

# Growth and morphology of three forest understorey species (Calluna vulgaris, Molinia caerulea and Pteridium aquilinum) according to light availability

Noémie Gaudio, Philippe Balandier, Yann Dumas, Christian Ginisty

## ▶ To cite this version:

Noémie Gaudio, Philippe Balandier, Yann Dumas, Christian Ginisty. Growth and morphology of three forest understorey species (Calluna vulgaris, Molinia caerulea and Pteridium aquilinum) according to light availability. Forest Ecology and Management, 2011, 261 (3), p. 489 - p. 498. 10.1016/j.foreco.2010.10.034 . hal-00590768

## HAL Id: hal-00590768 https://hal.science/hal-00590768

Submitted on 5 May 2011

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés. Author-produced version of the article published in Forest Ecology and Management, 2011, 261 (3), 489–498

The original publication is available at http://www.sciencedirect.com/

doi : 10.1016/j.foreco.2010.10.034

1	Growth and morphology of three forest understorey species (Calluna vulgaris, Molinia caerulea
2	and Pteridium aquilinum) according to light availability
3	
4	Noémie Gaudio <sup>a</sup> , Philippe Balandier <sup>a, b</sup> , Yann Dumas <sup>a</sup> , Christian Ginisty <sup>a</sup>
5	
6	<sup>a</sup> Cemagref Research Unit on Forest Ecosystems, Domaine des Barres, F-45290 Nogent-sur-Vernisson,
7	France
8	<sup>b</sup> INRA, UMR547 PIAF, F-63100 Clermont-Ferrand, France
9	Corresponding author: <u>noemie.gaudio@cemagref.fr</u> , Tel. + 33 2 38 95 03 49, Fax. + 33 2 38 95 03 59
10	
11	Key words
12	Understorey vegetation; light; growth
13	
14	Abstract
15	Calluna vulgaris, Molinia caerulea and Pteridium aquilinum are three forest understorey species that
16	compete with tree seedlings for environmental resources. Forest managers therefore seek to control
17	their growth, which is driven in part by the light available in the forest understorey.
18	An experiment was set up in a nursery in which the three understorey species C. vulgaris, M. caerulea
19	and P. aquilinum were planted at six light levels (6, 11, 22, 36, 48 and 100% of full sunlight)
20	replicated in three blocks. The different light levels other than 100% were obtained using neutral
21	shading nets. The response of the three species to light availability was estimated after two growing
22	seasons by their cover and height, their morphology, assessed by the foliar tuft height-to-width ratio
23	for C. vulgaris and M. caerulea and by the frond height-to-length ratio for P. aquilinum, and their
24	functional acclimation, assessed by a leaf trait (leaf mass on an area basis, LMA).
25	Vegetation cover changed with light availability following a bell-shaped curve. By contrast, vegetation
26	height remained approximately the same, irrespective of the light treatment, except for P. aquilinum,
27	which grew higher than the other two species at medium and high light levels. As a consequence,
28	vegetation individuals were more spindly in a dark environment. From the lowest light treatment,

*P. aquilinum* cover was high (75%) and intercepted a larger proportion of the light than the other two
 species. This species thus proved the most competitive for light.

31 All three species showed a notable acclimation to light availability by their LMA, though in different

32 ways. The LMA of C. vulgaris decreased in shaded conditions by an increase in leaf area, whereas

33 decrease in LMA for *P. aquilinum* was due to a decrease in leaf mass. For *M. caerulea*, the LMA

34 remained stable whatever the light conditions by a simultaneous increase in both leaf mass and leaf

35 area in shaded conditions.

- 36 Consequently, the in-forest development of *C. vulgaris* and *M. caerulea* could be managed through
- 37 small adult canopy thinnings, as both species grew well from light levels above 20%. Conversely, it
- 38 seems unrealistic to manage *P. aquilinum* in this way as its development was almost maximal even at
- 39 very low light levels.
- 40
- 41
- 42

#### 43 **1. Introduction**

In the forest understorey, tree seedlings and herbaceous or shrubby vegetation grow together and 44 45 interact in different ways, e.g. for environmental resources, namely light, water and nutrients (Davis et 46 al., 1999). Understorey vegetation can have a positive effect (process of facilitation) on tree seedlings 47 by providing protection against browsing (Farris and Filigheddu, 2008) or adverse microclimates such 48 as frosts or extreme temperatures (Callaway, 1995; Balandier et al., 2009). Conversely, understorey 49 vegetation can strongly compete for resources causing at least decreased growth and at worst the death 50 of tree seedlings (Malcolm et al., 2001; Frochot et al., 2002; Harmer and Morgan, 2007). The effect of 51 vegetation depends greatly on its morphology, physiological features and growth rate compared with 52 tree seedlings, and its capacity to deplete resources at their expense (Goldberg, 1990; Balandier et al., 53 2006a).

54

55 In many forests, management is currently oriented towards a silviculture that comes closer to natural 56 forest processes and dynamics (Schütz, 1999; Gamborg and Larsen, 2003). For instance, tree natural 57 regeneration and growth of trees in the understorey can be favoured by the creation of small gaps 58 within an adult forest stand, the latter providing a seed source. The creation of gaps results in 59 increased resources, particularly light (Aussenac, 2000; Clinton, 2003; Heithecker and Halpern, 2006), 60 which promotes tree seedling growth, but also enables the colonisation by light-demanding or at least 61 shade-intolerant species with fast growth rates (Lautenschlager, 1999). Some herbaceous or shrubby 62 understorey species display growth and physiological traits that confer an ability to rapidly colonise 63 newly-opened areas such as newly-created forest gaps (Aikens et al., 2007). In response to canopy 64 openness, these species can invade the gap, forming a dense, nearly single-species cover able to 65 exclude other species, whether they are trees in regeneration or herbaceous species that are not strong 66 competitors (Thomas et al., 1999). Various understorey species can be cited, such as Rubus idaeus, 67 R. fruticosus, Cytisus scoparius and Pteridium aquilinum (see e.g. Fotelli et al., 2001; Gaudio et al., 68 2008; Heinrichs and Schmidt, 2009). Depending on their lifespan and vigour, they can even delay the 69 plant succession dynamics for many years when they are fully developed (Den Ouden, 2000; Prévosto 70 et al., 2004; Royo and Carson, 2006).

71 As reviewed by Balandier *et al.* (2006a), the traits conferring a high colonisation rate are multiple, e.g. 72 high growth rate and morphology of root system and / or aerial parts, high leaf area index (LAI), 73 capacity to take up resources, etc. Thus it has been shown that some perennial grasses possess a dense 74 root system that can efficiently and rapidly colonise superficial soil zones (Aerts et al., 1991; Coll et 75 al., 2003). Some other species, such as certain ferns, have large, very fast-growing aerial organs (Den 76 Ouden, 2000; Parker et al., 2009; Gaudio et al., 2010). These traits are often linked to a strong effect 77 on resource availability, as defined by Goldberg (1990), and consequently a high competitive ability, 78 at least in forest understoreys where low light does not drastically inhibit growth.

However, as pointed out by Tilman (1990), competitive ability also depends on capacity to tolerate low resource levels, which is linked to various acclimation features such as slowed growth rate or shifts in functional traits that go from traits adapted for resource capture maximisation to traits adapted for resource storage efficiency. For instance, some functional leaf traits reflect ability to acclimate to low light levels. Thus the leaf mass on an area basis (LMA, g cm<sup>-2</sup>) has been shown to reflect the resource-induced stress encountered by plants (King, 2003; Aranda *et al.*, 2004; Provendier and Balandier, 2008; Gaudio *et al.*, 2010).

86

87 As understorey herbaceous and shrubby competitive species are mostly light-requiring, their growth 88 can be limited by light availability in the understorey, which in turn depends on adult tree canopy 89 cover density. Thus to prevent the entire gap being colonised by such monopolistic understorey 90 vegetation species, it is necessary to know and predict their behaviour in response to canopy opening 91 and increased light availability. The development of these species can be partly assessed by height and 92 cover (percentage of the ground occupied by the vertical projection of the foliage) (Aubin *et al.*, 2000; 93 Stadt and Lieffers, 2005; Gaudio et al., 2008). Wagner et al. (2010) in a review of growth patterns 94 according to light pointed out that some species respond to light availability according to either a 95 linear or a bell-shaped curve. For instance, Gaudio et al. (2008) showed that Cytisus scoparius cover 96 increased regularly from 0 to 80% of full sunlight, whereas *Rubus idaeus* cover followed a bell-shaped 97 curve, reaching a maximum at about 45% of full sunlight in the same light range. This shows that the 98 development of species commonly considered as light-requiring can be favoured by some shelter 99 compared with full light conditions. These types of study also highlight a minimal light level below 100 which the species considered is unable to develop. For example, Ricard and Messier (1996) showed 101 that Rubus idaeus was not found below light levels of 10% of full sunlight.

102

103 Despite the crucial role of competitive understorey vegetation in tree regeneration, studies 104 characterising and quantifying its development in response to abiotic factors are scant. Most of the 105 research on understorey vegetation has focused on its impact on tree seedlings (see e.g. 106 Lautenschlager, 1999; Harmer and Robertson, 2003; Provendier and Balandier, 2008) or is based on a 107 descriptive approach to their life cycle, abiotic preferences and area distribution (Rameau *et al.*, 1989; 108 Grime et al., 2007). In this approach, some studies (Weisberg et al., 2003; Royo and Carson, 2006) 109 underline our poor knowledge of "aggressive" understorey vegetation and advocate including it in 110 forest dynamics models, which is currently not done. However, the inclusion of a vegetation layer in 111 the understorey in modelling requires an ability to predict its development in response to light 112 availability, at least in temperate and tropical forests where light is assumed to be the most limiting 113 factor, below-ground resources being taken as most limiting in boreal and arid or warm-temperate 114 forests (Coomes and Grubb, 2000).

116 The ericaceous shrub Calluna vulgaris (L.), the grass Molinia caerulea (L.) Moench and the fern 117 Pteridium aquilinum (L.) Kuhn in Kersten, are three common understorey species in acidic temperate 118 forests and to a lesser extent in boreal forests. Their behaviour has been well researched in open areas 119 such as grass- or moorlands with regard to vegetation succession dynamics (see e.g. Aerts, 1989; 120 Mitchell et al., 2008; Chapman et al., 2009). Studies of forest ecosystems have already shown the 121 negative impact of these three species on tree seedling establishment and growth (see e.g. Dolling, 122 1996; Norberg et al., 2001; Gaudio et al., 2010) and their life cycle, reproduction and resource 123 requirements have been empirically described (for reviews, see Gimingham, 1960; Taylor et al., 2001; 124 Marrs and Watt, 2006). They are considered light-demanding species, with Ellenberg light-125 requirement indices of 6, 7 and 8 (on a scale of 9) for P. aquilinum, M. caerulea and C. vulgaris 126 respectively (Ellenberg et al., 1992), and tolerant to acid to highly acid poor soils, and to some extent 127 to waterlogging, which explains their broad distribution area in temperate and boreal forests. However, 128 these data are relatively empirical and need to be quantified to predict the behaviour of these three 129 understorey species and their dynamics in forest and especially in forest gaps.

A literature search on a scientific database (Web of Science, http://www.isiknowledge.com/) with the three species and light / growth added as keywords in the title yielded no results, illustrating the paucity of knowledge of the considered species.

133

134 This study set out to quantify i) the response curves of three understorey species (C. vulgaris, 135 *M. caerulea* and *P. aquilinum*) to light availability in terms of growth (assessed by cover and height), 136 morphology (assessed by the plant height-to-width ratio or for P. aquilinum, by the frond height-to-137 length ratio) and functional acclimation (LMA) and ii) the impact of the three species mainly on light 138 availability and to a lesser degree on the soil water content. The study presented here follows directly 139 on form the work of Gaudio et al. (2010), which underlined the negative impact of increasing densities 140 of the three understorey species on Scots pine seedling growth. Those authors considered out that the 141 development of these three species according to light availability should be quantified. This has been 142 done in the study reported here.

143

#### 144 **2. Materials and methods**

#### 145 2.1. Experimental site

In spring 2008 an experiment was set up in a nursery (Cemagref research centre, Nogent-sur-Vernisson, France,  $47^{\circ}50 \text{ N}-2^{\circ}44 \text{ E}$ ). The soil was sandy (79% sand, 13% loam and 8% clay) with a low organic matter content (24.8 g kg<sup>-1</sup>) and a pH<sub>water</sub> of 6.6. It was chemically poor (N: 0.922 g kg<sup>-1</sup>, P: 0.09 g kg<sup>-1</sup>, K: 0.156 g kg<sup>-1</sup>, Mg: 0.088 g kg<sup>-1</sup>) and presented a low cation exchange capacity (CEC: 7.095 cmol kg<sup>-1</sup>). The region where the experiment was carried out is characterized by a semioceanic climate with annual precipitation of 720 mm and mean annual temperature of 10.8°C (data recorded from 1971 to 2000). In 2009, a notable drought occurred from August to October: precipitation during this period was 86 mm in 2009, against a mean value of 184 mm for the samethree months in the years 1971-2000.

155

#### 156 2.2. Experimental design

The experiment was designed to quantify the response to light of three understorey species: *Calluna vulgaris* (L.) Hull, *Molinia caerulea* (L.) Moench and *Pteridium aquilinum* (L.) Kuhn in Kersten. Six

- 159 light treatments repeated in three randomised blocks were tested: 6, 11, 22, 36, 48 and 100% of full
- 160 sunlight. Except for the 100% light treatment, the different light levels were obtained using shading
- 161 nets, the spectral neutrality of which was checked using a spectrometer (USB2000, Ocean Optics,
- 162 Inc.). This resulted in 18 plots, 5 m long, 2 m wide and 1.2 m high when covered by a shading net,
- each containing three subplots of area 1 m<sup>2</sup> bordered by a 50 cm buffer zone and corresponding to the three understorey species. In each subplot,  $5 \times 5$  vegetation individuals were planted at regular 20 cm
- 165 intervals.

166 In March 2008, plant individuals were harvested in a forest located close to the nursery (Orleans 167 Forest) and immediately transferred to the nursery. They were at the seedling stage for *C. vulgaris* and 168 *M. caerulea*. For *P. aquilinum*, 10 cm segments of rhizome with a frond bud were collected at the 169 same time. Plant individuals were cautiously washed and then weighed. The plantation in the nursery 170 was set up so as to have the same mean biomass in each subplot for a given species.

- 171 Throughout the experiment all the plots were manually rid of all vegetation other than the three test 172 species.
- 173

### 174 *2.3. Measurements*

175 Most measurements were made in 2009, i.e. in the second year of vegetation growth, to ensure that the 176 observed response of the vegetation was due to current light conditions and not to the preceding forest 177 environment.

178

## 179 2.3.1. Soil water content (SWC) and temperature

SWC was measured in each subplot, which was equipped with a cylindrical TDR PVC tube that allowed SWC measurement in the first 20 cm of depth with a TDR probe (Trime-HD/IPH, IMKO GmbH, Germany). SWC measurements were made on August 8 and September 11, 2009, i.e. before and during the drought period. Temperature was measured and stored with one thermohygrometer (HOBO Pro Series, MicroDAQ.com Ltd, USA) per plot installed 90 cm from the ground. Measurements were made every 10 minutes throughout August and September 2009. Daily minimal and maximal temperatures were determined.

- 187
- 188 2.3.2. Light

189 Light was measured at three levels: i) outside the plots (full sunlight conditions), ii) just below the 190 shading nets but above the vegetation and iii) beneath the vegetation.

191 The photosynthetically active radiation (PAR 400–700 nm) available in each plot above vegetation 192 was measured in September 2009 using a 0.8 m-long ceptometer (Decagon Devices, Pullman, WA, 193 USA) composed of 80 photoelectric cells spaced every centimetre. Thirteen measurements were made 194 in every plot in order to assess the light variability in each plot. At the same time, incident PAR was 195 measured using another light sensor (Licor Inc., Lincoln, Nebraska, USA) located in full light. 196 Relative PAR above vegetation was calculated as the ratio between the PAR measured above 197 vegetation and the PAR measured in full light (× 100). The thirteen PAR values were pooled at the 198 plot level. Finally, PAR above vegetation had six light levels: 6, 11, 22, 36, 48 and 100% of incident 199 PAR.

200 In August 2009, the PAR was measured beneath the vegetation at 15 cm above the soil surface, due to 201 the size of the support, using a light sensor (PAR quantum SKP 215, Skye Instruments Ltd, UK) 202 connected to a datalogger (DataHog2, Skye Instruments Ltd, UK). Point light measurements were 203 made in all subplots every minute for 24 h. At the same time, incident PAR (outside the shading nets) 204 was measured with the same type of light sensor. The percentage of PAR beneath the vegetation was 205 calculated as the ratio between the PAR measured beneath the vegetation and the incident PAR 206  $(\times 100)$ . The PAR transmitted by the vegetation (transmittance) was calculated as the ratio between the 207 PAR measured beneath the vegetation and the PAR available above the vegetation in each plot (6, 11, 208 22, 36, 48 and 100% of incident PAR).

209

### 210 2.3.3. Vegetation characteristics

211 On September 7 2009, the cover (percentage of the ground occupied by the vertical projection of the 212 foliage) was visually estimated on each subplot. To minimise bias linked to the visual estimation of 213 cover, measurements were always made by the same two operators. The mean vegetation height 214 (in cm) was measured as the total height of most of the foliage or fronds, sparse higher or smaller 215 shoots, leaves or fronds being ignored. For *M. caerulea*, vegetation height did not include floral stalks. 216 The height and width of all C. vulgaris and M. caerulea individuals were also measured to calculate 217 the foliar tuft height-to-width ratio. For P. aquilinum, the height and length of each frond were also 218 measured and used to calculate the frond height-to-length ratio.

In October 2009, the leaf mass on an area basis (LMA, mg cm<sup>-2</sup>) was calculated on the nine central individuals of all the subplots. On each individual we collected two leaves for *M. caerulea*, two terminal shoot cuttings about 3 cm long (due to the small size of the leaves) for *C. vulgaris* and two frond cuttings with second order ramifications for *P. aquilinum*. The leaves harvested were scanned using an area meter (LiCor Inc., Li-3100C Area Meter) to compute the leaf area, dried at 65°C for 4 days and weighed. The LMA at the subplot level was computed from the LMA of the nine individuals pooled.

#### 227 2.4. Data analysis

228 Data were analysed using Statgraphics Plus software (Statpoint Inc., Virginia). To highlight a potential 229 effect of PAR treatment on vegetation growth (height and cover), morphological characteristics pooled 230 at the subplot level (foliar tuft height-to-width and frond height-to-length ratios) and leaf functional 231 trait (LMA, leaf mass and leaf area), ANOVAs were compiled with block considered as a random 232 factor and PAR treatment and species as fixed factors. ANOVAs were also compiled to analyse the 233 PAR treatment effect on each species separately and the differences among the three species within 234 each PAR treatment. When relevant (P < 0.05), means were separated with a Tukey test. Regressions 235 were used to link the characteristics of all three species to light availability. Models including SWC in 236 addition to light were tested for all vegetation characteristics, but this variable was never retained in 237 the best model fitted.

The relationship between transmittance and cover of the three species was explored using the Beer-Lambert law of light attenuation in a turbid medium to obtain a light extinction coefficient k for each species:

241 Transmittance = 
$$e^{-(k.cover)}$$

ANOVAs were also compiled to explore the variation of the transmittance and the SWC according toPAR treatments and the species considered.

For all ANOVAs, the homogeneity of variances was tested. If this condition was not met, a logarithmic transformation of the variable was carried out. Normality of residuals was checked visually.

247

## **3. Results**

249 3.1. Effect of PAR treatment on soil water content (SWC) and temperature

The PAR treatment had a significant negative impact on SWC (P < 0.0001, Fig. 1). This decrease was more pronounced at the peak of the drought period (September 11) than at the beginning (August 8) (P = 0.003).

The daily maximal temperatures recorded during August and September 2009 increased with light availability (P < 0.0001), whereas the opposite effect was observed for daily minimal temperatures (P < 0.0001). Thus the broadest temperature amplitude was recorded in PAR treatments of 100%. For August 8 and September 11, the SWC and the maximal temperature were negatively correlated (P < 0.05).

258

## 259 3.2. Vegetation development in response to light availability

260 The positive influence of PAR on vegetation cover differed among the three species (Table 1). Cover

261 was linked to PAR availability following a bell-shaped curve (Fig. 2) for C. vulgaris (P < 0.0001,

262  $R^2 = 90\%$ ), *M. caerulea* (P < 0.0001,  $R^2 = 86\%$ ) and *P. aquilinum* (P < 0.002,  $R^2 = 38\%$ ). The cover of

*P. aquilinum* already reached a high value of 75% at the PAR treatment of 6%. *C. vulgaris* and *M. caerulea* cover reached a maximum value around 50% and 45% of full sunlight respectively,
whereas this value was considerably lower for *P. aquilinum*, maximum cover being reached for a light
level of 20%.

At the two lowest PAR treatments (6% and 11%), *P. aquilinum* cover was significantly higher than that of *C. vulgaris* and *M. caerulea* ( $P \le 0.001$ ). At the PAR treatment of 6%, *M. caerulea* cover was

slightly higher than *C. vulgaris*, but the cover of the two species was equivalent at 11%. For PAR

treatments of 36 and 48%, the cover of all three species was statistically the same, reaching values

- 271 higher than 80%. At the PAR treatment of 100%, C. vulgaris cover was higher than M. caerulea
- 272 cover, with *P. aquilinum* intermediate between the two other species (P = 0.04).
- 273

The vegetation height did not vary with PAR treatment except for *P. aquilinum* (Table 1). For this species, the variation of height according to light availability followed the same pattern as cover, i.e. a bell-shaped curve increasing from 6 to 35% and decreasing for higher light levels (P < 0.0001,  $R^2 = 64\%$ ). From the PAR treatment of 22%, *P. aquilinum* was higher than the other two species (P < 0.05) and *C. vulgaris* was as high as or slightly smaller than *M. caerulea*. At the PAR treatment of 11%, there was no statistical difference among the three species, whereas at the lowest PAR treatment, *C. vulgaris* was the smallest species (P = 0.008).

281

## 282 3.3. Vegetation morphology in response to light availability

283 The foliar tuft height-to-width ratio decreased significantly with increasing light availability for C. vulgaris (P = 0.0005,  $R^2 = 51\%$ , Fig. 3a) and M. caerulea (P < 0.0001,  $R^2 = 82\%$ , Fig. 3b). For 284 285 C. vulgaris, the ratio decrease was due to a strong increase in foliar tuft width with increasing light 286 availability (P < 0.0001,  $R^2 = 71\%$ ), whereas tuft height barely changed (P = 0.05,  $R^2 = 16\%$ ). For 287 *M. caerulea*, this effect was less marked, but tuft width increased significantly and logarithmically 288 with light availability (P < 0.0001,  $R^2 = 80\%$ ), whereas the increase in tuft height followed a bell-289 shaped curve (P = 0.0001,  $R^2 = 59\%$ ). The frond height-to-length ratio of P. aquilinum increased with 290 light availability (P < 0.0001,  $R^2 = 93\%$ , Fig. 3c). This ratio was statistically the same in the three 291 lowest PAR treatments but it was not reached in the same way. The fronds growing in the PAR 292 treatment of 22% were systematically higher (P = 0.003) and longer (P = 0.01) than those growing in 293 the two lowest PAR treatments. Thus frond height followed a bell-shaped curve with increasing light 294 availability (P < 0.0001,  $R^2 = 72\%$ ), whereas frond length decreased exponentially (P = 0.03, 295  $R^2 = 23\%$ ).

296

#### 297 3.4. Leaf functional trait: the LMA

The LMA was influenced by the PAR treatment in a different way for each of the three species (Table 1, Fig. 4). LMA increased strongly with PAR availability for *C. vulgaris* (P < 0.0001,

- 300  $R^2 = 86\%$ ) and P. aquilinum (P < 0.0001,  $R^2 = 96\%$ ). For M. caerulea, a slight increase in LMA was 301 also recorded (P = 0.002,  $R^2 = 41\%$ ), but the differences between PAR treatments were not significant 302 (Table 1). The decrease in light availability had an impact on leaf mass, leaf area or both leaf mass and 303 area depending on the plant species considered. For C. vulgaris, the decrease in LMA in shaded 304 conditions was due to an increase in leaf area (P = 0.04,  $R^2 = 20\%$ ), whereas for *P. aquilinum*, it was 305 due to a decrease in leaf mass (P < 0.0001,  $R^2 = 61\%$ ). For *M. caerulea*, both leaf area (P = 0.002, 306  $R^2 = 42\%$ ) and leaf mass (P = 0.02,  $R^2 = 26\%$ ) increased when light availability decreased, so that 307 LMA stayed relatively unchanged whatever the PAR treatment.
- 308

## 309 *3.5. Impact of vegetation on light and SWC*

310 *3.5.1. Vegetation transmittance* 

311 The transmittance of C. vulgaris and P. aquilinum did not differ according to PAR treatment, whereas 312 for *M. caerulea* it decreased when light availability increased except at the PAR treatment of 100%, 313 where there was a slight increase in transmittance (Table 2). However, transmittance differed among 314 the three species for a given PAR treatment (Table 2). At the lowest PAR treatment, P. aquilinum 315 already intercepted a high proportion of light, resulting in a transmittance of only 10%, significantly 316 lower than the transmittance of the other two species. At the PAR treatment of 11%, the light 317 transmitted by *M. caerulea* decreased slightly, placing this species between *C. vulgaris* and 318 P. aquilinum. From the PAR treatments of 22% to 100%, M. caerulea and P. aquilinum transmitted an 319 equivalent proportion of light, significantly lower than C. vulgaris, except for the PAR treatment of 320 100% for which transmittance of *M. caerulea* was intermediate between the other two species.

- 321 Consistent with these results, the application of the Beer-Lambert law gave an extinction coefficient *k* 322 that was high for *P. aquilinum* (k = 0.029;  $R^2 = 11\%$ ), intermediate for *M. caerulea* (k = 0.017; 323  $R^2 = 68\%$ ) and much lower for *C. vulgaris* (k = 0.0004;  $R^2 = 3\%$ ) (Fig. 5).
- 324
- 325 *3.5.2. Soil water content (SWC)*

The SWC was negatively affected by PAR treatment and differed among the three species (Table 2), the SWC in the *M. caerulea* and *P. aquilinum* subplots being overall lower than the SWC in the *C. vulgaris* subplots. As the interaction between PAR treatment and the species effect was not significant, the SWC was in part species-dependent. However, the differences in SWC among the three species for a given PAR treatment were not significant except at the PAR treatment of 36%, where the SWC was slightly smaller in *M. caerulea* plots than in *C. vulgaris* plots, with *P. aquilinum* intermediate (P = 0.02).

- For *C. vulgaris* and *M. caerulea*, the SWC of the two lowest PAR treatments were equivalent and higher than all the other PAR treatments (P = 0.002 and P < 0.0001 respectively). SWC in
- *P. aquilinum* plots was statistically the same in all the PAR treatments, but the trend of the SWC
- decrease was nearly significant (P = 0.09).

## 338 **4. Discussion**

339 4.1. Vegetation growth in response to light availability

340 The cover of C. vulgaris and M. caerulea and to a lesser extent that of P. aquilinum increased with 341 light availability following a bell-shaped curve. Such a bell-shaped curve had already been recorded 342 for the cover of Rubus idaeus according to light (Gaudio et al., 2008) and for the growth of tree 343 species according to other abiotic factors (see e.g. Lyr, 1996). Another study of two ericaceous species 344 (Hawkins and Henry, 2004) also showed that plant aerial biomass was higher for a PAR level of 70% 345 than in full light conditions. Thus there was an optimum light level below and above which the cover 346 of the three species declined. In another study, Nabuurs (1996) described a model linking the cover of 347 the same three understorey species to light availability following logistic curves, at variance with our 348 results. However, the authors clearly specified that these curves were empirically built and need to be 349 validated by field measurements.

350 Nevertheless, PAR treatments of 100% were characterised by a low SWC linked to more extreme 351 temperatures induced by the absence of the shelter provided by the shading nets. However, SWC had 352 no significant impact on vegetation cover and was always higher than the SWC at the withering point 353 calculated as 3 to 5% for a sandy soil like the one in the experiment (Baize, 1988). We never found 354 SWC values below 9% at any time in the study, suggesting there was no pronounced water stress. 355 Thus the decrease in vegetation cover at the PAR treatment of 100% seems to be linked more to the 356 environmental conditions in full light, i.e. a high light level that could decrease photosynthetic activity, 357 extreme temperatures and potential low relative air humidity, than to any water deficit. The light 358 threshold above which cover decreased was highest for C. vulgaris and lowest for P. aquilinum, with 359 *M. caerulea* intermediate, consistent with the classification of Ellenberg (1992), i.e. light-requirement 360 indices of 6, 7 and 8 for P. aquilinum, M. caerulea and C. vulgaris respectively. However, our results 361 clearly show that the three species and especially P. aquilinum are not strictly light-requiring species 362 and that the differences between the three species in terms of light requirement are more pronounced 363 than the Ellenberg indices suggest. This is a reminder, as highlighted in other studies (Dzwonko, 364 2001), that the Ellenberg indices should be used with caution.

365 At the two lowest PAR treatments, the cover of *P. aquilinum* was significantly higher than that of the 366 other two species and almost at its maximum value, showing that even at very low light levels, this 367 species was well developed with a cover of 75% at only 6% of full sunlight. This explains the weak 368 influence of light on *P. aquilinum* cover, at least with a minimal light value of 6%. Thus *P. aquilinum* 369 is able to grow in shaded forest understoreys. However, foliage development was characterised only 370 by cover in this study, i.e. vertical projection of the foliage on the soil. The same cover can be 371 produced in different ways, with one or many leaf or frond layers, i.e. the same cover percentage can 372 correspond to different leaf area indices (LAI). Thus although cover is certainly a most useful variable 373 to illustrate the competitive effect of a species on light availability, it does not necessarily reflect a real

tolerance to shade. We see here that *P. aquilinum* is able to develop in the year following its establishment but we do not know whether it could maintain itself in the longer term at low light levels. The carbohydrates stored in *P. aquilinum* rhizomes might become exhausted after a few years of growth in very shaded conditions, leading to an inability to produce new fronds.

378 C. vulgaris and M. caerulea are more light-requiring and reached a high cover from 36% of full 379 sunlight. M. caerulea seems to be less light-requiring than C. vulgaris as its cover was higher at the 380 PAR treatment of 6%. The cover of all three species was equivalent and high (> 83%) at the PAR 381 treatments of 36% and 48%, but C. vulgaris slightly overtopped the other two species at the PAR 382 treatment of 100%, suggesting that it tolerates full sunlight better.

- 383 Unlike vegetation cover, vegetation height was not affected by light availability except for 384 *P. aquilinum*, where a height increase occurred with increasing PAR. From the PAR treatment of 22%, 385 *P. aquilinum* grew higher than the other two species. Vegetation cover therefore seems to be a better 386 variable than vegetation height to quantify the response of vegetation to light availability. 387 Nevertheless, in a forest context when considering tree seedlings, vegetation height can give 388 information on the time that an established tree seedling will spend in the shade provided by the 389 understorey vegetation. From this point of view, a tree seedling growing in *P. aquilinum* in a medium 390 or strongly lit understorey would be more impeded than one growing in C. vulgaris or M. caerulea, as 391 the time to overtake P. aquilinum would be longer. As described by Goldberg (1990), asymmetric 392 competition occurs when two plants differ in height. In this case, the smallest individual response to 393 competition is related to the resource level induced by the tallest individual, whereas if the competition 394 is symmetric (plants of the same height), both individuals can make a noticeable impact on resource 395 levels.
- 396

## 397 4.2. Vegetation morphology in response to light availability

398 The foliar tuft height-to-width ratio of C. vulgaris and M. caerulea decreased when light availability 399 increased by an increase in the foliar tuft width, whereas foliar tuft height varied little or not at all. 400 Thus individuals of the two species were stockier in strongly lit conditions. This effect is not 401 illustrated in the literature for herbaceous or shrubby species, but it can be placed in parallel with 402 results observed on tree response to light availability. Numerous studies have shown that the stem 403 height / diameter ratio of trees decreases with light availability, suggesting that shade affects stem 404 diameter growth more negatively than it does height growth (Petritan et al., 2009). For shade-405 intolerant species, a height increment can even occur in response to shade, in a "shade-avoidance 406 reaction", corresponding to a height increment added to potentially seek more light (Dehlin et al., 407 2004).

The frond height-to-length ratio of *P. aquilinum* increased with light availability. Thus the fronds growing in full light conditions were approximately as high as they were long, lending the frond an erect posture, whereas fronds in the PAR treatment of 6% were nearly twice as long as they were high, 411 with a spreading posture and fronds trailing on the ground. As noticed by Koop and Hilgen (1987) and

- 412 observed in dark forest understoreys (personal observation), this flexible posture in shaded conditions
- 413 allows *P. aquilinum* to climb along tree trunks and branches to seek more strongly lit environments.
- 414

#### 415 4.3. Leaf functional trait, LMA

416 The LMA has been shown to reflect adaptation of tree species to light (see e.g. King, 2003; Gaudio et 417 al., 2010; Rodriguez-Calcerrada et al., 2010). This leaf trait varied differently with light availability 418 according to the understorey species considered; the LMA of C. vulgaris and P. aquilinum increased 419 with light availability, but it remained nearly unchanged for *M. caerulea*. However, the variation of 420 LMA with light was not induced by the same processes for the two components of LMA, i.e. the leaf 421 mass and the leaf area. For C. vulgaris, the decrease in light availability led to an increase in leaf area, 422 while the leaf mass remained stable, i.e. it can be assumed that priority was given to the light 423 interception expressed by the leaf area at the expense of the light use efficiency linked to the amount 424 of cellular material involved in photosynthesis. However, although this species is able to maintain the 425 same leaf mass while increasing its leaf area in shaded conditions compared with strongly lit ones, the 426 lower cover in shaded conditions compared with strongly lit ones suggests the production of fewer 427 leaves. Other studies on ericaceous species have also highlighted a strong response of LMA (or SLA, 428 Specific Leaf Area, the reverse) to light availability, showing that leaf area always increases in shaded 429 conditions while the thickness of each leaf decreases (Messier, 1992; Moola and Mallik, 1998), which 430 may or may not be linked to a decrease in leaf mass.

For *P. aquilinum*, the decrease in light availability led to a decrease in leaf mass, whereas leaf area remained stable, as also shown for two *Dryopteris* sp. ferns (Rünk and Zobel, 2007). In the results of Den Ouden (2000), the decrease in the frond mass is assumed to be linked to a decrease in the investment in the support tissues of the fronds, i.e. stem and rachis. This was illustrated by the high flexible posture of the fronds at the low light levels.

- For *M. caerulea*, both leaf mass and area increased in the same proportions when light decreased, so that LMA did not vary with light availability. In shaded conditions, *M. caerulea* therefore produced fewer leaves (as shown by the low vegetation cover at the PAR treatment of 6%) that were particularly
- 439 efficient for both light interception and light use efficiency.
- 440 Thus although the three understorey species implemented different strategies to resist shade, they all
- 441 showed a notable acclimation to low light levels.
- 442

## 443 4.4. Impact of vegetation on light and SWC

444 In the study presented here, vegetation transmittance calculated from the Beer-Lambert's law used 445 vegetation cover rather than LAI, which is traditionally used. Two reasons justify this choice: i) cover

- 446 can be easily measured in the field by forest managers and ii) our results and some other studies found
- 447 a reliable relationship between cover and transmittance. For example, Stadt and Lieffers (2005), who

- 448 compared LAI and cover to predict transmittance, concluded that even if cover is slightly less accurate
- than LAI, the difference is minor, arguing for the use of cover rather than LAI.
- 450

451 The cover of *M. caerulea* was sparse at the lowest PAR treatment of 6% and became denser when 452 PAR level increased. For this reason, this species transmitted more light in the two shaded treatments 453 than in more strongly lit conditions. The transmittance increased slightly in the PAR treatment of 454 100%, probably because of the decrease in *M. caerulea* cover in the PAR treatment of 100% compared 455 with the PAR treatment of 48%. The light extinction coefficient of *M. caerulea* was 0.017, i.e. very 456 close to the value of 0.018 found in another study (Gaudio et al., 2010). By contrast, C. vulgaris 457 transmitted the same light proportion whatever the PAR treatment, although its cover increased with 458 light availability. However, light beneath vegetation was not measured at ground level but at 15 cm 459 above the ground because of the size of the light sensor. The foliar tuft morphology of C. vulgaris and 460 the fact that light beneath vegetation was measured at 15 cm above the ground might explain these 461 results. C. vulgaris foliar tuft is very compact near the ground, while in its upper part only a few 462 branches spread out. The light sensor was therefore probably too high compared with C. vulgaris 463 individual heights to give the true light amount reaching the soil level beneath this species. For this 464 reason, the light extinction coefficient calculated for C. vulgaris was very low (0.0004) compared with 465 the results of another study where k = 0.012 (Gaudio *et al.*, 2010). Unlike the two other species, 466 P. aquilinum was highly developed from the lowest PAR treatment and so transmitted less than 10% 467 of the light it received for all PAR treatments except at the PAR treatment of 100%, where the 468 transmittance increased slightly, as was observed for M. caerulea. For this reason, P. aquilinum exhibited the highest light extinction coefficient (k = 0.029) and can be considered as highly 469 470 competitive for light even in conditions as shaded as 6%. The light extinction coefficient k of 471 *P. aquilinum* (0.029) was slightly higher than that (0.022) found for this species in the study of Gaudio 472 et al. (2010). However, the experimental designs of the two studies were different. Here, P. aquilinum 473 grew under shading nets (except for the PAR treatment of 100%) that did not permit lateral input of 474 direct light. Our light conditions could thus be assumed to come closer to those of a forest 475 environment, so the *k* value is probably closer to the real *k* of *P*. aquilinum.

Differences between the three species concerning light interception are probably due to their foliar morphological characteristics. *P. aquilinum* forms dense covering foliage even for low light levels of 6% whereas the other two species have sparser foliage. Sonohat *et al.* (2002) compared light interception by the grass *Festuca arundinacea* and by the legume species *Trifolium repens*. The results showed that for the same LAI the light interception capacity of the grass was lower than that of the legume species due to its erect posture compared with the planophile posture of the other species.

482

483 Compared with the species effect on transmittance, the effect on SWC was low, no clearly marked 484 difference being found among the three species, except that SWC was lower overall in *P. aquilinum*  485 and *M. caerulea* subplots than in *C. vulgaris* subplots with all plots pooled. However, no difference 486 was recorded among the three species within the same treatment. Thus the three species may have the 487 same behaviour concerning water absorption, although the proximity of the three subplots within a 488 plot may have erased potential differences among the three species.

489

## 490 **5.** Conclusion

## 491 5.1. Practical implications

492 Our results showed C. vulgaris to be the most light-requiring species, followed by M. caerulea and 493 then by P. aquilinum. This last species is particularly tolerant to shade and showed a strong growth 494 and consequently a high light interception for light levels as low as 6% of full sunlight. Hence seeking 495 to promote tree regeneration through controlling *P. aquilinum* in a forest understorey by acting on the 496 adult tree canopy and the resulting light reaching the understorey seems unrealistic. The control of this 497 species will inevitably require mechanical or chemical intervention. As reviewed by Marrs and Watt 498 (2006), P. aquilinum is very difficult to eradicate. The two main mechanical techniques often used to 499 manage this species are ploughing to cut the rhizomes or frond cutting before frond maturity. 500 However, both techniques need to be repeated every year for at least five years to really ensure 501 *P. aquilinum* eradication. The herbicide mostly used to control *P. aquilinum* is asulam, but once again, 502 herbicide application must be repeated in time. Also, as herbicide use is being banned in more and 503 more countries, the mechanical treatment would certainly be the only appropriate treatment to control 504 P. aquilinum in-forest.

505 Conversely, C. vulgaris and M. caerulea reached high covers only for light levels above 20%. This 506 means that foresters could control the development of both species by decreasing light in the 507 understorey below 20%, which is dependent on adult tree density and identity. However, the possible 508 control of the two species depends mainly on the light requirement of the tree species that the foresters 509 want to regenerate. In acidic temperate forests, these two species are often encountered in the 510 understorey of Pinus sylvestris, P. pinaster or Quercus petraea and Q. robur stands. The two pines are 511 classified as light-demanding species and the two oaks as medium light-demanding species (Von 512 Lüpke, 1998; Richardson, 2000). As pointed out by Sonohat et al. (2004), transmittance below 20% in 513 *P. sylvestris* adult stands is linked to a basal area above  $35 \text{ m}^2 \text{ ha}^{-1}$ . As this basal area range is often 514 found in P. sylvestris stands (see e.g. Pérot et al., 2007; Chabaud and Nicolas, 2009), it seems that the 515 two understorey species could be controlled through adult canopy management in these stand types in 516 such a way as to ensure *P. sylvestris* regeneration, considering a light availability of 20% to be 517 sufficient for Scots pine regeneration, at least in temperate acidic forests. Conversely, Berbigier and 518 Bonnefond (1995) underlined that the maximum LAI measured in *P. pinaster* stands in the temperate zone was around 4 m<sup>2</sup> m<sup>-2</sup>, corresponding to a light transmittance of 30%. In this case, the amount of 519 520 light arriving in the understorey is always too high to allow C. vulgaris and M. caerulea control by 521 overstorey management. Concerning oaks, Balandier et al. (2006b) showed that a transmittance below

- 522 20% in the understorey was associated with a basal area above approximately  $18 \text{ m}^2 \text{ ha}^{-1}$ , which is 523 relatively low standing value compared with the current basal areas characteristic of oak stands, which 524 are around 25 m<sup>2</sup> ha<sup>-1</sup> (Jarret, 2004, for the Orleans forest). As the light requirement to ensure oak 525 regeneration is around 15 to 20% of full sunlight (Von Lüpke, 1998), the two understorey species 526 could probably not be controlled in oak stands to ensure oak regeneration.
- 527

## 528 5.2. Ecological implications

529 The monopolistic behaviour of the three species in-forest, especially *P. aquilinum*, seems to result 530 mainly from their capacity to develop a dense cover at low light levels. Thus a light availability of 531 10% allowed a cover around 90% for P. aquilinum and 50% for C. vulgaris and M. caerulea leading 532 to the dominance of the three species in the understorey. Indeed, the possibilities of development of 533 the three species in deep shade seem to have been underestimated in many cases, at least for 534 P. aquilinum. Besides other strategies of establishment such as the production of a large and persistent 535 seed bank or resprouting for C. vulgaris, the formation of a very dense and deep root system and 536 lateral vegetative spread for *M. caerulea* and again a persistent seed bank, the development of a highly 537 ramified and often clonal underground rhizome for P. aquilinum, the feature of rapid aerial 538 development forming a dense canopy in shade could explain the strong exclusion of other species in 539 stands where these species are present. According to Grime et al. (2007), P. aquilinum is classified as 540 a competitor (C) and the two other species as stress-tolerant competitors (SC). However, Grime (2001) 541 defined the competitors, displaying high growth rates, as being adapted to environmental conditions 542 with high resource availability, whereas stress-tolerators, with low growth rates, are adapted to 543 resource-limited environments. Our results partly conflict with the Grime classification of these three 544 species, as we found they displayed high aerial growth rates in shaded environments.

545

## 546 Acknowledgements

547 This work was supported by a grant from the "Office National des Forêts" (National Forestry
548 Commission) and from the "Région Centre" (Centre Region, France). The authors also thank Aurélien
549 Brochet, Vincent Seigner, Florian Vast, Michel Bonin and André Marquier for their valuable field
550 assistance.

|--|

553	Aerts, R., 1989.	Aboveground	biomass	and	nutrient	dynamics	of	Calluna	vulgaris	and	Molinia
554	<i>caerulea</i> in a dry	heathland. Oiko	os 56, 31-3	38.							

- 555
- Aerts, R., Boot, R.G.A., Vanderaart, P.J.M., 1991. The relation between aboveground and belowground biomass allocation patterns and competitive ability. Oecologia 87, 551-559.
- 558
- Aikens, M.L., Ellum, D., McKenna, J.J., Kelty, M.J., Ashton, M.S., 2007. The effects of disturbance
  intensity on temporal and spatial patterns of herb colonization in a southern New England mixed-oak
  forest. Forest Ecology and Management 252, 144-158.
- 562

Aranda, I., Pardo, F., Gil, L., Pardos, J.A., 2004. Anatomical basis of the change in leaf mass per area
and nitrogen investment with relative irradiance within the canopy of eight temperate tree species.
Acta Oecologica 25, 187-195.

- 566
- Aubin, I., Beaudet, M., Messier, C., 2000. Light extinction coefficients specific to the understory
  vegetation of the southern boreal forest, Quebec. Canadian Journal of Forest Research 30, 168-177.
- Aussenac, G., 2000. Interactions between forest stands and microclimate: ecophysiological aspects
  and consequences for silviculture. Annals of Forest Science 57, 287-301.
- 572

573 Baize, D., 1988. Guide des analyses courantes en pédologie. INRA eds, Orléans, France.

- 574
- 575 Balandier, P., Collet, C., Miller, J.H., Reynolds, P.E., Zedaker, S.M., 2006a. Designing forest 576 vegetation management strategies based on the mechanisms and dynamics of crop tree competition by 577 neighbouring vegetation. Forestry 79, 3-27.
- 578

579 Balandier, P., Sonohat, G., Sinoquet, H., Varlet-Grancher, C., Dumas, Y., 2006b. Characterisation, 580 prediction and relationships between different wavebands of solar radiation transmitted in the 581 understorey of even-aged oak (*Quercus petraea*, *Q. robur*) stands. Trees 20, 363-370.

- 582
- Balandier, P., Frochot, H., Sourisseau, A., 2009. Improvement of direct tree seeding with cover crops
  in afforestation: Microclimate and resource availability induced by vegetation composition. Forest
  Ecology and Management 257, 1716-1724.
- 586

- 587 Berbigier, P., Bonnefond, J.M., 1995. Measurement and modelling of radiation transmission within a
- 588 stand of maritime pine (*Pinus pinaster* Ait). Annals of Forest Science 52, 23-42.
- 589
- 590 Callaway, R.M., 1995. Positive interactions among plants. Botanical Review 61, 306-349.
- 591
- 592 Chabaud, L., Nicolas, L., 2009. Guide des sylvicultures. Pineraies des plaines du Centre et du Nord-
- 593 Ouest. Office National des Forêts (eds), Paris, France.
- 594
- Chapman, D.S., Termansen, M., Quinn, C.H., Jin, N.L., Bonn, A., Cornell, S.J., Fraser, E.D.G.,
  Hubacek, K., Kunin, W.E., Reed, M.S., 2009. Modelling the coupled dynamics of moorland
  management and upland vegetation. Journal of Applied Ecology 46, 278-288.
- 598
- Clinton, B.D., 2003. Light, temperature, and soil moisture responses to elevation, evergreen
  understory, and small canopy gaps in the southern Appalachians. Forest Ecology and Management
  186, 243-255.
- 602

603 Coll, L., Balandier, P., Picon-Cochard, C., Prevosto, B., Curt, T., 2003. Competition for water between
604 beech seedlings and surrounding vegetation in different light and vegetation composition conditions.
605 Annals of Forest Science 60, 593-600.

606

607 Coomes, D.A., Grubb, P.J., 2000. Impacts of root competition in forests and woodlands: A theoretical
608 framework and review of experiments. Ecological Monographs 70, 171-207.

- 609
- Davis, M.A., Wrage, K.J., Reich, P.B., Tjoelker, M.G., Schaeffer, T., Muermann, C., 1999. Survival,
  growth, and photosynthesis of tree seedlings competing with herbaceous vegetation along a waterlight-nitrogen gradient. Plant Ecology 145, 341-350.
- 613
- Dehlin, H., Nilsson, M.C., Wardle, D.A., Shevtsova, A., 2004. Effects of shading and humus fertility
  on growth, competition, and ectomycorrhizal colonization of boreal forest tree seedlings. Canadian
  Journal of Forest Research 34, 2573-2586.
- 617
- 618 Den Ouden, J., 2000. The role of bracken (*Pteridium aquilinum*) in forest dynamics. Thesis.
  619 Wageningen University, Netherlands, 218p.
- 620
- 621 Dolling, A.H.U., 1996. Interference of bracken (Pteridium aquilinum L. Kuhn) with Scots pine (Pinus
- 622 sylvestris L.) and Norway spruce (Picea abies L. Karst.) seedling establishment. Forest Ecology and
- 623 Management 88, 227-235.

- 624
- Dzwonko, Z. 2001. Assessment of light and soil conditions in ancient and recent woodlands by
  Ellenberg indicator values. Journal of Applied Ecology 38, 942-951.
- 627
- 628 Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., Paulißen, D., 1992. Zeigerwerte von
- 629 Pflanzen in Mitteleuropa, Scripta Geobotanica, Göttingen, Germany.
- 630
- 631 Farris, E., Filigheddu, R., 2008. Effects of browsing in relation to vegetation cover on common yew
- 632 (*Taxus baccata* L.) recruitment in Mediterranean environments. Plant Ecology 199, 309-318.
- 633
- 634 Fotelli, M.N., Gessler, A., Peuke, A.D., Rennenberg, H., 2001. Drought affects the competitive
- 635 interactions between *Fagus sylvatica* seedlings and an early successional species, *Rubus fruticosus*:
- responses of growth, water status and delta C-13 composition. New Phytologist 151, 427-435.
- 637
- Frochot, H., Armand, G., Gama, A., Nouveau, M., Wehrlen, L., 2002. La gestion de la végétation
  accompagnatrice : état et perspective. Revue forestière française 6, 505-520.
- 640
- 641 Gamborg, C., Larsen, J.B., 2003. 'Back to nature' a sustainable future for forestry? Forest Ecology642 and Management 179, 559-571.
- 643
- Gaudio, N., Balandier, P., Marquier, A., 2008. Light-dependent development of two competitive
  species (*Rubus idaeus*, *Cytisus scoparius*) colonizing gaps in temperate forest. Annals of Forest
  Science 65, 104.
- 647
- Gaudio, N., Balandier, P., Philippe, G., Dumas, Y., Jean, F., Ginisty, C., 2010. Light-mediated
  influence of three understorey species (*Calluna vulgaris, Pteridium aquilinum, Molinia caerulea*) on
  the growth of *Pinus sylvestris* seedlings. European Journal of Forest Research, doi 10.1007/s10342010-0403.
- 652
- 653 Gimingham, C.H., 1960. Biological flora of the British Isles. *Calluna vulgaris* (L.) Hull. Journal of
  654 Ecology 48, 455-483.
- 655
- Goldberg, D.E., 1990. Components of resource competition in plant communities. In: Grace, J.B.,
  Tilman, D. (Eds.), Perspectives on plant competition. Academic Press, London, Great Britain, pp. 27-
- 658 49.
- 659

- 660 Grime, J.P., 2001. Plant strategies, vegetation processes, and ecosystem properties. John Wiley and 661 sons (2nd ed.), Chichester, Great Britain.
- 662
- 663 Grime, J.P., Hodgson, J.G., Hunt, R., 2007. Comparative plant ecology, a functional approach to 664 common British species. Castlepoint Press, Chippenham, Great Britain.
- 665
- Harmer, R., Morgan, G., 2007. Development of *Quercus robur* advance regeneration following
  canopy reduction in an oak woodland. Forestry 80, 137-149.
- 668
- Harmer, R., Robertson, M., 2003. Seedling root growth of six broadleaved tree species grown in
  competition with grass under irrigated nursery conditions. Annals of Forest Science 60, 601-608.
- 671
- Hawkins, B., Henry, G., 2004. Effect of nitrogen supply and irradiance on seedling survival and
  biomass in two evergreen, ericaceous species. Scandinavian Journal of Forest Research 19, 415-423.
- 674
- Heinrichs, S., Schmidt, W., 2009. Short-term effects of selection and clear cutting on the shrub and
  herb layer vegetation during the conversion of even-aged Norway spruce stands into mixed stands.
  Forest Ecology and Management 258, 667-678.
- 678
- Heithecker, T.D., Halpern, C.B., 2006. Variation microclimate associated with dispersed-retention
  harvests in coniferous forests of western Washington. Forest Ecology and Management 226, 60-71.
- 681
- Jarret, P., 2004. Guide des sylvicultures. Chênaie atlantique. Office National des Forêts (eds), Paris,
  France.
- 684
- King, D.A., 2003. Allocation of above-ground growth is related to light in temperate deciduoussaplings. Functional Ecology 17, 482-488.
- 687
- Koop, H., Hilgen, P., 1987. Forest dynamics and regeneration mozaic shifts in unexploited beech
  (*Fagus sylvatica*) stands at Fontainebleau (France). Forest Ecology and Management 20, 135-150.
- 690
- Lautenschlager, R.A., 1999. Environmental resource interactions affect red raspberry growth and its
   competition with white spruce. Canadian Journal of Forest Research 29, 906-916.
- 693
- Lyr, H., 1996. Effect of the root temperature on growth parameters of various European tree species.Annals of Forest Science 53, 317-323.
- 696

- 697 Malcolm, D.C., Mason, W.L., Clarke, G.C., 2001. The transformation of conifer forests in Britain -
- regeneration, gap size and silvicultural systems. Forest Ecology and Management 151, 7-23.
- 699
- 700 Marrs, R.H., Watt, A.S., 2006. Biological flora of the British Isles: *Pteridium aquilinum* (L.) Kuhn.
- 701 Journal of Ecology 94, 1272-1321.
- 702
- Messier, C., 1992. Effects of neutral shade and growing media on growth, biomass allocation, and
   competitive ability of *Gaultheria shallon*. Canadian Journal of Botany 70, 2271-2276.
- 705
- Mitchell, R.J., Rose, R.J., Palmer, S.C.F., 2008. Restoration of *Calluna vulgaris* on grass-dominated
  moorlands: The importance of disturbance, grazing and seeding. Biological Conservation 141, 21002111.
- 709
- 710 Moola, F.M., Mallik, A.U., 1998. Morphological plasticity and regeneration strategies of velvet leaf
- blueberry (*Vaccinium myrtilloides* Michx.) following canopy disturbance in boreal mixedwood forests.
- 712 Forest Ecology and Management 111, 35-50.
- 713
- Nabuurs, G.J., 1996. Quantification of herb layer dynamics under tree canopy. Forest Ecology andManagement 88, 143-148.
- 716
- Norberg, G., Dolling, A., Jaderlund, A., Nilsson, M.C., Zackrisson, O., 2001. Control of heather
  (*Calluna vulgaris* (L.) Hull) by steam treatment: Effects on establishment and early growth of Scots
  pine. New Forests 21, 187-198.
- 720
- Parker, W.C., Pitt, D.G., Morneault, A.E., 2009. Influence of woody and herbaceous competition on
  microclimate and growth of eastern white pine (*Pinus strobus* L.) seedlings planted in a central
  Ontario clearcut. Forest Ecology and Management 258, 2013-2025.
- 724
- Pérot, T., Perret, S., Meredieu, C., Ginisty, C., 2007. Prévoir la croissance et la production du Pin
  sylvestre : le module Sylvestris sous Capsis 4. Revue Forestière Française 1, 57-84.
- 727
- 728 Petritan, A.M., von Lupke, B., Petritan, I.C., 2009. Influence of light availability on growth, leaf
- morphology and plant architecture of beech (Fagus sylvatica L.), maple (Acer pseudoplatanus L.) and
- ash (*Fraxinus excelsior* L.) saplings. European Journal of Forest Research 128, 61-74.
- 731
- Prévosto, B., Robert, A., Coquillard, P., 2004. Development of *Cytisus scoparius* L. at stand and
  individual level in a mid-elevation mountain of the French Massif Central. Acta Oecologica 25, 73-81.

775	Dresse lier D. Deley lier D. 2008. Commend offerte of commetitien her energy (C
735	Provendier, D., Balandier, P., 2008. Compared effects of competition by grasses ( <i>Graminoids</i> ) and
/30	broom ( <i>Cytisus scoparius</i> ) on growth and functional traits of beech saplings ( <i>Fagus sylvatica</i> ). Annals
131	of Forest Science 65, 510.
/38	Pamaay I.C. Mansian D. Dymá C. Timbal I. Lagainta A. Dynant D. Kallar D. 1080 Elara
739 740	forestière française, Plaines et collines. IDF / ENGREF, France.
741	
742	Ricard, J.P., Messier, C., 1996. Abundance, growth and allometry of red raspberry ( <i>Rubus idaeus</i> L)
743	along a natural light gradient in a northern hardwood forest. Forest Ecology and Management 81, 153-
744	160.
745	
746	Richardson, D.M., 2000. Ecology and biogeography of Pinus. Cambridge University Press,
747	Cambridge, Great Britain.
748	
749	Rodriguez-Calcerrada, J., Cano, F.J., Valbuena-Carabana, M., Gil, L., Aranda, I., 2010. Functional
750	performance of oak seedlings naturally regenerated across microhabitats of distinct overstorey canopy
751	closure. New Forests 39, 245-259.
752	
753	Royo, A.A., Carson, W.P., 2006. On the formation of dense understory layers in forests worldwide:
754	consequences and implications for forest dynamics, biodiversity, and succession. Canadian Journal of
755	Forest Research 36, 1345-1362.
756	
757	Rünk, K., Zobel, K., 2007. Phenotypic plasticity and biomass allocation pattern in three Dryopteris
758	(Dryopteridaceae) species on an experimental light-availability gradient. Plant Ecology 193, 85-99.
759	
760	Schütz, J.P., 1999. Close-to-nature silviculture: is this concept compatible with species diversity?
761	Forestry 72, 359-366.
762	
763	Sonohat, G., Balandier, P., Ruchaud, F., 2004. Predicting solar radiation transmittance in the
764	understory of even-aged coniferous stands in temperate forests. Annals of Forest Science 61, 629-641.
765	
766	Stadt, K.J., Lieffers, V.J., 2005. Comparing PAR transmission models for forest understorey
767	vegetation. Applied Vegetation Science 8, 65-76.
768	
769	Taylor, K., Rowland, A.P., Jones, H.E., 2001. Molinia caerulea (L.) Moench. Journal of Ecology 89,
770	126-144.

772	Thomas, S.C., Halpern, C.B., Falk, D.A., Liguori, D.A., Austin, K.A., 1999. Plant diversity in
773	managed forests: Understory responses to thinning and fertilization. Ecological Applications 9, 864-
774	879.
775	
776	Tilman, D., 1990. Mechanisms of plant competition for nutrients: the elements of a predictive theory
777	of competition. In: Grace, J.B., Tilman, D. (Eds.), Perspectives on plant competition. Academic Press,
778	London, Great Britain, pp. 117-141.
779	
780	Von Lüpke, B., 1998. Silvicultural methods of oak regeneration with special respect to shade tolerant
781	mixed species. Forest Ecology and Management 106, 19-26.
782	
783	Wagner, S., Fisher, H., Huth, F., 2010. Canopy effects on vegetation caused by harvesting and
784	regeneration treatments. European Journal of Forest Research doi 10.1007/s10342-010-0378-z.
785	
786	Weisberg, P.J., Hadorn, C., Bugmann, H., 2003. Predicting understorey vegetation cover from
787	overstorey attributes in two temperate mountain forests. Forstwissenschaftliches Centralblatt 122, 273-
788	286.
789 790	

- 791 Fig 1: Relationships between soil water content (SWC) and light availability (PAR) on August 8 and
- 792 September 11, 2009 under shading nets. Regression equations, SWC =
- 793 August 8:  $26.1736 1.2668*\sqrt{PAR} (R^2 = 34\%, P < 0.0001)$
- 794 September 11: 35.8645\*PAR<sup>-0.25707</sup> ( $R^2 = 59\%$ , P < 0.0001)



- 807 Fig 2: Cover (%) of Calluna vulgaris, Molinia caerulea and Pteridium aquilinum (c) in September
- 808 2009 according to light (PAR) in a nursery experiment. Regression equations, Cover =
- *C. vulgaris*: 80.7458 1.10349\*PAR + 29.0551\*LOG(PAR<sup>2</sup>) (*R*<sup>2</sup> = 90%)
- *M. caerulea*: -54.3864 1.10152\*PAR + 25.4721\* LOG(PAR<sup>2</sup>) ( $R^2 = 86\%$ )
- *P. aquilinum*:  $49.4357 0.588658*PAR + 9.16872* LOG(PAR<sup>2</sup>) (<math>R^2 = 38\%$ )



- 828 Fig 3: Foliar tuft height / width ratios of *Calluna vulgaris* (a) and *Molinia caerulea* (b) and frond
- 829 height / length ratio of *Pteridium aquilinum* (c) in September 2009 according to light in a nursery
- 830 experiment. Regression equations, foliar tuft height / width or frond height / length rartios =
- *C. vulgaris*:  $11.2784*PAR^{-0.36508}$  ( $R^2 = 51\%$ , P = 0.0005)
- *M. caerulea*: 24.0746\*PAR<sup>-0.424424</sup> ( $R^2 = 82\%$ , P < 0.0001)
- *P. aquilinum*:  $0.256794 + 0.0657518*\sqrt{PAR}$  ( $R^2 = 93\%$ , P < 0.0001)



<u>Fig 4</u>: Relationships between the leaf mass on an area basis (LMA) of three understorey species
 (*Calluna vulgaris, Molinia caerulea, Pteridium aquilinum*) planted under shading nets in a nursery
 experiment in spring 2008 and the light availability (PAR) in September 2009. Regression equations,
 LMA =

- *C. vulgaris*:  $4.70695*PAR^{0.344563}$  ( $R^2 = 86\%$ , P < 0.0001)
- *M. caerulea*:  $5.25173 + 0.29451*\sqrt{PAR}$  ( $R^2 = 41\%$ , P = 0.002)

-C. vulgaris

M. caerulea

quilinum

Incident PAR (%)

*P. aquilinum*:  $0.732736*PAR^{0.572848}$  ( $R^2 = 96\%$ , P < 0.0001)

LMA (mg cm-2)





- 890 Fig 5: Relationships between vegetation cover of three understorey species (Calluna vulgaris, Molinia
- *caerulea*, *Pteridium aquilinum*) and the light they transmitted (transmittance) in a nursery experiment.
- 892 Regression equations, transmittance =
- *C. vulgaris*: exp -(0.00377792\*Cover) ( $R^2 = 3\%$ )
- *M. caerulea*: exp -(0.0167476\*Cover) ( $R^2 = 68\%$ )
- *P. aquilinum*: exp -(0.0288637\*Cover) ( $R^2 = 10\%$ )



908 <u>Table 1</u>: Cover, height and leaf mass on an area basis (LMA) in September 2009 of three understorey species

909 (*Calluna vulgaris*, *Molinia caerulea*, *Pteridium aquilinum*) planted under six PAR treatments in a nursery in 910 spring 2008.

		Cover (%)	Height (cm)	LMA (mg cm <sup>-2</sup> )
PAR (%) =	6	$10 \pm 0 (c)^{C}$	$20 \pm 6 (a)^{B}$	$8.7 \pm 1.5 (c)^{A}$
	11	$57 \pm 6 (b)^{B}$	$24 \pm 5 (a)^{A}$	$10.4 \pm 0.6 (bc)^{A}$
	22	$77 \pm 8 (a)^{B}$	$32 \pm 11 (a)^{C}$	$13.7 \pm 3.3 (bc)^{A}$
	36	$83 \pm 3 (a)^{A}$	$30 \pm 8 (a)^{B}$	$18.4 \pm 1.8 \text{ (ab)}^{A}$
	48	$93 \pm 3 (a)^{A}$	$29 \pm 6 (a)^{C}$	$17.7 \pm 1.1 \text{ (ab)}^{A}$
	100	$78 \pm 8 (a)^{A}$	$27 \pm 10 (a)^{B}$	$21.8 \pm 2.5 (a)^{A}$
PAR (%) =	6	$23 \pm 3 (c)^{B}$	$31 \pm 3 (a)^{A}$	$5.9 \pm 0.4 (a)^{A}$
	11	$67 \pm 6 (b)^{B}$	$36 \pm 6 (a)^{A}$	$6.4 \pm 1.0 \text{ (a)}^{B}$
	22	$80 \pm 5 (ab)^{AB}$	$44 \pm 14 (a)^{B}$	$6.8 \pm 1.4 (a)^{B}$
	36	$83 \pm 3 (ab)^{A}$	$43 \pm 10 (a)^{B}$	$7.0 \pm 1.3 (a)^{B}$
	48	$88 \pm 8 (a)^{A}$	$42 \pm 6 (a)^{B}$	$6.7 \pm 0.2 (a)^{B}$
	100	$71 \pm 10 (ab)^{B}$	$30 \pm 3 (a)^{B}$	$8.5 \pm 0.6 (a)^{B}$
$\mathbf{D}\mathbf{A}\mathbf{D}(0/) =$	(	75 + 5 (h)A	27 + 5 (a) <sup>A</sup>	$21 + 0.1 (1)^{C}$
PAK (%) –	0	$73 \pm 3(0)$	$27 \pm 3$ (c) $27 \pm 16$ (b c) <sup>A</sup>	$2.1 \pm 0.1 (u)$
	11	$93 \pm 3$ (ab)	$37 \pm 10 (bc)$	$2.8 \pm 0.6$ (cd)
	22	$95 \pm 5 (ab)^{-1}$	$58 \pm 11 (abc)^{11}$	$4.0 \pm 0.5 (c)^{B}$
	36	$88 \pm 10 (ab)^{4}$	$60 \pm 18 \text{ (ab)}^{4}$	$6.2 \pm 0.2$ (b) <sup>B</sup>
	48	$98 \pm 3 (a)^{A}$	$69 \pm 2 (a)^{A}$	$6.9 \pm 0.7 (b)^{B}$
	100	$75 \pm 10 (b)^{AB}$	$51 \pm 3 (abc)^{A}$	$10.0 \pm 1.1 (a)^{B}$
		NS	0.0001	NS
		0.0006	0.0003	< 0.0001
		< 0.0001	0.009	< 0.0001
		< 0.0001	0.003	< 0.0001
	PAR (%) = PAR (%) = PAR (%) =	PAR (%) = $\begin{pmatrix} 6 \\ 11 \\ 22 \\ 36 \\ 48 \\ 100 \end{pmatrix}$ PAR (%) = $\begin{pmatrix} 6 \\ 11 \\ 22 \\ 36 \\ 48 \\ 100 \end{pmatrix}$ PAR (%) = $\begin{pmatrix} 6 \\ 11 \\ 22 \\ 36 \\ 48 \\ 100 \end{pmatrix}$	$PAR (\%) = \begin{cases} 6 & 10 \pm 0 (c)^{C} \\ 11 & 57 \pm 6 (b)^{B} \\ 22 & 77 \pm 8 (a)^{B} \\ 36 & 83 \pm 3 (a)^{A} \\ 48 & 93 \pm 3 (a)^{A} \\ 100 & 78 \pm 8 (a)^{A} \end{cases}$ $PAR (\%) = \begin{cases} 6 & 23 \pm 3 (c)^{B} \\ 11 & 67 \pm 6 (b)^{B} \\ 22 & 80 \pm 5 (ab)^{AB} \\ 36 & 83 \pm 3 (ab)^{A} \\ 48 & 88 \pm 8 (a)^{A} \\ 100 & 71 \pm 10 (ab)^{B} \end{cases}$ $PAR (\%) = \begin{cases} 6 & 75 \pm 5 (b)^{A} \\ 11 & 93 \pm 3 (ab)^{A} \\ 22 & 95 \pm 5 (ab)^{A} \\ 36 & 88 \pm 10 (ab)^{A} \\ 48 & 98 \pm 3 (a)^{A} \\ 100 & 75 \pm 10 (b)^{AB} \end{cases}$ $NS \\ 0.0006 \\ <0.0001 \\ <0.0001 \end{cases}$	$PAR (\%) = \begin{cases} 6 & 10 \pm 0 (c)^{C} & 20 \pm 6 (a)^{B} \\ 11 & 57 \pm 6 (b)^{B} & 24 \pm 5 (a)^{A} \\ 22 & 77 \pm 8 (a)^{B} & 32 \pm 11 (a)^{C} \\ 36 & 83 \pm 3 (a)^{A} & 30 \pm 8 (a)^{B} \\ 48 & 93 \pm 3 (a)^{A} & 29 \pm 6 (a)^{C} \\ 100 & 78 \pm 8 (a)^{A} & 27 \pm 10 (a)^{B} \end{cases}$ $PAR (\%) = \begin{cases} 6 & 23 \pm 3 (c)^{B} & 31 \pm 3 (a)^{A} \\ 11 & 67 \pm 6 (b)^{B} & 36 \pm 6 (a)^{A} \\ 22 & 80 \pm 5 (ab)^{AB} & 44 \pm 14 (a)^{B} \\ 36 & 83 \pm 3 (ab)^{A} & 43 \pm 10 (a)^{B} \\ 48 & 88 \pm 8 (a)^{A} & 42 \pm 6 (a)^{B} \\ 100 & 71 \pm 10 (ab)^{B} & 30 \pm 3 (a)^{B} \end{cases}$ $PAR (\%) = \begin{cases} 6 & 75 \pm 5 (b)^{A} & 27 \pm 5 (c)^{A} \\ 11 & 93 \pm 3 (ab)^{A} & 37 \pm 16 (bc)^{A} \\ 22 & 95 \pm 5 (ab)^{A} & 58 \pm 11 (abc)^{A} \\ 36 & 88 \pm 10 (ab)^{A} & 60 \pm 18 (ab)^{A} \\ 48 & 98 \pm 3 (a)^{A} & 69 \pm 2 (a)^{A} \\ 100 & 75 \pm 10 (b)^{AB} & 51 \pm 3 (abc)^{A} \end{cases}$ $NS & 0.0001 \\ 0.0006 & 0.0003 \\ <0.0001 & 0.009 \\ <0.0001 & 0.009 \end{cases}$

915 Lower case in parenthesis indicates a statistical difference (P < 0.05) between PAR treatments within the same 916 plant species. Upper case indicates a statistical difference among the three plant species for a given PAR

917 treatment. NS = non-significant.

923 <u>Table 2</u>: Transmittance and soil water content (SWC) in September 2009 within three understorey species

924 (Calluna vulgaris, Molinia caerulea, Pteridium aquilinum) planted under six PAR treatments in a nursery in

925 spring 2008.

926

			Transmittance (%)	SWC (%)
C. vulgaris	PAR (%) =	6	$86 \pm 5 (a)^{A}$	$23 \pm 3 (a)^{A}$
		11	$90 \pm 13 (a)^{A}$	$23 \pm 1 (a)^{A}$
		22	$57 \pm 13 (a)^{A}$	$20 \pm 5 (ab)^A$
		36	$82 \pm 9 (a)^{A}$	$19 \pm 1 (ab)^{A}$
		48	$74 \pm 18 (a)^{A}$	$14 \pm 2 (bc)^{A}$
		100	$72 \pm 16 (a)^{A}$	$11 \pm 1 (c)^{A}$
M. caerulea	PAR (%) =	6	$74 \pm 4 (a)^{A}$	$23 \pm 3 (a)^{A}$
		11	$49 \pm 13 (ab)^{B}$	$24 \pm 3 (a)^{A}$
		22	$17 \pm 11 \text{ (c)}^{\text{B}}$	$14 \pm 3 (b)^{A}$
		36	$14 \pm 3 (c)^{B}$	$11 \pm 2 (b)^{B}$
		48	$18 \pm 3 (c)^{B}$	$11 \pm 1 (b)^{A}$
		100	$33 \pm 7 (bc)^{AB}$	$11 \pm 2 (b)^{A}$
P. aquilinum	PAR (%) =	6	$10 \pm 6 (a)^{B}$	$19 \pm 3 (a)^{A}$
		11	$8 \pm 5 (a)^{C}$	$19 \pm 9 (a)^{A}$
		22	$7 \pm 3 (a)^{B}$	$18 \pm 0 (a)^{A}$
		36	$6 \pm 1 (a)^{B}$	$14 \pm 2 (a)^{AB}$
		48	$5 \pm 1 (a)^{B}$	$12 \pm 2 (a)^{A}$
		100	$16 \pm 13 (a)^{B}$	$12 \pm 2 (a)^{A}$
ANOVA (P)				
Block			NS	NS
Species			< 0.0001	0.006
PAR			0.003	< 0.0001
Species*PAR			0.002	NS

927

928 Lower case in parenthesis indicates a statistical difference (P < 0.05) between PAR treatments within the same 929 plant species. Upper case indicates a statistical difference among the three plant species for a given PAR 930 treatment. NS = non-significant.

931

932

933 934

. . .

935

936