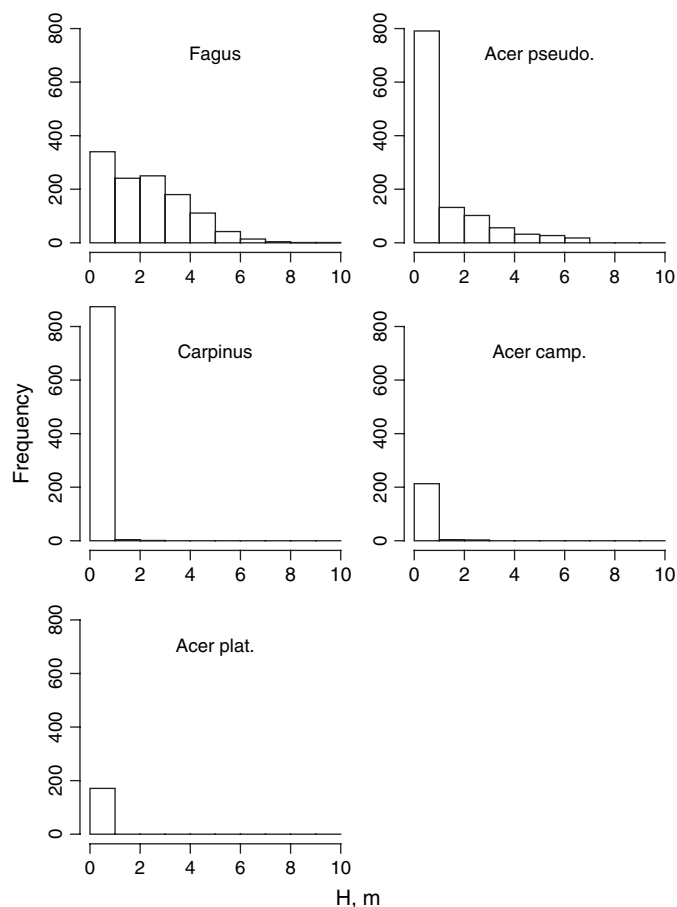


Figure 3. Frequency distribution of seedling basal diameter for the five main species encountered in the inventory quadrats.

The observed probability of presence of the five species was plotted against several variables related to regeneration development in the plot (total seedling density, total basal area, mean plot height and maximum plot height) or against variables describing the growth conditions (PACL). The best relationships were obtained with maximum plot height (height of the tallest seedling in the plot) (Figure 7).

For *Fagus*, the probability of presence was ~0.4 in plots containing only small seedlings (maximum height < 1 m), and rapidly increased when maximum plot height increased. In plots with taller seedlings (maximum height ≥ 2 m), the probability of presence of *Fagus* was close

to 1 (ANODEV probability value for maximum height < 0.0001 for *Fagus*). For *A. pseudoplatanus*, the probability of presence did not change with maximum height and was ~0.7 (ANODEV *P*-value: 0.8). For *Carpinus*, *A. campestre* and *A. platanoïdes*, the probability of presence decreased with maximum plot height. For these three species, the probability of presence in the plots with small seedlings (maximum height < 1m) was 0.3, 0.5 and 0.35, respectively (ANODEV *P*-values < 0.05 for each of the three species).

Similar relationships were established between the probability of presence of the five species and PACL measured in the plots (graphics not shown). Statistically significant values for the

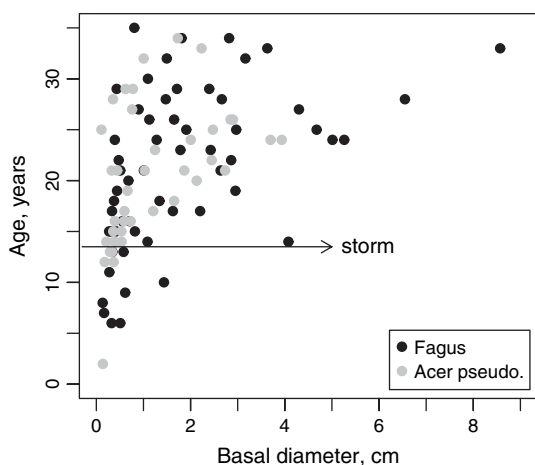


Figure 4. Seedling age as a function of seedling basal diameter, estimated on *Fagus sylvatica* and *Acer pseudoplatanus* seedlings harvested in the stand. The horizontal arrow separates the seedlings that germinated before or after the 1990 storm (above or below the arrow, respectively).

effects of PACL were obtained in the ANODEV for *Fagus* ($P < 0.001$) and for *A. platanoides* ($P = 0.001$): when PACL increased from 5 to 70 per cent, the probability of presence increased from 0.6 to 0.95 for *Fagus* and decreased from 0.3 to 0.1 for *A. platanoides*. For *A. pseudoplatanus*, *Carpinus* and *A. campestre*, the probability of presence was not significantly related to PACL ($P > 0.1$). For each of the five species, the residual deviance was always lower for the model with maximum height than for the model with PACL, indicating that maximum plot height was a better predictor of the species probability of presence than PACL.

In plots with a mean height below 3.5 m, *Fagus* seedlings were generally dominant and had a mean height higher than the mean plot height (all species pooled) and *A. pseudoplatanus* was slightly dominated (Figure 8). In plots with taller seedlings (mean height > 3.5 m), *Fagus* was co-dominant with *A. pseudoplatanus*, with a species mean height close to the plot mean height for both species. When they were present, *Carpinus*, *A. campestre* and *A. platanoides* were generally dominated by other species, and the difference between the species mean height and the plot mean height was greater in plots with tall seedlings.

Discussion

Dominance of Fagus and A. pseudoplatanus seedlings

In 1990, just before the storm, the stand had a large basal area with a closed canopy. It was dominated by *Fagus*, *Quercus* and *Carpinus*, and contained a large number of other broadleaved species. The storm created gaps of various sizes (from 0.01 to 0.5 ha); 13 years after the storm, the regeneration was abundant in the gaps and under the closed canopy and was largely dominated by *Fagus* and *A. pseudoplatanus* seedlings.

A first notable result is the absence of dominant *Quercus* or *Carpinus* seedlings in the study. A number of factors may explain the absence among the dominant seedlings of these two species. The quasi-absence of *Quercus* seedlings in the two study plots (14 *Quercus* seedlings out of a total number of 3714 seedlings measured) is most likely related to the low light levels and to the high inter-seedling competition that existed in most plots after the coppice-with-standards management ended. The low light levels measured in most of the plots probably precluded the long-term survival of *Quercus* seedlings in these plots: only 25 per cent of the plots received > 10 per cent of above canopy light and 15 per cent of the plots received > 20 per cent of above canopy light, which are two threshold values commonly given for the survival and growth of *Quercus* seedlings (Ziegenhagen and Kausch, 1995; von Lüpke, 1998). Most plots with high light availability (PACL > 20 per cent) were characterized by a high competitive pressure among the seedlings (large seedling basal area and tall seedlings). This competition, mainly caused by *Fagus* and *A. pseudoplatanus* seedlings, towards which *Quercus* seedlings have a clear competitive disadvantage, prohibited the development of most *Quercus* seedlings that may have established (von Lüpke, 1998; Vera, 2000). The third factor that may have limited the development of *Quercus* seedlings is browsing. Counts made by the local hunting society indicated an abundance of 12 roe deers per 100 ha in the forest where the study was conducted. At this level of abundance, roe deer usually cause significant damage to young oak seedlings, which are among its

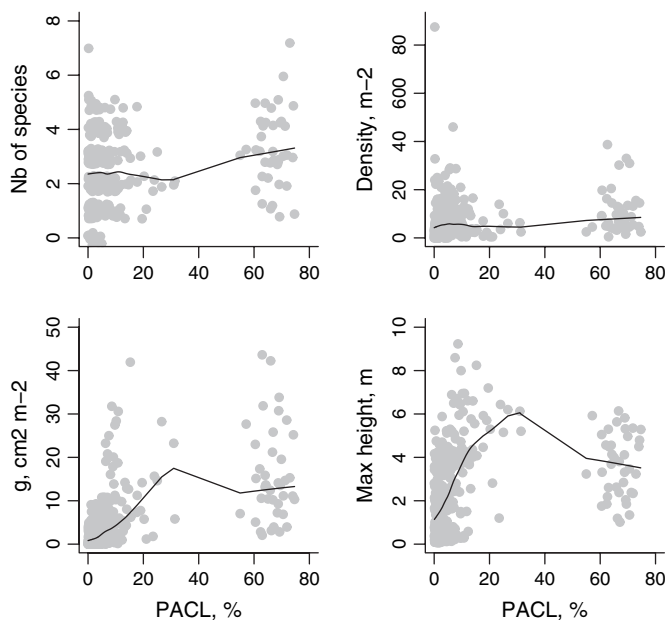


Figure 5. Number of tree species per plot, seedling density, total seedling basal area and maximum seedling height (height of the tallest seedling in the plot), in relationship to the simulated PACL value, 3 m above the ground. In each graph, a local polynomial regression line adjusted on the data (smoother span=2/3) is drawn. In the first graph, jittered values of the number of species were used to separate the overlapped points.

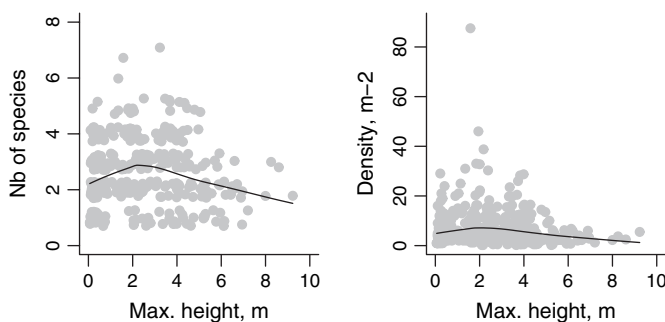


Figure 6. Number of tree species per plot and total seedling density in relationship to maximum seedling height (height of the tallest seedling in the plot). In each graph, a local polynomial regression line adjusted on the data (smoother span=2/3) is drawn. Empty plots (with no seedlings) are not represented because maximum seedling height is not defined for these plots.

preferred species (Harmer, 2001; Drexhage and Colin, 2003; Palmer *et al.*, 2004; Decocq *et al.*, 2005), decreasing the competitiveness of oak seedlings towards the other tree species. Low light availability, high competition among seedlings

and high browsing pressure are three factors that may explain the absence of *Quercus* seedlings among the dominant seedlings, and their relative importance would be difficult to evaluate in our study.

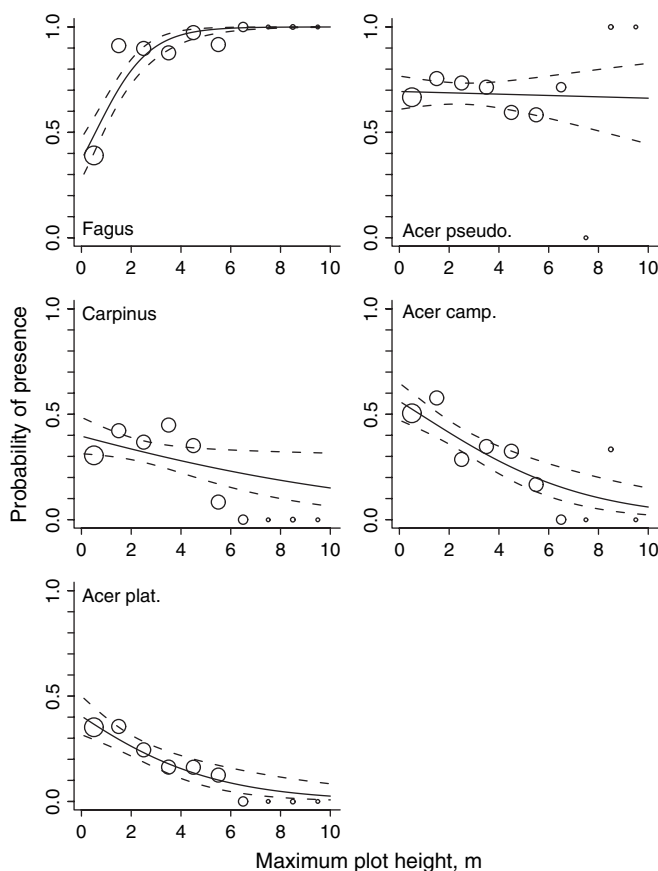


Figure 7. Probability of presence of the five main species encountered in the inventory quadrats (*Fagus*, *Acer pseudoplatanus*, *Carpinus*, *Acer campestre* and *Acer platanoides*) as a function of maximum seedling height (height of the tallest seedling in the quadrat). The dotted lines draw the pointwise asymptotic 95 per cent confidence band for the predictor, and the dots are the observed proportions of presence for quadrats in successive classes of maximum height. For each height class, dot size is proportional to the number of quadrats observed in the class. Empty plots (with no seedlings) are not taken into account because maximum seedling height is not defined for these plots.

Just like *Quercus*, *Carpinus* was also clearly not a dominant species in the regeneration. As for *Quercus*, the existing *Carpinus* seedlings were small (87 per cent of the seedlings were <0.5 m tall). However, *Carpinus* seedlings were much more present (879 *Carpinus* seedlings inventoried in the two study plots). *Carpinus* seedlings were able to germinate and survive for at least a few years, but they were not able to increase in size. Compared with *Quercus* seedlings, *Carpinus* seedlings are more shade tolerant and they are

better competitors, but they are also very attractive to browsers (Le Duc and Havill, 1998). In our study, the high sensitivity of *Carpinus* seedlings to browsing may have been the main factor that limited their development.

Since potential seed trees of other species (*A. campestre*, *Acer platanoides*, *S. torminalis*, *S. aria*, *Fraxinus* and *Tilia*) were present in the study plots or in their close vicinity, these species were also initially expected to be found among the dominant species of the regeneration. Their

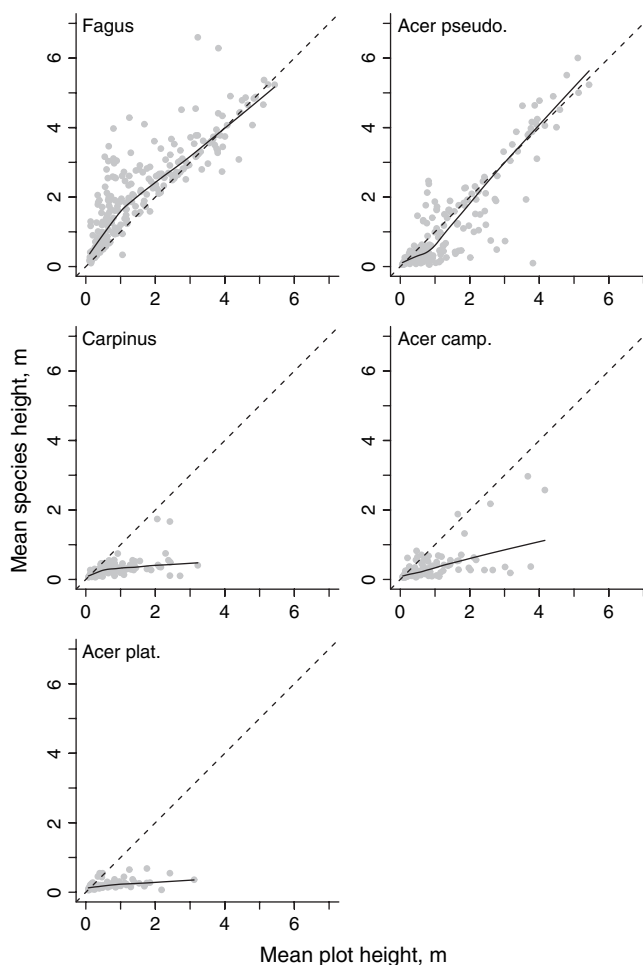


Figure 8. Mean species height (mean height of all seedlings of the species in the quadrat) as a function of mean plot height (mean height of all seedlings in the quadrat), for the five main species encountered in the inventory quadrats (*Fagus*, *Acer pseudoplatanus*, *Carpinus*, *Acer campestre* and *Acer platanoides*). In each graph, the identity line (dotted line) and a local polynomial regression line adjusted on the data (smoother span = 2/3) (solid line) are drawn. For each species, dots corresponding to monospecific plots are located on the identity line.

quasi-absence (*S. torminalis*, *S. aria*, *Fraxinus* and *Tilia*) or their lack of dominance (*A. campestre* and *Acer platanoides*) can also be ascribed to a combination of the same set of factors: low light availability, high competition among seedlings and high browsing pressure. It was not possible in the present study to estimate the relative contribution of these three factors, which most probably varied among the species.

Importance of advance regeneration

In the Graouilly forest, the seedlings that dominated the regeneration were almost exclusively *Fagus* or *A. pseudoplatanus* seedlings. For these two species, advance regeneration accounted for a considerable proportion of the dominant seedlings. We calculated that 85 per cent of the dominant seedlings were already established when the

storm occurred and, since seedling age was probably underestimated (Collet *et al.*, 2002), this is also probably a minimum value.

The importance of advance regeneration after canopy disturbance in some forests has been shown in many other studies (Kneeshaw and Bergeron, 1996; Messier *et al.*, 1999; Antos *et al.*, 2005). To evaluate the prospect for advance regeneration, three stages must be considered: the amount of advance regeneration present before the disturbance, the survival through the disturbance and subsequent survival and growth (Parish and Antos, 2005). In the present study, we considered that the composition and structure of the regeneration in the undisturbed part of the stand remained stable from 1990 to 2003, and the regeneration in the plots under closed canopy inventoried in 2003 was used to estimate the amount of advance recruits present before the 1990 storm. Five species are able to develop and persist under closed canopy: *Fagus*, *A. pseudoplatanus*, *Carpinus*, *A. campestre* and *A. platanoïdes*, which were all present in more than one-third of the plots. Thirteen years after the disturbance, the latter three species were either absent or completely dominated by *Fagus* and *A. pseudoplatanus* in the gap plots, revealing difficulties for these three species to take advantage of openings.

On the contrary, *Fagus* and *A. pseudoplatanus* were able to rapidly adjust to the new open environment and recover active height and diameter growth (data not shown), as has been shown in several earlier studies (Collet *et al.*, 2001; Wohlgemuth *et al.*, 2002; Collet and Chenost, 2006; Nagel *et al.*, 2006). *Fagus* seemed slightly more dominant than *A. pseudoplatanus*, especially in plots with small seedlings. In plots with large seedlings, the two species were strictly co-dominant. These two species are known to have close ecological requirements and similar growth dynamics in their early stages. However, *A. pseudoplatanus* is more sensitive to browsing than *Fagus* (Modry *et al.*, 2004; Cermak and Mrkva, 2006), and this difference may explain the slight advantage of *Fagus* in plots with small seedlings.

The absence of light-demanding species in the gap plots and the lack of significant relationships between the amount of light available in the understory and any of the variables used to describe regeneration development (tree species diversity,

seedling density and total seedling basal area) contradicts the classical gap theory where disturbance events usually promote the development of rapidly growing pioneer species. However, this has already been shown in several North American (Batista *et al.*, 1998; Battaglia *et al.*, 1999; Webb and Scanga, 2001; Harcombe *et al.*, 2002; Kwit and Platt, 2003) or European (Nagel *et al.*, 2006) studies. It has been related to a regime of periodic wind disturbance of intermediate intensity that (1) creates small-sized interconnected gaps in a matrix of undisturbed forest and engenders understory light conditions particularly favourable to pre-established shade-tolerant seedlings and (2) results in a succession of open and closed canopy episodes that eventually promote shade-tolerant species. Periods of closed canopy conditions filter the regeneration against light-demanding species and progressively enrich the stand understory in shade-tolerant species, and subsequent periods of canopy opening enable these seedlings to develop. These successive episodes of canopy opening and closure not only affect the composition of the understory seedling bank but also its structure, with seedlings characterized both by a wide range of sizes and ages, where size and age are not necessarily well correlated.

Implications for management

In the Graouilly forest, the total amount of advance regeneration or new recruits was adequate to fully stock the gaps created by the windstorm. Although the spatial pattern of seedling distribution was highly variable, with distinct clumps of seedlings within larger areas characterized by more regular distribution, very few inventory plots located in the gaps contained <1 seedling m⁻², suggesting that the seedlings were well enough distributed to ensure full stocking with well-spaced stems.

In the closed stand, a large seedling bank of shade-tolerant species (*Fagus*, *A. pseudoplatanus*, *Carpinus*, *A. campestre* and *A. platanoïdes*) existed, whose structure was characterized by a high degree of variability in seedling age and size. Among the species constituting the seedling bank, *Fagus* and *A. pseudoplatanus* seedlings were able to rapidly respond to canopy openings. Because they did not start as germinants, these seedlings

had a competitive advantage over potential competitors from the neighbouring vegetation, showed active height and diameter growth and were rapidly able to fill small gaps. If the management objective is to obtain a mixed *Fagus*–*A. pseudoplatanus* stand, the natural regeneration will effectively provide all necessary material to fully stock the site, with very few silvicultural operations required.

On the contrary, if the management objective is to obtain a more diverse stand, it will be necessary to perform a series of silvicultural operations to counteract the natural dynamics of the regeneration that will otherwise dramatically reduce the tree species diversity existing in the initial seedling bank. The purpose of these tending or cleaning operations would be to reduce the development of the advance of *Fagus* and *A. pseudoplatanus* seedlings and to favour the establishment, survival and growth of other tree species, which may already be present in the seedling bank (*Carpinus*, *A. campestre*, *A. platanoïdes*) or which may appear after canopy opening as new recruits (*Quercus*, *S. torminalis*, *S. aria*, *Fraxinus*, *Tilia*, *Prunus*).

The Graouilly forest is a former coppice-with-standards mixed-species stand, a type of stand that covers a large surface area in northeastern France. The stand presently has a high species and structure diversity and the potential to regenerate into a stand with similar diversity. However, if no silvicultural operations are performed during the regeneration phase to counteract the natural dynamics, this diversity may be lost in a single generation.

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