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EFFECTS OF CANOPY OPENING ON CARBON BALANCE AND HYDRAULIC CONSTRAINTS IN NATURALLY REGENERATED *FAGUS SYLVATICA* AND *ACER PSEUDOPLATANUS* SEEDLINGS

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Introduction

Beech (*Fagus sylvatica* L) and sycamore (*Acer pseudoplatanus* L) are often found in mixture in the forests of western and central Europe. Natural regeneration is the usual regeneration scheme for these mixed beech-sycamore stands. During the first stages of the regeneration process, seedlings grow under the canopy of adult trees which are progressively removed.

Low light intensities under the forest canopy limit severely growth and survival of tree seedlings. The current consensus is that shade tolerance results from a complex interplay between several traits involving seedling architecture, growth dynamics, carbon gain capacity and carbon balance at individual level, all contributing to seedling survival under low irradiance (Givnish 1988, Messier et al. 1999, Walters and Reich 1999). One of the components of shade tolerance resides in the ability of individuals to optimise carbon gain under low light environments, by maximising light interception and use of the intercepted light, while minimising carbon loss by respiration (Walters and Reich 1999, 2000). Plants in shade have higher light interception efficiency (Sterck, 1999). The photosynthetic capacity of leaves is known to display a large plasticity in response to different levels of irradiance, characterised by a large variety of structural and physiological changes including increased carbon assimilation and respiration, and greater reserve content (Robakowski et al 2003, Gansert and Sprick 1998). In addition, seedlings grown in shade show low hydraulic conductance and high xylem vulnerability to cavitation (Shumway et al. 1993, Cochard et al. 1999). Shade-exposed seedlings express a series of morphogenetic, hydraulic and trophic constraints.

Following canopy opening, changes in microclimatic conditions induce morphogenetic, hydraulic and trophic alterations that might affect seedling carbon balance. The objective of the present study is to assess the responses of naturally regenerated seedlings of beech and sycamore during two years following canopy opening, in terms of growth dynamics and ecophysiological traits. The following hypotheses were tested: (1) canopy opening induces higher height and diameter growth, as shown by Collet et al. (2002); (2) this higher growth is associated with higher assimilation and transpiration of seedlings and with changes in hydraulic traits; (3) the acclimation to high irradiance levels takes several growing seasons.

Materials and Methods

In a deciduous stand of North-eastern France (Graoully forest, Moselle), two mixed regeneration patches containing beech and sycamore seedlings and located under closed canopy were selected. Seedling height ranged between 10 cm and 1m. In January 2005, each of these plots was split in two subplots, one remaining under shade, while the canopy over the other one was removed. A third plot was further selected in a several-year-old gap.

In each species, ten seedlings under canopy (shade seedlings, S), ten in recent gaps (shade to light seedlings, S->L) and three in the old gap (sun seedlings, L) were sampled for ecophysiological measurements.

Relative light intensity reaching the plants was estimated by analysing hemispherical photographs, and seedling 3D architecture was reconstructed after digitizing the seedlings. This enabled to estimate interception of photosynthetically active radiation (PAR) and to simulate seedling photosynthesis and carbon balance. Light-saturated assimilation and stomatal conductance were recorded monthly using an open gas exchange system (LiCor LI6400).

Hydraulic properties were assessed by leaf specific conductance (measured with a high-pressure flow meter, HPFM) and xylem vulnerability to cavitation (measured with a centrifugation technique developed by Cochard et al. (2005)).

Height and diameter of beech and sycamore seedlings growing in gap or under closed canopy were measured on a total of 3415 seedlings in March and December 2005.

Linear mixed effect models with plot as random effect were fitted to test for canopy opening and species effects.

Results and Discussion

Beech and sycamore exhibited an immediate reaction to canopy opening. For sycamore seedlings, mean annual seedling height and diameter increments were 2.42 cm and 0.95 mm respectively one year after canopy opening and 1.45 cm and 0.50 mm respectively under canopy. For beech, height and diameter increments were 5.53 cm and 1.83 mm respectively in gap versus 3.37 cm and 0.54 mm respectively in shade.

During the first year after canopy opening, PAR interception efficiency did not changed significantly in both species. But seedlings of beech exhibited a slight increase of light-saturated CO_2 assimilation (Asat reached 7.10 µmole m^{-2} s^{-1}) and stomatal conductance (gsat reached 0.14 mole m^{-2} s^{-1}), compared to seedlings that remained under close canopy (S plants, Asat and gsat were 5.52 µmole m^{-2} s^{-1} and 0.10 mole m^{-2} s^{-1} respectively). However, for both species, the rates remained much lower than those of sun-acclimated seedlings (L plants, Asat and gsat were 13.59 µmole m^{-2} s^{-1} and 0.37 mole m^{-2} s^{-1} respectively for beech). In addition S->L beech seedlings, contrary to sycamore, show higher stem hydraulic conductance (7.10^{-4} versus 2.10^{-4} kg s^{-1} m^{-2} Mpa^{-1} in average) and higher xylem vulnerability to cavitation than S seedlings. The xylem water potential level producing 50% loss of hydraulic conductivity (PLC50) is higher in S->L plants than in S plants (-3 Mpa versus –4.07 MPa in average).

This results suggested that hydraulic constraints remained high in S->L seedlings. Indeed in the newly created gaps, air evaporative demand was higher leading to higher transpiration rate, compared to the shaded seedlings (S seedlings). However, we show that assimilation and stomatal conductance remained weak compared to seedlings in old gaps (L seedlings). The maintenance of xylem integrity, through stomatal aperture control, might impose a limitation to maximum plant transpiration rates (Cochard et al. 1996, Jones and Sutherland 1991).

Asat and gsat of seedlings from the opened plots (S->L plants) decreased from July to September in both species. This variation was amplified in seedlings from the opened area plots. At the same time, the rate Asat/gsat decreased, suggesting a biochemical limitation of photosynthesis (Grassi and Magnani 2005).

In a next step we will estimate interception of PAR from hemispherical photographs and 3D architecture of seedlings and then simulate saplings photosynthesis and their carbon balance. These simulations will be further compared to measured whole plant gas exchange.

In conclusion, the first year after canopy opening, seedling height and diameter growth were enhanced. However net CO_2 assimilation and transpiration increased slightly compared to S plants. This might be linked to persistence of hydraulic constraints. Then, light acclimatisation would take more one growing season.

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