

Six-year time course of light-use efficiency, carbon gain and growth of beech saplings (*Fagus sylvatica*) planted under a Scots pine (*Pinus sylvestris*) shelterwood

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Summary Two-year-old *Fagus sylvatica* L. saplings were planted under the cover of a *Pinus sylvestris* L. stand in the French Massif Central. The stand was differentially thinned to obtain a gradient of transmitted photosynthetically active radiation (PAR_t ; 0–0.35). Eighteen *Fagus* saplings were sampled in this gradient, and their growth (basal stem diameter increment) was recorded over six years. Over the same period, morphological parameters (leaf area, number and arrangement in space) were monitored by 3D-digitization. Photosynthetic parameters were estimated with a portable gas-exchange analyzer. Photosynthesis was mainly related to light availability, whereas sapling morphology was mainly driven by sapling size. Annual stem diameter increment was related to the amount of light-intercepting foliage (silhouette to total leaf area ratio (STAR) \times total sapling leaf area (LA)) and light availability above the saplings (PAR_t). However, light-use efficiency, i.e., the slope of the relationship between STAR \times LA \times PAR_t and stem diameter increment, decreased over time as a result of a relative decrease in the proportion of photosynthetic tissues to total sapling biomass.

Keywords: forest regeneration, leaf nitrogen content, photosynthetic parameters, silhouette to total leaf area ratio (STAR).

Introduction

In France, and more generally in Europe, the use of shelterwood or partial cutting is becoming increasingly widespread, particularly to establish shade-tolerant late-successional spe-

cies such as *Fagus sylvatica* L. (Balandier et al. 2004). This practice aims to keep a sufficient number of adult trees in the overstorey to prevent the development of the most competitive light-demanding species of the understorey vegetation while allowing tree seedling and sapling growth, although not at maximum rates (Schütz 2004, Balandier et al. 2006). Therefore, optimal use of shelterwoods requires detailed information on the light requirement or shade tolerance of species.

Reductions in tree seedling and sapling growth in response to shade have been widely reported (e.g., Loach 1970, Canham 1988, Givnish 1988, Welander and Ottosson 1998, Walters and Reich 2000a). Shade-intolerant species have greater growth potential in high light than shade-tolerant species, whereas shade-tolerant species are sometimes reported to have higher growth potential in low light, but not always (Walters and Reich 1999, 2000a, Portsmouth and Niinemets 2006). Young seedlings have various adaptive responses to shade, such as: preferential investment of biomass in leaves resulting in a high leaf mass or area ratio (a characteristic response of shade-intolerant species), or conversely, a reduction in growth as a result of preferential investment of biomass in stems or roots for carbon storage (low leaf mass ratio, shade-tolerant species); a reduction in respiratory costs and maintenance of a positive carbon balance; a spatial arrangement of leaves that limits self-shading; and a low light compensation point and dark respiration rate allowing net carbon gain even at low light availabilities (Planchais and Sinoquet 1998, Messier et al. 1999, Walters and Reich 1999, 2000b, Collet et al. 2002, Valladares et al. 2002, Poorter et al. 2003, Craine and Reich 2005). Globally, there is a general trade-off between the ability

to survive in low light and to grow rapidly in high light (Walters and Reich 1999, Sanchez-Gomez et al. 2006). An increasing number of recent studies have shown that many of the traits that are supposed to confer shade tolerance in some species are highly dependent on ontogeny and seedling or sapling size (Sack and Grubb 2001, King 2003, Delagrangé et al. 2004, 2006, Niinemets 2006, Kneeshaw et al. 2006). However, data on morphological and physiological responses to light of saplings over long periods are scarce. Furthermore, most data come from experiments with seedlings in pots under shading nets that provide a diffuse light with a distribution quite unlike that in the forest understory (e.g., Delagrangé et al. 2006).

These experimental conditions make it difficult to link the rate of plant growth unequivocally to particular morphological or physiological traits. Canopy enclosure systems allow monitoring of gas exchanges of a whole tree at the seasonal scale (Daudet 1987), but they are rarely used in forests because of the technical difficulties associated with in situ measurements. Therefore, gas exchange measurements are often made on only a small sample of leaves and over a short period of time (Ceulemans and Saugier 1991). Linking growth to total leaf area (LA), or better still, to the amount of intercepted light, should provide more integrative measures of whole-canopy and whole-season variations than point photosynthetic measurements. This approach was attempted with success by Cannell et al. (1987) on willow. Growth or biomass production (G) can be linked directly to light absorption or interception (I) through a coefficient of light-conversion efficiency (ϵ):

$$G(t) = \epsilon I \Delta t \quad (1)$$

where Δt is the time interval (Monteith 1977).

Canopy light interception has been assessed by various techniques, from aerial photographs to rough estimates of the exposed crown area of adult trees (percentage of tree canopy not overtopped by any other tree; Wyckoff and Clark 2005) to detailed descriptions of leaf distribution and orientation by 3D-digitizing techniques for younger trees (Sinoquet et al. 1998, Farque et al. 2001).

The objective of our study was to analyze the growth of *F. sylvatica* saplings in relation to photosynthetically active radiation (PAR) availability over a six-year period and to test the assumption that sapling size significantly changes morphological and physiological traits associated with shade-tolerance mechanisms. The response to light was divided into two components: (1) the efficiency with which light is intercepted as determined by the 3D-digitizing technique; and (2) the efficiency with which carbon is incorporated into carbohydrates as determined by measurements of the main photosynthetic variables. We also explored the applicability of the light-conversion efficiency approach as a means to analyze growth variations according to sapling size. *Fagus sylvatica* saplings were grown in natural conditions in the French Massif Central under a heterogeneous cover of *Pinus sylvestris* L. that provided different light availabilities.

Material and methods

Study site

Measurements were performed in a 25-year-old natural *P. sylvestris* stand in the Chaîne des Puys, a mid-elevation volcanic mountain range situated in the Auvergne region of France (45°42' N, 2°58' E). The elevation of the forest stand studied is 900 m a.s.l. The climate is montane with oceanic influence in the Western part of the range. Mean annual rainfall is about 820 mm, and for the years of measurement (2001–2004 and 2006), rainfall during the growing season (May to September) was 416, 424, 306, 496 and about 400 mm, respectively. The year 2003 was characterized by severe droughts. Mean annual temperature was about 7 °C. The year 2003 was uncharacteristic, with unusually high summer temperatures: mean daily June to August temperature of 18.6 °C versus 15.3 and 15.0 °C in 2001 and 2002, respectively. The soil is developed on volcanic ash and belongs to the Andisol family, with a pH of 6.0 and a rich organic upper layer (Prévosto et al. 2004). Nutrients are fully available, with a CEC of 33 mEq per 100 g (Curt et al. 2005), and in most years, with the exception of 2003, tree growth was not limited by soil water (Balandier et al. 2004).

Experimental design

Two-year-old bare root *Fagus sylvatica* saplings from a local nursery were planted in November 2000 in a *Pinus sylvestris* stand that had been thinned to different degrees (final density varying from 500 to 4000 stem ha⁻¹) to obtain a gradient of transmitted solar radiation in the understory. Based on this gradient, 18 *F. sylvatica* saplings were sampled over the PAR transmittance range of 0.1 to 0.4. When present, the herbaceous vegetation within a 0.5 m radius around the sapling was cut at ground level.

Measurements

Fagus sylvatica stem basal diameter was measured with a caliper rule at the end of each growing season from 2001 to 2006. For each sapling, measurements at right angles were averaged.

Transmitted solar irradiance above each *F. sylvatica* sapling was measured three times (in 2001, 2005 and 2006) with tube solarimeters (300–3000 nm) in 2001, and PAR quantum sensors (400–700 nm) in 2005 and 2006. Measurements were made over a 24-h period. Transmittance was thus the ratio of values measured in the understory to incident values measured during the same 24 h in an open area. All transmittance data are given for the PAR range based on the relationship described by Sonohat et al. (2003) to convert transmitted total solar radiation (300–3000 nm; TSR_t) to transmitted PAR (PAR_t) under the cover of *P. sylvestris* ($PAR_t = 0.8903 TSR_t$, $r^2 = 0.99$). Between 2001 and 2006, transmittance decreased by about 0.07 for all saplings. Therefore, the transmittance values for years where light was not measured (i.e., 2002, 2003 and 2004) were linearly extrapolated from the 2001 and 2006 values. Values in 2006 ranged from 0.033 for the most shaded sapling to 0.34 for the most well lit sapling.

The canopy structure (i.e., arrangement of leaves in space) of the 18 *Fagus* saplings was described each year in July (after full leaf expansion) from 2001 to 2004 and in 2006 based on a 3D-digitizing technique (Sinoquet and Rivet 1997) and software Pol95 (Adam 1999). The position and orientation of each leaf in 3D-space were recorded in the field with a digitizing device including a pointer (Polhemus 1993). The operator digitizes each leaf with the pointer located at the junction between petiole and lamina and set parallel to the lamina plane and the midrib (Sinoquet et al. 1998). In this way, azimuth, the inclination angle of the midrib and the rolling angle of leaf lamina around the midrib are recorded. In addition, the length (L) and width (W) of each leaf were measured to calculate the leaf surface area (LA): $LA = kLW$, where k is a parameter; this relationship has been shown to be highly accurate for *F. sylvatica* (Planchais and Sinoquet 1998). Based on these data, sapling leaf number, sapling LA, mean LA and mean leaf inclination were calculated for each year.

Light-interception efficiency (LIE) can be assessed as the ratio between LA projected orthogonally in the direction of the light source and total LA. This ratio is often named STAR (silhouette to total LA ratio). A STAR value of 1 means that there is no overlap among leaves and that all leaves are arranged perpendicular to incoming light. The STAR values were computed with the free software VegeSTAR (Adam et al. 2002) available at <http://www2.clermont.inra.fr/piaf/eng/download/download.php>. VegeSTAR combines visualization features of the 3D-digitized plants with image processing subroutines, which allows estimation of the projected foliage area in any view direction. The STAR values are directional and must be integrated over the whole sky vault ($STAR_{sky}$) to take into account radiation from all directions. A "turtle" arrangement, dividing the sky into 46 solid angles of similar size, was used (den Dulk 1989). The STAR values were calculated for the central directions (Ω) of the 46 solid angles. The contribution of each solid angle to incident radiation above the tree saplings is likely to change because of directional changes in both gap fraction $P_o(\Omega)$ of the pine canopy above the saplings and incident radiation above the pine canopy $I_o(\Omega)$. As a result, the sky-integrated $STAR_{sky}$ value was computed as:

$$STAR_{sky} = \frac{\sum_{\Omega=1}^{46} I_o(\Omega)P_o(\Omega)STAR(\Omega)}{\sum_{\Omega=1}^{46} I_o(\Omega)P_o(\Omega)\sin(h_{\Omega})} \quad (2)$$

where h is the elevation angle associated with direction Ω . The denominator in Equation 2 indicates that $STAR_{sky}$ is defined with respect to a horizontal surface, i.e., where $STAR(\Omega)$ is $\sin(h_{\Omega})$.

Gap fraction $P_o(\Omega)$ was computed from a fisheye photograph taken above each sapling. Photographs were digitized with the software PiafPhotem (UMR PIAF, INRA, France). Otherwise, incident radiation above the pine canopy $I_o(\Omega)$ was assumed to obey the standard overcast (SOC) distribution.

Leaf photosynthetic capacities were determined with an

LI-6400 gas-exchange analyzer (Li-Cor, Lincoln, NE). Because preliminary measurements of leaf photosynthesis made on several leaves of the same sapling showed no significant variation, only one leaf per sapling located in the upper part of the sapling and in full sun was sampled at the end of July (after full leaf expansion) of each year, except for 2003 where unusually high July temperatures prevented accurate measurement. Thus, the mean of a measurement in June and a measurement in early September was used for 2003, after having checked in 2001 and 2002 that photosynthesis variables were constant from June to September (data not shown) as in previous studies (Parelle et al. 2006). Maximum carboxylation rate (V_{cmax} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) and maximum electron transport rate (J_{max} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) were derived from assimilation (A)/internal CO_2 concentration (C_i) curves (10 to 15 points per curve with C_i ranging from 10 to 190 Pa). During measurements, light and temperature were set at $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ and 25°C , respectively. Dark respiration (R_d ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) was estimated by direct measurements about 20 minutes after switching off the illumination of the Li-Cor chamber in 2001–2003 or by extrapolation of the A/C_i curves in 2004 and 2006. Leaves were collected immediately after measurements to determine dry matter and nitrogen (N) concentration. Each leaf was dried by lyophilization before quantification of N with an elemental micro-analyzer. The amount of N was then divided by LA to express N concentration on an area basis (N_a) or by leaf dry mass to express N concentration on a mass basis (N_m).

Data analysis

Fagus sylvatica sapling growth variables, morphological variables (i.e., sapling LA, leaf number, mean LA, mean leaf angle and $STAR_{sky}$) and photosynthetic variables were related to PAR_t and year of growth by multifactor analysis of variance (ANOVA). The PAR_t (mean of the 6 years) was divided into three classes (0–0.1, 0.1–0.2 and 0.2–0.37) to balance the size of each class (6, 6, 6). The variances of each class were not statistically different (Cochran's C test). A type III error calculation was used in the ANOVA. The light by year interaction was included in the model. When the ANOVA result was significant, means were separated by a Newman-Keuls test (significance threshold set at 5%). Sapling stem diameter was the covariable in an analysis of covariance (ANCOVA) to take into account a possible sapling size effect on all studied variables. Area-based leaf nitrogen concentration and V_{cmax} were related to PAR_t and N_a , respectively, by nonlinear regressions. As the product of PAR_t with $STAR_{sky}$ represents relative foliar irradiance, it was used to predict N_a . Annual stem diameter increment was linked to the product $PAR_t \times STAR_{sky} \times LA$. Individually, none of these variables gave higher r^2 values than their product. The different variables are also not independent and cannot be used in a multiple regression. The product is a means to express light interception by saplings at the season scale. By analogy to Monteith's research (Equation 1), the slope of the regression can be regarded as an expression of ϵ .

Results

Fagus sylvatica sapling growth

One year after planting, there was no difference in basal stem diameter between the three light classes, but there was a significant difference after 6 years because the saplings at the higher PAR_t had approximately 1.5-fold larger diameters than the other saplings (Table 1). The annual basal stem diameter increment increased significantly with the PAR_t class, but differences between classes, although maintained, were less marked when stem diameter was set as a covariable in the analysis, indicating that diameter increment is affected by sapling size (Table 1). There were interannual variations in diameter incre-

Table 1. Mean beech sapling growth values relative to transmitted photosynthetic active radiation (PAR_t) divided into three classes and year of growth after planting in November 2000. Abbreviations: BSD_1 and BSD_6 , basal stem diameter at the end of the first and sixth year, respectively; INC, annual basal stem diameter increment; and INC_d , annual basal stem diameter increment with diameter as a covariable. Different letters indicate significant differences between means ($\alpha = 0.05$).

	BSD_1 (mm)	BSD_6 (mm)	INC (mm)	INC_d (mm)
PAR_t 0–0.1	6.8	16.3 a	1.7 a	2.2 a
PAR_t 0.1–0.2	7.2	22.5 b	2.7 b	2.3 a
PAR_t 0.2–0.35	7.3	26.9 b	3.8 c	2.9 b
Year 2001			1.5 A	3.0 C
Year 2002			3.4 CD	3.8 D
Year 2003			2.2 AB	2.2 B
Year 2004			2.7 BC	1.9 AB
Year 2006			4.1 D	1.5 A
<i>P</i> value PAR_t	0.68	0.0037	< 0.0001	0.0042
<i>P</i> value Year			< 0.0001	< 0.0001
<i>P</i> value PAR_t × year			0.0008	< 0.0001

ment, with years 1, 3 and 4 yielding a smaller diameter increment. The interaction between light class and year was significant, mainly because the positive effect of light on growth increased with time after planting.

Morphological sapling variables related to light interception

Generally, PAR_t and year after planting significantly influenced mean sapling total LA, mean sapling leaf number (PAR_t not significant for this variable), mean LA, mean leaf inclination and mean $STAR_{sky}$ (Table 2). The light × year interaction was significant for sapling total LA and mean LA because of the much larger values for these variables in 2006. Leaf number and LA increased with year. Leaf inclination increased significantly with higher PAR_t values (more vertical leaves with increasing light), whereas leaf angle showed only slight variations with years. Values of $STAR_{sky}$ were significantly greater for the first class of PAR_t (0–0.1) and decreased with year, and this decrease was more marked for year (0.67 to 0.48) than for light (0.64 to 0.56). Stem diameter set as a covariable in the analysis had a significant effect on total sapling LA ($P < 0.0001$), leaf number ($P < 0.0001$) and $STAR_{sky}$ ($P = 0.0022$), but not on mean LA ($P = 0.24$) and leaf inclination ($P = 0.30$).

Fagus sylvatica leaf photosynthetic capacity

Leaf nitrogen concentration on an area basis increased significantly with PAR_t (Table 3, Figure 1). There were slight variations according to year, with 2002 and 2001 showing the smallest and the largest N_a , respectively. Differences were much smaller for N_m . Leaf dry matter content per area (M_a) increased with PAR_t , and no year-related variation was recorded for 2002 to 2006 (data for 2001 not available). Maximum leaf carboxylation rate, J_{max} and R_d increased slightly with PAR_t (Table 3). Year did not influence J_{max} , whereas V_{cmax} increased with year and R_d was significantly lower in 2002 and 2003 (2004 data not available). When significant, the light × year interaction was due to the absence of significant variation between PAR_t classes in the first year (2001), which was not the

Table 2. Mean values of beech-sapling morphological variables relative to transmitted photosynthetically active radiation (PAR_t) and the year of growth after planting. Abbreviation: $STAR_{sky}$, silhouette to total leaf area ratio integrated on the whole sky vault. Different letters indicate significant differences between means ($\alpha = 0.05$).

	Sapling total leaf area (m ²)	Leaf number	Leaf area (cm ²)	Leaf inclination (°)	$STAR_{sky}$
PAR_t 0–0.1	0.406 a	378	9.1 a	15.6 a	0.64 b
PAR_t 0.1–0.2	0.710 b	572	9.1 a	18.0 b	0.55 a
PAR_t 0.2–0.35	0.754 b	479	11.2 b	20.1 c	0.56 a
Year 2001	0.074 A	118 A	6.4 A	15.8 A	0.67 C
Year 2002	0.163 A	205 A	8.1 B	19.9 B	0.60 B
Year 2003	0.255 A	297 A	8.8 B	19.8 B	0.59 B
Year 2004	0.452 A	506 B	9.0 B	19.6 B	0.59 B
Year 2006	2.174 B	1255 C	16.8 C	14.5 A	0.48 A
<i>P</i> value PAR_t	0.0084	0.099	0.0025	< 0.0001	< 0.0001
<i>P</i> value Year	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
<i>P</i> value PAR_t × year	0.0014	0.33	0.0063	0.7076	0.19

Table 3. Mean values of beech sapling photosynthetic variables relative to transmitted photosynthetically active radiation (PAR_t) and year of growth after planting. Abbreviations: N_a , leaf nitrogen concentration per unit area; N_m , leaf nitrogen concentration per unit mass; M_a , leaf dry matter content per unit area; V_{cmax} , maximum leaf carboxylation rate; J_{max} , maximum electron transport rate; and R_d , dark respiration rate. Different letters indicate significant differences between means ($\alpha = 0.05$).

	N_a ($g\ m^{-2}$)	N_m ($g\ g^{-1}$)	M_a ($g\ m^{-2}$)	V_{cmax} ($\mu mol\ m^{-2}\ s^{-1}$)	J_{max} ($\mu mol\ m^{-2}\ s^{-1}$)	R_d ($\mu mol\ m^{-2}\ s^{-1}$)
PAR_t 0–0.1	0.89 a	2.33 a	35.4 a	27.6 a	68.5 a	–0.69 a
PAR_t 0.1–0.2	1.13 b	2.59 b	43.0 b	38.7 b	90.6 b	–0.73 a
PAR_t 0.2–0.35	1.28 c	2.51 b	52.2 c	37.3 b	89.5 b	–0.93 b
Year 2001	1.18 B	–	–	30.3 A	83.5	–1.00 C
Year 2002	0.98 A	2.43	40.6	32.8 A	88.5	–0.43 A
Year 2003	1.11 AB	2.59	43.0	30.2 A	78.7	–0.73 B
Year 2004	1.11 AB	2.39	45.7	37.7 B	87.7	–
Year 2006	1.11 AB	2.49	44.9	41.7 C	75.8	–0.96 C
P value PAR_t	< 0.0001	0.0006	< 0.0001	< 0.0001	< 0.0001	0.0094
P value Year	0.0258	0.21	0.20	< 0.0001	0.19	< 0.0001
P value PAR_t × year	0.003	0.098	0.90	0.0001	0.0003	0.059

case for the following years (examples for N_a and V_{cmax} given in Figures 1 and 2). The V_{cmax} was logarithmically significantly linked to N_a , with some limited differences between years (same slope, $P = 0.81$, but different origins, $P < 0.0001$; Figure 2). The stem diameter covariable was significant on N_a ($P = 0.0002$), M_a ($P = 0.0053$) and V_{cmax} ($P = 0.0005$), but only slightly on N_m ($P = 0.0391$), and was not significant on J_{max} ($P = 0.11$) or R_d ($P = 0.71$).

Light-use efficiency

Fagus sylvatica annual stem diameter increment was significantly related to the amount of foliage ($STAR_{sky} \times LA$) that participated in harvesting a fraction of PAR_t , but with strong between-year variations (Figure 3). In the first and second year

after planting, ϵ (slope of regression) was high, but decreased dramatically in the third and fourth years (Figure 3B) and even more in 2006 (Figure 3A). The product $STAR_{sky} \times LA \times PAR_t$ increased exponentially with stem diameter ($P < 0.0001$ and $r^2 = 0.85$), whereas there was no relationship between relative diameter increment (diameter increment/diameter) and its product ($P = 0.13$ and $r^2 \cong 0$).

Discussion

Fagus sapling growth at low irradiances

As previously reported (e.g., Ammer 2003, Coll et al. 2003, Dreyer et al. 2005), *F. sylvatica* can survive and grow in deep shade, but grows much better at higher irradiances (0.35 of PAR_t in our experiment). We measured the effects of irradi-

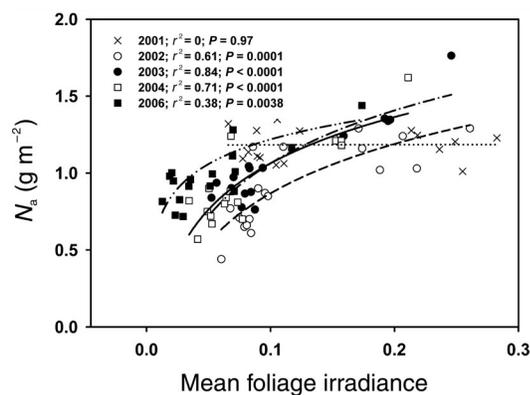


Figure 1. Leaf nitrogen concentration (area basis, N_a) of *Fagus sylvatica* saplings at the end of July as a logarithmic function of the mean foliar irradiance ($PAR_t \times STAR_{sky}$) for different years of growth after planting in November 2000 under the cover of *Pinus sylvestris*. Dotted line, 2001; dashed line, 2002; dash-dotted line, 2003; unbroken line, 2004; and dash-double dotted line, 2006. Abbreviations: PAR_t , transmitted photosynthetically active radiation; and $STAR_{sky}$, silhouette to total leaf area ratio integrated on the whole sky vault.

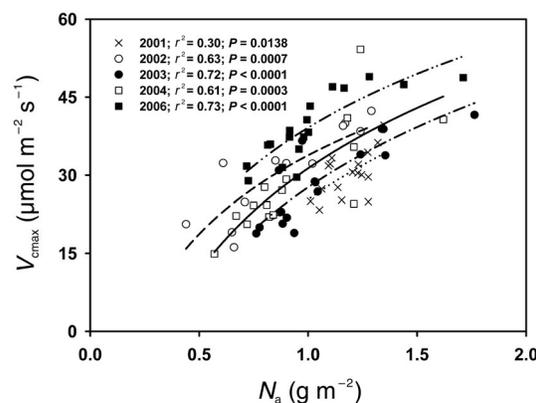


Figure 2. Maximum carboxylation rate (V_{cmax}) of leaves of *Fagus sylvatica* saplings at the end of July as a logarithmic function of leaf nitrogen concentration (area basis, N_a) for different years of growth after planting in November 2000 under the cover of *Pinus sylvestris*. Dotted line, 2001; dashed line, 2002; dash-dotted line, 2003; unbroken line, 2004; dash-double dotted line, 2006.

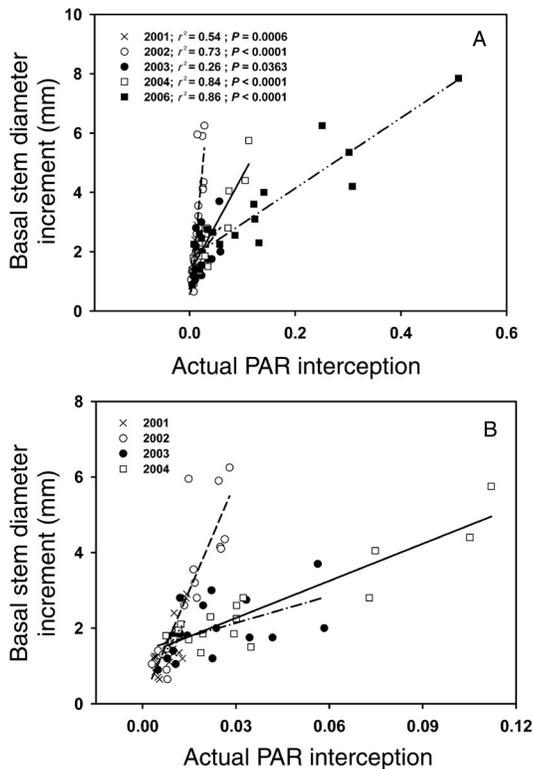


Figure 3. *Fagus sylvatica* sapling growth (annual basal stem diameter increment) according to the quantity of PAR intercepted by leaves at the season scale ($PAR_t \times STAR_{sky} \times LA$) for different years of growth after planting under the cover of *Pinus sylvestris*. Dotted line, 2001; dashed line, 2002; dash-dotted line, 2003; unbroken line, 2004; dash-double dotted, 2006. (A) All years and (B) details for 2001–2004. Abbreviations: PAR_t , transmitted photosynthetically active radiation; $STAR_{sky}$, silhouette to total LA ratio integrated on the whole sky vault; and LA, leaf area.

ance only on stem diameter growth, but irradiance also affects stem height (data not shown), although the effect is less marked because height growth is disturbed by confounding effects such as stem curvature with increasing shade (Vinkler 2005). All saplings displayed similar growth, morphological characteristics and physiological parameters in the first year after planting (2001), regardless of the light conditions, indicating that studies of the effects of varying irradiances on saplings, at least of *Fagus sylvatica*, coming from nurseries and then planted in the field must extend over at least two years. We also found that the growth conditions of year $n - 1$ had a strong influence on the morphological and physiological features of beech saplings in year n (Aranda et al. 2001, Ammer 2003, Cochard et al. 2005). For instance, leaf N concentration responded to light availability only in the second year after planting (Figure 1). This result contrasts with findings reported by Kimura et al. (1998) for *Fagus japonica* Maxim., where current light conditions had significant effects on M_a and the chlorophyll:nitrogen ratio. Other species such as *Juglans nigra* L. \times *regia* L. also show high morphological and physiological plasticity to the current light environment (Frak

et al. 2001, 2006). However, some authors have shown that the ability of a species to acclimate (morphologically and physiologically) to current (and changing) light conditions is strongly limited by leaf anatomy via mesophyll plasticity (Oguchi et al. 2005), which in *Fagus* spp. is generally determined during bud formation by previous light conditions (Eschrich et al. 1989).

Morphological plasticity of *F. sylvatica* saplings

Variables related to light harvesting, such as sapling total LA, leaf number and arrangement, LA and leaf angle, all showed significant variations with changing light availability (cf. Planchais and Sinoquet 1998). Sapling leaf number and mean leaf angle increased with light availability, as shown for *Quercus petraea* (Matt.) Liebl. (Farque et al. 2001). Although mean LA showed strong variations in response to light in *Quercus* (Lichtenthaler et al. 1981, Farque et al. 2001), we observed a weak response in *Fagus sylvatica*. Similarly, sapling total LA responded more to year than to PAR_t , which can be interpreted as an effect of sapling size (Delagrange 2004, Dreyer et al. 2005). The silhouette to total LA ratio integrated at the whole-sky vault scale decreased with both year and light availability, with a larger effect for year than for light. Higher STAR values on plants growing in low irradiances than in high irradiances have previously been reported (e.g., Farque et al. 2001 for *Q. petraea*) and may indicate a mechanism for increasing light-interception efficiency in shade. The decrease in STAR over time, which we did not predict, could be interpreted as a sapling size effect rather than a light effect (Delagrange 2004, Dreyer et al. 2005). This interpretation is supported by the finding that, when stem diameter was set as a covariable in the analysis, it had a significant effect on variations in sapling total LA, leaf number and $STAR_{sky}$. Two variables were insensitive to increases in stem diameter, mean LA and leaf inclination, indicating that these variables could be good markers of light conditions because they are independent of sapling size.

Physiological plasticity of *F. sylvatica* saplings

As reported by Niinemets et al. (1998), Curt et al. (2005) and Dreyer et al. (2005), we found low M_a at low light availability. Values ranged from 35 to 52 g m⁻², which is in good agreement with the values of 30–100 and 35–65 g m⁻² reported by Ceulemans and Saugier (1991) and Dreyer et al. (2005), respectively, for *F. sylvatica*. Leaf N concentration on an area basis was positively linked to light availability, as previously reported for different species (Reich et al. 1995, Niinemets et al. 1998, Le Roux et al. 1999, Anten et al. 2000, Valladares et al. 2002), whereas irradiance had much less effect on nitrogen concentration on a mass basis (N_m), as found in other studies (Parelle et al. 2006). This result, together with the finding that LA was driven by light availability independently of sapling size, supports the suggestion that the main trait associated with variations in irradiance is an adjustment in M_a , (e.g., Montgomery 2004, Curt et al. 2005, Shipley et al. 2005). Both N_a and M_a were sensitive to stem diameter set as a covariable, suggesting a size effect. The product of $PAR_t \times STAR_{sky}$, i.e., the

foliar irradiance relative to incident radiation, was more accurate in predicting N_a than transmittance alone, indicating that N distribution among leaves in a tree depends on the light environment in the canopy (Anten et al. 2000) and thus, on structural traits of the canopy, such as leaf overlap. Because $STAR_{sky}$ was also size-dependent (increased leaf overlap with size), the size effect on N_a and, to some extent, M_a is consistent, whereas N_m is only slightly modified.

Both V_{cmax} and J_{max} increased slightly with N_a and N_m , and also with light transmittance (cf. Ducrey 1981, Aranda et al. 2004, Parelle et al. 2006). These photosynthetic parameters were also strongly correlated with one another ($r = 0.86$; unpublished data), thereby presumably balancing the use of light and CO_2 by the leaf (Niinemets et al. 1998). When PAR_t increased from 0.1 to 0.35, V_{cmax} increased 30% from 27 to 37 $\mu mol\ m^{-2}\ s^{-1}$, which is much less than the increases reported for potted seedlings (Dreyer et al. 2005, V_{cmax} from about 20 to 60 $\mu mol\ m^{-2}\ s^{-1}$ for *Fagus sylvatica*) and for species like *Quercus robur* L. (maximum assimilation rate from 4 to about 16 $\mu mol\ m^{-2}\ s^{-1}$, i.e., an increase of 75% from 15 to 50% light, Valladares et al. 2002). Because our measurements of V_{cmax} were made without taking account of stomatal conductance, V_{cmax} may have been underestimated (Piel et al. 2002), particularly under conditions of great changes in M_a (cf. Warren and Adams 2006, Niinemets et al. 2006).

Sapling growth and light capture

We used a modified form of the conceptual framework proposed by Monteith (1977) to relate sapling growth to light capture. The initial framework expresses dry matter production as the result of light interception by the canopy and conversion of intercepted light into total dry matter production, including roots and shoots. This framework has been used in many studies on agricultural crops (e.g., Sinclair and Horie 1989, Muchow et al. 1993) and also in some studies on tree canopies (Cannell et al. 1987, Bartelink et al. 1997). We introduced some modifications to the initial framework. First, the method was used at the plant scale rather than the canopy scale, to allow us to account for growth variability at the individual scale. Second, light interception was expressed as the product $PAR_t \times STAR_{sky} \times LA$; this is the actual light interception in the studied system because it combines light availability due to the pine canopy cover (PAR_t) and interception by the sapling as a result of the spatial display of foliage ($STAR_{sky} \times LA$). Third, dry matter production was replaced with annual diameter growth. Diameter increment was used so that we could study the plants over several years rather than harvesting a selection of them after each year of study, and because there is a close relationship between annual increments of stem diameter and total sapling biomass (Curt et al. 2005).

The modified framework had two advantages. First, using a yearly time-scale avoided the necessity of a more mechanistic approach where carbon gain has to be computed at an hourly or daily time-step to scale leaf photosynthesis to the tree scale. Such an approach was avoided because it involves many uncertainties when integrating at the year scale, namely the effect

of incident radiation, spatial and temporal changes in tree structure and leaf photosynthetic parameters. Second, reliance on annual stem diameter increment avoided the necessity for time-dependent data, which may be a limitation of the Monteith growth analysis approach (Demetriades-Shah et al. 1992). This shortcoming mainly arises when applied over a growing season, and dealing with cumulative rather than incremental values. However, we are aware that our modified form is not a predictive model of beech growth, mostly because it does not explicitly deal with tree respiration and allocation to stem growth. Instead, it allowed us to show only how tree growth is correlated to light capture by saplings.

For the six years of the study, the variability in diameter increment explained by, for example, V_{cmax} or PAR_t was always lower (by at least 10%) than that explained by the product $PAR_t \times STAR_{sky} \times LA$. For most years, intercepted light appeared to be the main factor driving beech sapling growth, but apparently with varying efficiency (Figure 3): there was a general decrease in ϵ with increasing sapling age, i.e., for the same value of intercepted light, diameter growth was higher in 2001 or 2002 than in 2003 or 2004, and more marked in 2006. The year 2003 showed a pronounced spring and summer drought in most parts of France, with maximum temperatures above 35 °C (Picon Cochard, INRA, France, Pers. comm.). Therefore, in 2003, shortfalls in soil water supply or high water demand by leaves, or both, would have limited growth in addition to the limitation due to light availability (Monteith 1977), thus explaining the low value of the slope between stem diameter increment and the amount of intercepting foliage for that year.

Numerous studies have shown stomatal limitation of photosynthesis with increasing water deficit (Tognetti et al. 1994, Dreyer 1997, Jarvis and Davies 1998, Aranda et al. 2004). Therefore, the year 2003 would probably have shown ϵ values (slope) between those of 2002 and 2004 in the absence of drought and high temperatures. Also, we cannot totally exclude the possibility that, in 2004, ϵ was lower than expected because of a delayed effect of drought in 2003.

Finally, we transformed diameter measurements into biomass increments based on the relationship given by Curt et al. (2005) and used them to plot biomass increment according to the product $LA \times STAR_{sky} \times PAR_t$. Both diameter and biomass increment gave similar results, i.e., a decrease in ϵ with year, but the relationships were not so good for biomass as for diameter because biomass was approximated by calculation rather than measured (data not shown).

Influence of sapling size

A number of studies have shown that tree seedling or sapling size has a fundamental influence on growth and biomass distribution, both above- and belowground, independent of any effect on light availability (Sack and Grubb 2001, Cheng et al. 2005, Claveau et al. 2005, Niinemets 2006, Delagrangé et al. 2006, Kneeshaw et al. 2006). The proportion of non-photosynthetic tissues (NPT) increases faster than that of photosynthetic tissues (PT) as tree size increases. Consequently, it is

generally assumed that tall individuals have a greater light requirement than short individuals as a result of the increase in respiration and construction costs, particularly for NPT (Claveau et al. 2005). Our approach, using morphological sapling characterization with 3D-digitizing to estimate intercepted light at the growing season scale, supports such a hypothesis. Leaf area ratio (LAR, the ratio between tree LA and aerial biomass in $\text{cm}^2 \text{g}^{-1}$), which is used to assess PT/NPT (Messier and Nikinmaa 2000), was approximately 50% lower in the largest saplings ($76 \text{ cm}^2 \text{g}^{-1}$ in about 0.35 PAR_t) than in the smallest saplings ($158 \text{ cm}^2 \text{g}^{-1}$ in about 0.05 PAR_t). The LAR values were in the range of those reported for some boreal species (80–178 versus 55–120 $\text{cm}^2 \text{g}^{-1}$ in low versus high light environments; Messier and Nikinmaa 2000) and some species of the northwest USA (e.g., 100–45 $\text{cm}^2 \text{g}^{-1}$ for *Prunus serotina* Ehrh., Gottschalk 1994). Values of LAR were also in the range of values reported by Dreyer et al. (2005) for *Fagus sylvatica* calculated based on total seedling biomass instead of only aerial biomass: from 25 to 50 $\text{cm}^2 \text{g}^{-1}$, which corresponds to 50 to 100 $\text{cm}^2 \text{g}^{-1}$ if the same weighting is given to the root system as to the aerial part. We also recorded higher dark respiration rates with increasing irradiance, probably because of higher maintenance costs (Niinemets et al. 1998). Overall, dark respiration rates were close to those given in the literature ($0.7 \mu\text{mol m}^{-2} \text{s}^{-1}$; Ceulemans and Saugier 1991).

In conclusion, although the experiment should be replicated in other stands to allow for generalizations, the results obtained in natural conditions confirm the observation that morphological parameters are driven more by sapling size than by light availability (Delagrèze et al. 2004, 2006) with the exception of mean LA and leaf inclination, which responded to light independently of tree size. Physiological leaf parameters related to carbon gain were slightly linked to light availability and seemed to be driven largely by changes in M_a . Annual sapling growth was linked to the amount of intercepting foliage and light availability according to a modified version of Monteith's formalism, providing a useful concept for analyzing growth variations. The slope of the relationship decreased over time, probably because the proportion of photosynthetic tissues decreased more in relation to total sapling biomass.

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