Growth and mortality of naturally regenerated beech seedlings in relationships with canopy closure and seedling density

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GROWTH AND MORTALITY OF NATURALLY REGENERATED BEECH SEEDLINGS IN RELATIONSHIPS WITH CANOPY CLOSURE AND SEEDLING DENSITY

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Introduction

During the initial phase of naturally regenerated forest stands, great spatial heterogeneity in growth conditions occurs, which affects the growth and survival of tree seedlings. Among the factors showing important spatial variation, light availability and seedling density are two factors that strongly influence seedling growth. Since light availability and seedling density are the factors that may be the most easily regulated through silvicultural actions, they constitute the main tools to control the development of natural regeneration. In order to identify the most appropriate silvicultural action to perform in a given stand to optimize regeneration development, it is therefore necessary to have a good knowledge of the combined effects of light availability and local seedling density on seedling development.

A series of experiments were performed in naturally regenerated beech (*Fagus sylvatica* L.) stands of northeastern France to quantify the effects of canopy opening and local competition on seedling development.

Effects of light availability and local competition on seedling growth

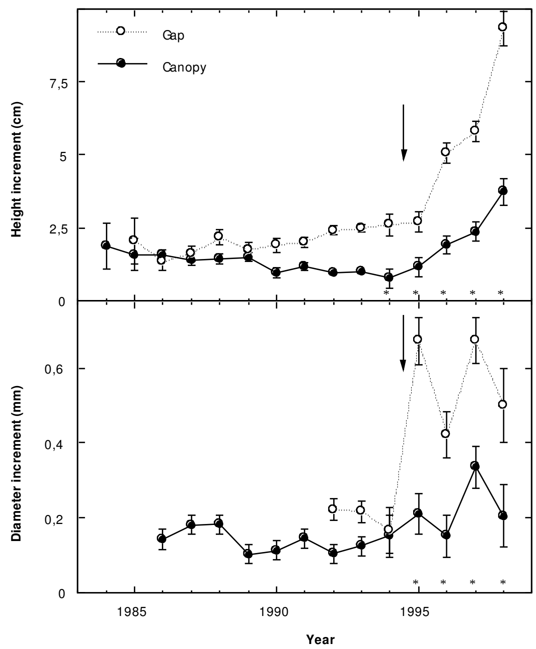
In order to analyze the growth dynamics of beech seedlings growing under changing canopy conditions, a beech stand in which two types of canopy opening (canopy release or gap creation) had been applied in 1995 was selected in 1997 in the Forest of Haye near Nancy. Three and four years after the canopy had been opened, 155 naturally regenerated seedlings were sampled in gaps or under the canopy. Seedling height ranged between 5 and 50 cm, and seedling age between 2 and 19 years. No relationship was found between seedling age and seedling size (height or diameter).

The effects of canopy closure and seedling age on height and diameter growth were analyzed on 113 seedlings using mixed models. Under closed canopy, average annual seedling height and diameter increments were 1.2 cm and 0.18 mm, respectively (Fig.1). Diameter growth increased in the first year after the canopy had been opened, and exhibited considerable inter-annual variation related to climatic conditions. Conversely, height growth did not increase immediately after canopy opening, but increased regularly in the following years. Four years after the gap had been created, annual seedling height and diameter growth were 9.5 cm and 0.49 mm respectively in the gaps, and 3.8 cm and 0.21 mm respectively under released canopy. Age did not affect the dynamics of seedling growth.

A second experiment was conducted in the same stand (Forest of Haye) in order to analyze the combined effects of canopy opening and local competition on seedling growth. In 1997, five regeneration patches located under different canopy closure degrees were selected. Percent of above canopy light (PACL) ranged between 5 and 45%. Two years later (in 1999), the canopy was felled by a storm, and the five patches were under full light (PACL=100%).

The effects of local density were examined using neighborhood analysis. Different competition indices (CI) and neighborhood radii ranging from 10 to 200 cm were tested. Models including PACL and CI accounted for between 0.56 and 0.64% of the variation in individual seedling annual diameter or height growth. Local density had a strong negative influence on diameter growth, and a much smaller influence on height growth. PACL was positively correlated with diameter and height growth before canopy opening. Differed effects of PACL (measured before the storm) on height growth were observed immediately after canopy opening, but disappeared after two years. No differed effects of PACL on diameter growth after canopy opening were observed.

Figure 1: Annual height and diameter increments for seedlings sampled under canopy or in gaps (least-squares mean ±SEM) in the Forest of Haye. The arrow indicates the year in which the canopy was released (seedlings sampled under canopy) or the gaps created (seedlings sampled in gaps). The difference in annual height or diameter increment between the seedlings sampled under canopy and the seedlings sampled in gaps was tested for each year between 1994 and 1998 (*: significant F-ratio at the p<0.05 level of probability).



Mortality in relationship with seedling growth and local competition

The data from the second experiment in the Forest of Haye were used to establish growth-mortality relationships. Logistic models were used to predict the probability of mortality from different combinations of size (height or diameter), growth (height or diameter increment) and competition index (CI). The best models were obtained using (1) diameter increment over the last two years, and (2) CI one year before and initial height (Fig.2).

Effects of canopy opening on seedling morphology

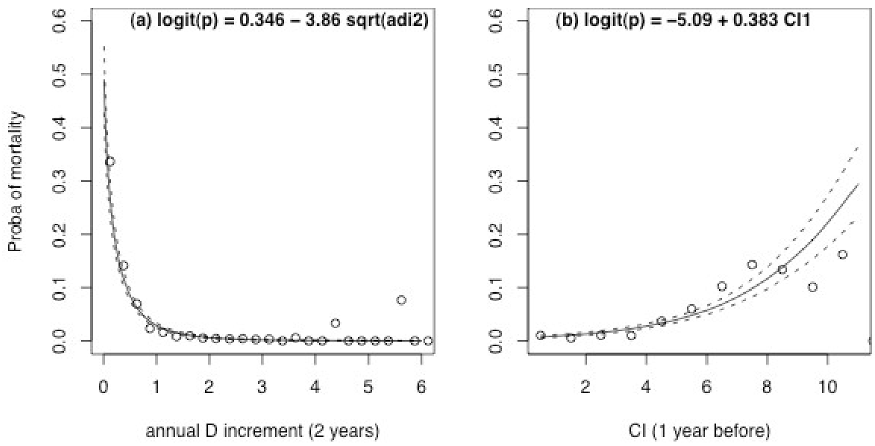
In many mature beech stands, a bank of seedlings exists. We have shown that this advance regeneration is able to recover rapid growth after canopy opening. However, questions remain about the morphological quality of the advance regeneration. Most seedlings that grew under closed canopy developed a typical shade morphology, with plagiotropic axes, large branches and forks, and it is not known if these branching defects will persist or disappear when the mature stand is opened.

A first survey was performed in 2003, in a beech stand that was partly felled by a storm in 1999 (Forest of Saint-Amond). Four years after the storm, 100 beech seedlings were selected in a plot located in a gap, and 100 seedlings in a plot located under closed canopy. It was shown that the seedlings in the gap were able to resume active growth and had less branching defects, compared to the seedlings that remained under closed canopy.

A second experiment was set up in the Graoully Forest, where fifteen 0.75 to 2.4 m-high seedlings growing under closed canopy (PACL=5%) were selected in November 2004. In January 2005, canopy trees were felled around the seedlings and PACL (measured in summer 2005) ranged between 30% and 50%. The elongation and the inclination of the dominant axis and the main branches were measured in January 2005 and in November 2006. One year after canopy opening, the main axis became more vertical for 9 seedlings, less vertical for 5 seedlings and remained unchanged for 1 seedling.

The results from both studies clearly suggest that after canopy opening (1) the morphology of beech seedlings undergo rapid changes and (2) the overall morphological quality of the seedlings improves.

Figure 2: Annual probability of mortality as a function of (a) annual diameter increment (2-year average, adi_2) and (b) competition index (calculated one year earlier as the sum of the squared basal diameter of the neighbors located in a 80-cm-radius disc around the target seedling, CI_1). The equation of the probability function is indicated for each model. The broken lines draw the point wise asymptotic 95% confidence band for the predictor, and the dots are the observed proportions of dead trees in successive classes of annual diameter increment or competition index.



Conclusion

The results gained in this series of experiments may be used in regeneration simulators where the development of beech seedlings is predicted as a function of local intra-specific competition and canopy closure. More data are still needed on the effects of competition and canopy closure on seedling morphology, in order to evaluate the changes in seedling morphological quality, and to predict the ability of the seedlings to produced high quality trees.