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1 **Beech seedling (*Fagus sylvatica* L.) growth in response to light availability in forest**  
2 **understorey: morphological and physiological plasticity of carbon gain.**

3  
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21 Running head : Beech carbon gain and growth in response to light

22

1 **Summary**

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4

5 *Keywords: forest regeneration, leaf nitrogen content, light interception, photosynthesis*

6 *parameters, silhouette to total leaf area ratio (STAR)*

7

1 **Introduction**

2 While in the past decades in France, and more generally in Europe, most forest  
3 regenerations were made by artificial tree plantation after clear-cutting, there is nowadays a  
4 trend to use more natural tools ensuring forest sustainability (Balandier et al. 2004). The  
5 use of shelterwood or partial cutting is becoming more and more popular, particularly to  
6 establish shade-tolerant late-successional species such as *Fagus sylvatica* or *Picea abies*  
7 (Lieffers and Stadt 1994; Holgen and Hanell, 2000; Nilsson et al. 2002). The objective is to  
8 use and keep a sufficient number of adult trees in the overstorey to i) insure seed  
9 production, ii) reach a light value that allow tree seedling growth even if not at its  
10 maximum rate but iii) prevent the development of the most competing light-demanding  
11 species of the understorey vegetation (Schütz 2004, Balandier et al. 2005). While this  
12 technique is relatively simple in its principle, problems often arise from unknown or badly  
13 known tree seedlings responses, in terms of morphological and physiological plasticities  
14 and growth adjustment to different light values (Vinkler 2005).

15 Decreasing light availability is often reported to induce reduced growth and morphological  
16 changes of seedlings, at least for plastic species (Kunstler et al. 2005). Tree seedlings are  
17 generally smaller under shade and allocate more biomass to stem length growth relatively  
18 to radial growth (Collet et al., 2002). Leaves are generally more horizontal to better  
19 intercept reduced light amount and space-arranged to avoid leaf over-lapping and self-  
20 shading at the plant level (Planchais and Sinoquet 1998).

21 Global photosynthetic abilities are strongly reduced in shade for probably all species but  
22 shade-tolerant species such as *Fagus sylvatica* have better carbon fixation rate in low light  
23 environment than light-requiring early-successional species in the same conditions (Bazzaz  
24 1996). Light compensation point and dark respiration for shade-tolerant species are lower

1 than for shade-intolerant species (Kozlowski et al. 1991), allowing carbon fixation even at  
2 very low light availability. Despite this fact, carbon fixation is globally reduced and leaves  
3 of shade-tolerant species contain lower levels of Rubisco and constituents of the electron  
4 transport chain (Kozlowski et al. 1991), reducing maximum photosynthesis rate.

5  
6 This has consequences on tree seedling growth. Depending on tree species, two growth  
7 strategies are reported in response to increasing shade, an increase in stem height increment  
8 to rapidly escape from shade (shade-intolerant species), and at the opposite a reduction in  
9 growth, both in diameter and stem length to reduce organ respiratory and building costs and  
10 keep a positive carbon balance (Madsen 1995), a strategy reported for shade-tolerant  
11 species such as *Fagus sylvatica*. Moreover the plasticity in response to light has two  
12 components, morphological or physiological, and shade-intolerant species such as *Quercus*  
13 *robur* showed a higher physiological plasticity (photosynthetic carbon gain in response to  
14 light) than *Fagus sylvatica* while this latter had a higher morphological plasticity (light  
15 harvesting, Valladares et al. 2002).

16 A reduction in photosynthesis often leads to a different carbon partitioning among tree  
17 seedlings organs, mainly an increase of carbon in aerial organs and a concomitant reduction  
18 of carbon towards root system (Kozlowski et al. 1991). Reduced root growth can limit  
19 water and nutrients supplying of the whole plant and the shade intolerance of some species  
20 could be more due to drought or nutrients deficiency problems rather than light level per se  
21 (Rundel and Yoder 1998).

22  
23 Even in the case where water and nutrients are not limiting, linking plant growth directly to  
24 photosynthesis is not easy, mainly because photosynthesis can only be measured on a

1 reduced sample of leaves and in a short time (Ceulemans and Saugier 1991; Kozlowski et  
2 al. 1991). In a certain way linking growth to total leaf area or intercepted light should be  
3 more integrative of the whole canopy and the whole season variations rather than to  
4 punctual photosynthesis measurements. Such an attempt has been made with success for  
5 instance by Cannell et al. (1987) on willow. Growth or biomass production (W) can be  
6 linked directly to light absorption or interception (I) via a coefficient of light conversion  
7 efficiency ( $\varepsilon$ ):

$$8 \quad W(t) = \varepsilon \cdot I \cdot \Delta t \quad (1)$$

9 with  $\Delta t$  the time interval (Monteith 1977; Kozlowski et al. 1991).

10

11 Canopy light interception has been assessed through different techniques, roughly from  
12 aerial photographs in order to determine exposed crown area of rather adult trees  
13 (percentage of tree's canopy not overtopped by any other tree, Wyckoff and Clark 2005) to  
14 more detailed description of leaves distribution and orientation with 3D-digitizing  
15 technique for rather smaller trees (Sinoquet et al. 1998 ; Farque et al. 2001).

16

17 Such an attempt has been made here for young beech seedlings grown under different light  
18 availabilities in the French Massif central. In addition to the characterization of  
19 physiological and morphological plasticities to light, the applicability of using the light  
20 conversion efficiency approach was explored as an attempt to better predict beech seedling  
21 growth according to light harvesting.

22

23

1 **Material and methods**

2 *Natural site*

3 Measurements were done in a 25 year old natural *Pinus sylvestris* stands in the Chaîne des  
4 Puys, a mid-elevation volcanic mountain range situated in Auvergne, France (lat. 45°42,  
5 long. 2°58). The elevation of the considered forest stand is 900 m a.s.l. The climate is close  
6 to a mountain type with oceanic influence in the West part of the range. Mean annual  
7 rainfall is about 820 mm and for the years of measurement (from 2001 to 2004) rainfall  
8 during seasonal growth (from approximately May to September) was 416, 424, 306 and  
9 496 mm, respectively. The year 2003 was consequently characterized by severe drought  
10 periods during tree growth. The mean annual temperature is about 7°C. Again 2003 is a  
11 particular year with unusual high temperatures in summer: the mean daily temperature for  
12 the months June to August was 15.3°C in 2001, 15.0°C in 2002 and 18.6°C in 2003 where  
13 temperatures greater than 35°C were recorded some days (Picon-Cochard, personal  
14 communication). The soil is developed on volcanic ashes and belongs to the Andisol  
15 family, with a pH<sub>water</sub> of 6.0, and a rich organic upper layer. Nutrients are fully available  
16 with a CEC of 33 mEq per 100g (Curt et al. 2005), and most years, soil water content is not  
17 a limiting factor for tree growth in this stand (Balandier et al. 2004).

18 *Pinus sylvestris* in the area established naturally from the 1950's in abandoned mountain  
19 agricultural lands. However the natural vegetation of the area is a mixed *Fagus sylvatica* /  
20 *Abies alba* forest and one issue for forest managers is to restore the *Fagus* forest from  
21 pioneer *Pinus* stands (Balandier et al. 2004). The study reported here is part of a project  
22 aiming at determining the conditions of *Fagus* development in the area.

23

24 *Experimental design*

1 Two year old *Fagus sylvatica* seedlings coming from a local nursery were planted in  
2 November 2000 in the *Pinus sylvestris* stand thinned to different levels to get a gradient of  
3 transmitted solar radiation in the understorey. From this experiment, 18 *Fagus* seedlings  
4 were sampled *a priori* to cover approximately the 0.1 to 0.4 range of transmittance.  
5 Measurements (see hereafter) showed that this range was in fact partially covered with a  
6 lack of individuals in the middle of the range (around 0.2).

7

### 8 *Measurements*

9 *Fagus sylvatica* growth related to solar radiation availability was divided in its two  
10 components: 1) the efficiency to which light is intercepted, and 2) the efficiency to which  
11 carbon is incorporated into carbohydrate compounds (photosynthesis).

12

13 *Fagus* stem basal diameter was measured with a calliper rule at the end of each growing  
14 season (October) from 2001 to 2004. For each seedling, measurements were made in two  
15 opposite directions and the mean of this two values is used in this article.

16

17 Transmitted solar radiation above *Fagus* seedlings was measured twice, in 2002 and in  
18 2005, using tube solarimeters (Delta-T<sup>®</sup>, wavelength range from 300 to 3000 nm) and PAR  
19 quantum sensors (LICOR<sup>®</sup>, 400-700 nm) in 2005. Measurements were done during 24  
20 hours to integrate the daily solar pathway in the sky. Transmittance is then the ratio of  
21 values measured in the understorey to incident values measured during the same 24 hours  
22 in an open area.

23



1 The canopy structure related to light interception (arrangement of leaves in the space) of the  
2 18 *Fagus* seedlings was described each year in July (after full leaf expansion) from 2001 to  
3 2004 using the 3D-digitising technique (Sinoquet and Rivet 1997). The position and  
4 orientation in the 3D-space of each leaf were recorded in the field using a digitising device  
5 (Polhemus, USA) which includes a magnetic source and a pointer. The position and  
6 orientation of the pointer in the space (x, y, and z coordinates and rolling and inclination)  
7 are computed from the measurements of induction currents in the magnetic field (Planchais  
8 and Sinoquet 1998). In addition to these measurements, the length (L) and width (W) of  
9 each leaf were measured in order to calculate the area (S) of each leaf using the following  
10 relationship,  $S=kLW$ , with k a parameter, relationship which was proved to be very  
11 accurate for *Fagus* (Planchais and Sinoquet 1998). From these data, seedling leaf number,  
12 seedling leaf area, mean leaf area, mean leaf inclination were calculated for each year. The  
13 light interception efficiency (LIE) can be assessed as the ratio between projected leaf area  
14 in a given direction and total leaf area, often named STAR (Silhouette to total leaf area  
15 ratio). A STAR of 1 means that there is no overlapping among leaves and that all are  
16 arranged perpendicular to incoming radiations. The STAR can be integrated on the whole  
17 heaven vault ( $STAR_{sky}$ ) to take into account diffuse radiations coming from every  
18 directions of the vault. Here's a "turtle" arrangement was used dividing the sky in 46 solid  
19 angles of same surface. As the contribution of low elevations above horizon are lesser than  
20 those from high elevations, a weight was attributed to each solid angle following a standard  
21 overcast (SOC) distribution.

22

23 Leaf photosynthetic capacities were determined by a LI-6400 gas-exchange analyser  
24 (LICOR<sup>®</sup>, USA) on one leaf per *Fagus* seedling at the end of July (after full leaf expansion)

1 of each year, except for 2003 where unusual very high temperatures in July (see here-  
2 above) prevented to have correct measurement. Then the mean of a measure in June and a  
3 measure in early September is used for 2003. The maximum carboxylation rate ( $V_{c_{max}}$  in  
4  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), the maximum electron transport rate ( $J_{max}$  in  $\mu\text{mol e}^- \text{ m}^{-2} \text{ s}^{-1}$ ) and dark  
5 respiration ( $R_d$  in  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) were derived from Assimilation ( $A$ )/internal  $\text{CO}_2$   
6 concentration ( $C_i$ ) curves. During measurements light was set at  $1500 \mu\text{mol photon m}^{-2} \text{ s}^{-1}$   
7 and temperature at  $25^\circ\text{C}$ . . Leaf was immediately collected after measurements to determine  
8 dry matter and nitrogen content. Each leaf was dried by lyophilization before quantification  
9 of N content by an elemental micro-analyser .... N is then divided by leaf area to express N  
10 content on an area basis ( $\text{g m}^{-2}$ ).

11

## 12 *Data analysis*

13 Statistical analysis were performed with the software Statgraphics®. *Fagus* seedling growth  
14 variables, morphological variables (i.e. tree leaf number, mean leaf area, mean leaf angle  
15 and  $\text{STAR}_{\text{sky}}$ ) and photosynthetic capacity variables were related to light availability and  
16 year of growth by multiple factor ANOVA. Light was divided into 3 classes (0-14%; 14-  
17 28% and 28-42%) to try to equilibrate size of each class. Despite this, classes were slightly  
18 unbalanced (7; 5; 6) but the variances of each class are not statistically different (Cochran's  
19 C test). A type III error calculation was used in the ANOVA. The interaction light by year  
20 is included in the model. When significant, means were separated by a Newman-Keuls test  
21 (threshold of signification 5%). For stem diameter increment analysis, seedling stem  
22 diameter was also used as a co-variable using an ANCOVA to take into account a possible  
23 seedling size effect. Leaf nitrogen content (N) and  $V_{c_{max}}$  were related to transmittance and

1 N, respectively, by non-linear regressions. As the product of Transmittance by STAR<sub>sky</sub>  
2 (i.e. the fraction of transmittance which is really intercepted by leaves due to their  
3 overlapping) gave better coefficient of determination, it was used to predict N leaf content.  
4 Basal stem diameter and diameter increment were linked to the product Transmittance \*  
5 STAR<sub>sky</sub> \* Leaf area, which is a mean to express the quantity of leaf area which is really  
6 included in light harvesting (m<sup>2</sup>). By analogy to the Monteith's work (equation 1), the slope  
7 of the regression can be likened to a coefficient of light use efficiency ( $\epsilon$ ).

8

9

## 10 **Results**

### 11 *Fagus seedling growth*

12 One year after the plantation, basal stem diameter was not different among the three light  
13 classes, but there was a significant difference after 4 years, the seedlings under 28 to 42%  
14 light having a diameter nearly two-fold larger than the other (table 1). The annual basal  
15 stem diameter increment was significantly higher for the third class of transmittance (28-  
16 42%), but differences between classes were less when stem diameter was set as a co-  
17 variable in the analysis, probably meaning that diameter increment is affected by seedling  
18 size (table 1). There were inter-annual variations of diameter increment, the 3<sup>rd</sup> and 4<sup>th</sup> year  
19 showing smaller diameter increment. The interaction between light class and year is  
20 significant, mainly due to the fact that the positive effect of light increased with year after  
21 plantation (i.e. the difference between class was much more higher 3 to 4 years after  
22 plantation than just after).

23

1 *Morphological seedling variables related to light interception*

2 Light and year after plantation influenced significantly mean tree leaf number, mean leaf  
3 area, mean leaf inclination and mean STAR<sub>sky</sub> (Table 2). The interaction light by year is  
4 never significant. Curiously, leaf number was significantly higher for the middle class of  
5 light availability (14-28%) which can be related to a significant smaller leaf area. Leaf  
6 number increased with year while leaf area became constant after the first year. Leaf  
7 inclination increased significantly with light (leaves more vertical with increasing light).  
8 After the first year, leaf angle was stable along years. STAR<sub>sky</sub> was significantly higher for  
9 the first light class (0-14%) and also evolved with year, with a general decrease from 0.83  
10 the first year to 0.67 after 4 years.

11

12 *Fagus sylvatica leaf photosynthetic capacity*

13 Leaf nitrogen content (N, on an area basis) increased significantly with light (table 3 and  
14 figure 1). There were slight variations according to year, 2002 and 2001 showing the  
15 smallest and the highest N content, respectively. Leaf dry matter content was significantly  
16 higher for the 3<sup>rd</sup> class of light (28-42%) and no variation was recorded according to year  
17 2002 to 2004 (data for 2001 not available). The leaf maximum carboxylation rate ( $V_{C_{max}}$ ),  
18 maximum electron transport rate ( $J_{max}$ ) and dark respiration (Rd) increased significantly  
19 with light (table 3). The factor year did not influenced  $V_{C_{max}}$  and  $J_{max}$  but Rd was  
20 significantly divided by two after the first year (data of year 2004 not available). When  
21 significant, the interaction light by year is due to the fact that the first year (2001) did not  
22 displayed any significant variation between light classes which was not the case for the  
23 following years (example for N and  $V_{C_{max}}$  in figures 1 and 2).  $V_{C_{max}}$  was significantly

1 linked logarithmically to leaf N content, with some limited differences between years (same  
2 slope,  $p=0.68$ , but different origins,  $p=0.0004$ , figure 2).

3

4 *Light use efficiency ( $\epsilon$ )*

5 *Fagus* stem diameter increment was significantly linearly linked to the amount of light  
6 intercepting foliage but with strong variations between years (figure 3B). The first and  
7 second years after plantation light use efficiency ( $\epsilon$ , slope of regression) was high but  
8 decreased dramatically the third and fourth years. In consequence, the increase of stem  
9 diameter with the amount of intercepting foliage was not linear but followed a  
10 multiplicative curve with an exponent of 0.385 (figure 3A).

11

12

### 13 **Discussion**

14

15 As already reported (Ammer 2003, Coll et al. 2003; Dreyer et al. 2005) *Fagus sylvatica* is  
16 able to survive and grow under limited light supply but it is also able to answer and grow  
17 much better under higher light level (until 40 % light in this experiment). Only stem  
18 diameter growth was presented in this article but the response to light is also true for stem  
19 height (data not shown) while not so clear because height growth is perturbed by confusing  
20 effect such as the tendency of the main stem to curve with increasing shade (Vinkler 2005).  
21 All seedlings presented the same growth, morphological characteristics and physiological  
22 parameters in the first year after plantation (2001) whatever the light conditions. This  
23 confirms the fact that studies with planted seedlings coming from nursery must at least last

1 2 years before give tangible effect. This also confirms that the growth conditions of the year  
2 n-1 have a strong influence on the morphological and physiological features of tree  
3 seedlings in year n (in Ammer 2003). For instance here, leaf nitrogen content responded  
4 fully to light availability only three years after plantation (better  $R^2$ , figure 1).

5  
6 As previously reported, variables linked with light harvesting such as leaf number and  
7 arrangement, leaf area, leaf angle, etc. showed all a significant variation according to light  
8 availability (Planchais and Sinoquet 1998). The seedling leaf number and mean leaf angle  
9 increased with light as shown for *Quercus petraea* (Farque et al. 2001). At the opposite,  
10 mean leaf area in the same study on oak as well as in other studies (Lichtenthaler et al.  
11 1981) showed great variations while in our case *Fagus sylvatica* showed only slight  
12 variations for that variable in response to light. The silhouette to total leaf area ratio  
13 integrated on the whole heaven vault ( $STAR_{sky}$ ) decreased both with light availability and  
14 year, the effect of year (from 0.83 to 0.67 from year 1 to year 4) being higher than that of  
15 light (from 0.81 to 0.70 from about 10 to 40% light). Such a STAR decrease with  
16 increasing light was already reported (Farque et al. 2001 on *Quercus petraea*). The STAR  
17 decrease with year is more singular. Such a decrease could be interpreted as a seedling size  
18 effect and not, or not only, as a light effect (Dreyer et al. 2005).

19  
20 As reported by Niinemets et al. (1998), Curt et al. (2005) or Dreyer et al. (2005), we  
21 founded a low value of leaf dry mass (on an area basis) at low light availability. The values  
22 ranged between 37 and 65 g m<sup>-2</sup>, well in accordance with those given by Ceulemans and  
23 Saugier (1991) for *Fagus sylvatica* (30-100 g m<sup>-2</sup>) or Dreyer et al. (2005, 35-65 g m<sup>-2</sup>).

24

1 There was a strong correlation between photosynthetic capacity ( $V_{C_{max}}$ ,  $J_{max}$ ,  $R_d$ ) and leaf  
2 nitrogen content (N), leaf nitrogen content being also positively linked to light availability  
3 as already recorded for different species (Reich et al. 1995; Niinemets et al. 1998; Le Roux  
4 et al. 1999; Anten et al. 2000; Valladares et al. 2002). Here, the product Transmittance by  
5  $STAR_{sky}$  was more accurate in predicting N, meaning that leaf overlapping must be  
6 considered. Therefore the N content of a considered leaf could result both from the direct  
7 exposure to light of the considered leaf but also to the global geometry of the crown, i.e. the  
8 number of shaded leaves (ref ?).

9  
10  $V_{C_{max}}$  and  $J_{max}$  increased with light transmittance as in other studies (Ducrey 1981) and  
11 were strongly correlated together ( $r=0.86$ , data not shown) as reported in many studies,  
12 probably to avoid excess capacity of one variable while the other is limiting (Niinemets et  
13 al. 1998).  $V_{C_{max}}$  increased with light but only slightly (from 25 to 35  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  that  
14 is to say an increase of about 30% when moving from about 10% to 40% light) in  
15 comparison with other studies dealing with seedlings in pots (Dreyer et al. 2005,  $V_{C_{max}}$   
16 from about 20 to 60  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  for *Fagus sylvatica*) or species like *Quercus robur*  
17 (maximum assimilation rate,  $A_{max}$  from 4 to about 16  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , i.e. an increase of  
18 75% from 15 to 50% light, Valladares et al. 2002). The increase in photosynthetic capacity  
19 with increasing light could be associated with a higher chloroplast content per leaf area  
20 unit, and the sun-type chloroplasts also possess more electron transport chains on a  
21 chlorophyll basis (*Fagus sylvatica*, Lichtenthaler et al. 1981).

22

1 Beech seedling growth can be linked directly to intercepted light following the formalism  
2 of Monteith (1977). Here stem diameter increment was used instead of plant biomass but  
3 there is a direct link between stem diameter increment and total plant biomass increment  
4 (Curt et al. 2005). For most years intercepted light seemed to be the main factor driving  
5 beech seedling growth in our conditions but apparently with different efficiency (figure 3):  
6 there was a general decrease of light use efficiency ( $\epsilon$ ) with increasing age of the seedlings,  
7 i.e. for the same value of intercepting foliage, diameter growth was better in 2001 or 2002  
8 than in 2003 or 2004. The year 2003 was a year with a pronounced spring and summer  
9 drought in most parts of France with scorching temperatures (see the Materials and Methods  
10 section). Therefore for that particular year, short soil water supply and/or high water  
11 demand from leaves would have limited growth in addition of the effect of light availability  
12 (Monteith 1977) explaining the low value of the slope between stem diameter increment  
13 and the amount of intercepting foliage for that year. Many studies showed the stomatal  
14 limitation of photosynthesis with increasing water stress (ref.). Therefore probably the year  
15 2003 would have had a  $\epsilon$  value (a slope) between those of 2002 and 2004 in the absence of  
16 water stress and high temperatures.

17

18 More and more studies are showing that tree seedling or sapling size has a fundamental  
19 influence on growth and biomass distribution in addition with light effect, both above- and  
20 below-ground (Cheng et al. 2005; Claveau et al. 2005). The proportion of non-  
21 photosynthetically tissues (NPT) increases faster than photosynthetically tissues (PT) as  
22 tree size increases. Consequently, it is generally assumed that tall individuals have a higher  
23 light requirement than small individuals due to an increase of respiration and construction



1 cost in particular for NPT (in Claveau et al. 2005). Our results support such an hypothesis.  
2 Here, the leaf area ratio (LAR, the ratio between tree leaf area and aerial biomass in  $\text{cm}^2 \text{g}^{-1}$   
3 <sup>1</sup>) which is a mean to assess PT/NPT (Messier and Nikinmaa 2000), measured on some  
4 beech seedling harvested to quantify biomass allocation (Curt et al. 2005; Prévosto,  
5 unpublished data) was approximately two fold lesser for the largest trees ( $76 \text{ cm}^2 \text{ g}^{-1}$  under  
6 approximately 40% light) than for the smallest ones ( $158 \text{ cm}^2 \text{ g}^{-1}$  under approximately 10%  
7 light). LAR values are in the range of those (80 to 178 vs. 55 to 120  $\text{cm}^2 \text{ g}^{-1}$  in low vs. high  
8 light environments, respectively reported for some boreal species by Messier and Nikinmaa  
9 (2000) or some species of NW of USA ( for instance from approximately 100 to 45  $\text{cm}^2 \text{ g}^{-1}$   
10 for *Prunus serotina*, Gottschalk 1994). There are also in the range of values reported by  
11 Dreyer et al. (2005) for a *Fagus sylvatica* LAR calculated from a total seedling biomass and  
12 not only aerial biomass: from 25 to 50  $\text{cm}^2 \text{ g}^{-1}$ , which can correspond to values from 50 to  
13 100  $\text{cm}^2 \text{ g}^{-1}$  if we give the same weight to the root system than to the aerial part. We also  
14 recorded higher values of dark respiration with increasing light levels probably because of  
15 higher maintenance costs (Niinemets et al. 1998). Globally,  $R_d$  values were close to values  
16 given in the literature ( $0.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , Ceulemans and Saugier 1991).

17

18

## 19 **Conclusion**

20 The results of this experiment tends to confirm the general observation that leaf  
21 physiological parameters related to C gain are mainly linked to light availability while  
22 morphological parameters are more driven by tree seedling size (Delagrange et al. 2004).  
23 Annual seedling growth can be predicted with accuracy by the amount of intercepting

1 foliage and light availability following the formalism proposed by Monteith. However the  
2 slope of the relationship (light conversion efficiency,  $\epsilon$ ) decreases with year, at least for  
3 young tree seedlings and the species studied here, *Fagus sylvatica*. This decrease is  
4 probably due to a size effect, i.e. a relative decrease of the proportion of photosynthetic  
5 tissues in comparison with the total biomass of the seedling.

6

7

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11

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2 Table 1: Mean values of beech seedling growth according to light availability divided in 3  
 3 classes and year of growth after plantation (Fontfreyde, France).

	Basal stem diameter at the end of the first year (mm)	Basal stem diameter at the end of the fourth year (mm)	Annual basal stem diameter increment (mm)	Annual basal stem diameter increment, with diameter as a co- variable (mm)
Light 0-14%	6.7	11.7 a <sup>#</sup>	1.5 a	2.0 a
Light 14-28%	7.4	14.0 a	2.0 a	2.0 a
Light 28-42%	7.3	18.5 b	3.3 b	2.7 b
Year 2001			1.5 A	2.5 B
Year 2002			3.0 B	3.2 C
Year 2003			2.0 A	1.7 A
Year 2004			2.6 B	1.6 A
p-value Light	0.39	0.0006	<0.0001	0.0187
p-value Year			<0.0001	<0.0001
p-value Light × year			0.0006	<0.0001

4 <sup>#</sup> significant differences between means are separated by different letters ( $\alpha=0.05$ )

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6

1 Table 2: Mean values of morphological beech seedling variables related to light  
 2 interception according to light availability divided in 3 classes and year of growth after  
 3 plantation (Fontfreyde, France).

	Leaf number	Leaf area (cm <sup>2</sup> )	Leaf inclination (°)	STAR <sub>sky</sub>
Light 0-14%	197 a <sup>#</sup>	8.7 b	15.9 a	0.81 a
Light 14-28%	338 c	7.0 a	18.1 b	0.74 b
Light 28-42%	259 b	8.9 b	20.9 c	0.70 b
Year 2001	121 A	6.3 A	16.0 A	0.83 A
Year 2002	183 A	8.3 B	19.7 B	0.76 B
Year 2003	274 B	9.2 B	18.6 B	0.76 B
Year 2004	480 C	9.0 B	19.1 B	0.67 C
p-value Light	<0.0001	<0.0001	<0.0001	<0.0001
p-value Year	<0.0001	<0.0001	<0.0001	<0.0001
p-value Light × year	0.06	0.74	0.43	0.38

4 <sup>#</sup> significant differences between means are separated by different letters ( $\alpha=0.05$ )

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2 Table 3: Mean values of beech seedling variables related to photosynthetic capacities  
 3 according to light availability divided in 3 classes and year of growth after plantation  
 4 (Fontfreyde, France).

	Leaf nitrogen content per area (g m <sup>-2</sup> )	Leaf dry matter content per area (g m <sup>-2</sup> )	V <sub>C</sub> <sub>max</sub> (μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	J <sub>max</sub> (μmol e <sup>-</sup> m <sup>-2</sup> s <sup>-1</sup> )	Rd (μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )
Light 0-14%	0.88 a <sup>#</sup>	34.3 a	25.0 a	66.8 a	-0.58 a
Light 14-28%	0.98 b	37.5 a	29.8 b	77.7 b	-0.68 a
Light 28-42%	1.27 c	52.6 b	34.9 c	93.0 c	-0.99 b
Year 2001	1.18 C	-	30.3	83.5	-1.00 B
Year 2002	0.92 A	39.2	30.4	81.1	-0.56 A
Year 2003	1.08 B,C	42.2	29.3	76.1	-0.69 A
Year 2004	0.98 A,B	42.9	29.6	75.9	-
p-value Light	<0.0001	<0.0001	0.0001	<0.0001	<0.0001
p-value Year	<0.0001	0.18	0.96	0.48	<0.0001
p-value Light × year	0.001	0.93	0.03	0.004	0.001

5 <sup>#</sup> significant differences between means are separated by different letters (α=0.05)

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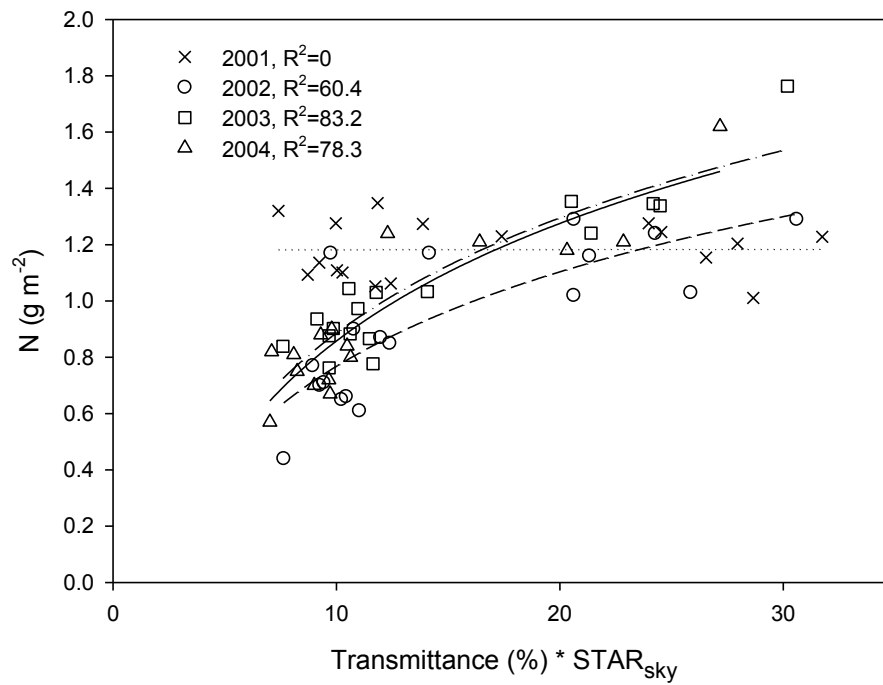
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2 Figure 1: *Fagus sylvatica* seedling leaf nitrogen content (on an area basis) at the end of July  
3 as a logarithmic function of the fraction of light which is actually intercepted for different  
4 years of growth after plantation under the cover of *Pinus sylvestris* (Fontfreyde, France).

5 Dotted line, 2001; dashed line, 2002; dash-dotted line, 2003; and unbroken line, 2004.

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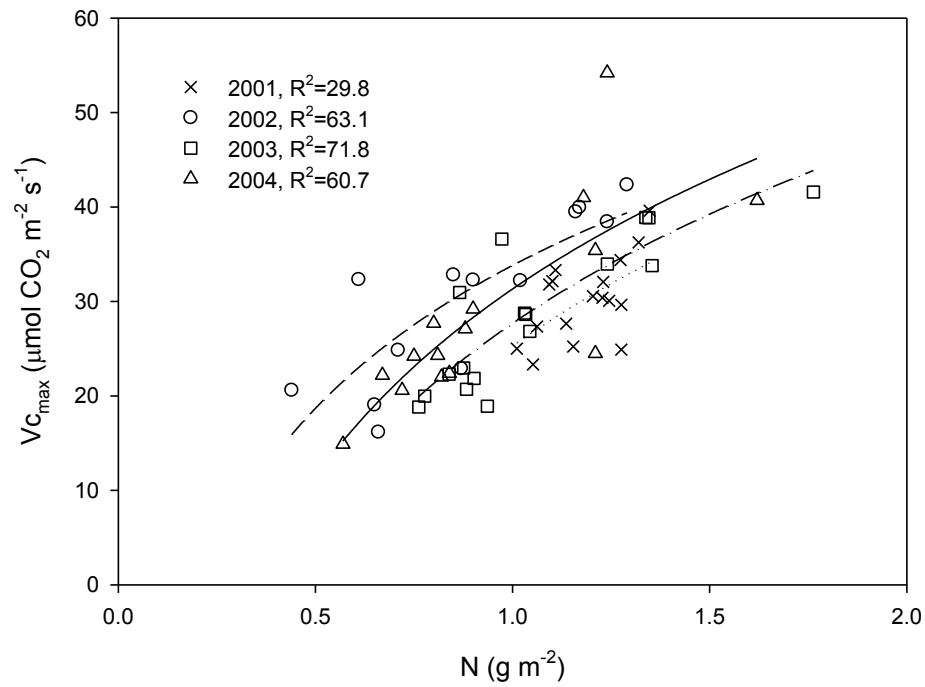
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2 Figure 2: Maximum carboxylation rate of *Fagus sylvatica* seedling leaves at the end of July  
3 as a logarithmic function of leaf nitrogen content (on an area basis) for different year of  
4 growth after plantation under the cover of *Pinus sylvestris* (Fontfreyde, France). Dotted  
5 line, 2001; dashed line, 2002; dash-dotted line, 2003; and unbroken line, 2004.

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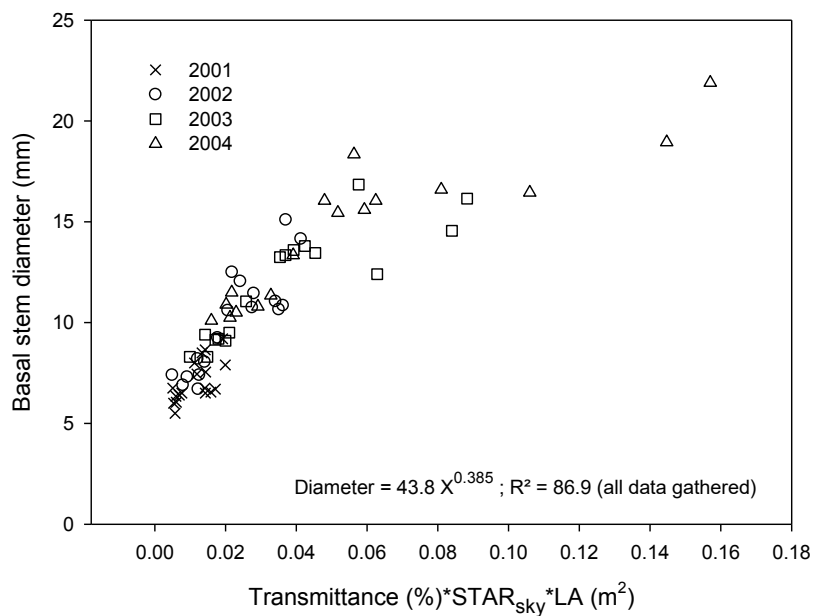
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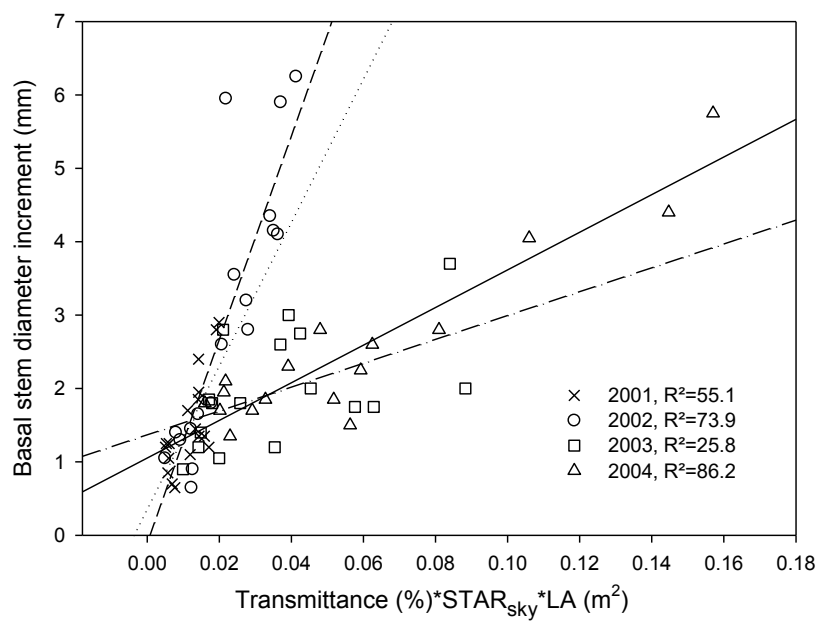
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1 Figure 3: *Fagus sylvatica* seedling growth according to the quantity of leaf area which  
 2 actually included in light harvesting for different year of growth after plantation under the  
 3 cover of *Pinus sylvestris* (Fontfreyde, France). A) Basal stem diameter; B) Annual basal  
 4 stem diameter increment. Dotted line, 2001; dashed line, 2002; dash-dotted line, 2003; and  
 5 unbroken line, 2004.



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