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

3  
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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,  
29 *P. aquilinum* cover was high (75%) and intercepted a larger proportion of the light than the other two  
30 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**

44 In the forest understorey, tree seedlings and herbaceous or shrubby vegetation grow together and  
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.

79 However, as pointed out by Tilman (1990), competitive ability also depends on capacity to tolerate  
80 low resource levels, which is linked to various acclimation features such as slowed growth rate or  
81 shifts in functional traits that go from traits adapted for resource capture maximisation to traits adapted  
82 for resource storage efficiency. For instance, some functional leaf traits reflect ability to acclimate to  
83 low light levels. Thus the leaf mass on an area basis (LMA, g cm<sup>-2</sup>) has been shown to reflect the  
84 resource-induced stress encountered by plants (King, 2003; Aranda *et al.*, 2004; Provendier and  
85 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).

115

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.

130 A literature search on a scientific database (Web of Science, <http://www.isiknowledge.com/>) with the  
131 three species and light / growth added as keywords in the title yielded no results, illustrating the  
132 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 from 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*

146 In spring 2008 an experiment was set up in a nursery (Cemagref research centre, Nogent-sur-  
147 Vernisson, France, 47°50 N-2°44 E ). The soil was sandy (79% sand, 13% loam and 8% clay) with a  
148 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>,  
149 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  
150 (CEC: 7.095 cmol kg<sup>-1</sup>). The region where the experiment was carried out is characterized by a semi-  
151 oceanic climate with annual precipitation of 720 mm and mean annual temperature of 10.8°C (data  
152 recorded from 1971 to 2000). In 2009, a notable drought occurred from August to October:

153 precipitation during this period was 86 mm in 2009, against a mean value of 184 mm for the same  
154 three months in the years 1971-2000.

155

## 156 2.2. *Experimental design*

157 The experiment was designed to quantify the response to light of three understorey species: *Calluna*  
158 *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,  
163 each containing three subplots of area 1 m<sup>2</sup> bordered by a 50 cm buffer zone and corresponding to the  
164 three understorey species. In each subplot, 5×5 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*

180 SWC was measured in each subplot, which was equipped with a cylindrical TDR PVC tube that  
181 allowed SWC measurement in the first 20 cm of depth with a TDR probe (Trime-HD/IPH, IMKO  
182 GmbH, Germany). SWC measurements were made on August 8 and September 11, 2009, i.e. before  
183 and during the drought period. Temperature was measured and stored with one thermohygrometer  
184 (HOBO Pro Series, MicroDAQ.com Ltd, USA) per plot installed 90 cm from the ground.  
185 Measurements were made every 10 minutes throughout August and September 2009. Daily minimal  
186 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 ( $\times 100$ ). 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.

219 In October 2009, the leaf mass on an area basis (LMA,  $\text{mg cm}^{-2}$ ) was calculated on the nine central  
220 individuals of all the subplots. On each individual we collected two leaves for *M. caerulea*, two  
221 terminal shoot cuttings about 3 cm long (due to the small size of the leaves) for *C. vulgaris* and two  
222 frond cuttings with second order ramifications for *P. aquilinum*. The leaves harvested were scanned  
223 using an area meter (LiCor Inc., Li-3100C Area Meter) to compute the leaf area, dried at 65°C for  
224 4 days and weighed. The LMA at the subplot level was computed from the LMA of the nine  
225 individuals pooled.



226

#### 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.

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

$$241 \quad \text{Transmittance} = e^{-(k \cdot \text{cover})}$$

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

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

247

### 248 3. Results

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

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

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

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

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

267 At the two lowest PAR treatments (6% and 11%), *P. aquilinum* cover was significantly higher than  
268 that of *C. vulgaris* and *M. caerulea* ( $P \leq 0.001$ ). At the PAR treatment of 6%, *M. caerulea* cover was  
269 slightly higher than *C. vulgaris*, but the cover of the two species was equivalent at 11%. For PAR  
270 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  
274 The vegetation height did not vary with PAR treatment except for *P. aquilinum* (Table 1). For this  
275 species, the variation of height according to light availability followed the same pattern as cover, i.e. a  
276 bell-shaped curve increasing from 6 to 35% and decreasing for higher light levels ( $P < 0.0001$ ,  
277  $R^2 = 64\%$ ). From the PAR treatment of 22%, *P. aquilinum* was higher than the other two species  
278 ( $P < 0.05$ ) and *C. vulgaris* was as high as or slightly smaller than *M. caerulea*. At the PAR treatment  
279 of 11%, there was no statistical difference among the three species, whereas at the lowest PAR  
280 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  
284 *C. vulgaris* ( $P = 0.0005$ ,  $R^2 = 51\%$ , Fig. 3a) and *M. caerulea* ( $P < 0.0001$ ,  $R^2 = 82\%$ , Fig. 3b). For  
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*

298 The LMA was influenced by the PAR treatment in a different way for each of the three species  
299 (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)

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

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

337

#### 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

374 tolerance to shade. We see here that *P. aquilinum* is able to develop in the year following its  
375 establishment but we do not know whether it could maintain itself in the longer term at low light  
376 levels. The carbohydrates stored in *P. aquilinum* rhizomes might become exhausted after a few years  
377 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).

408 The frond height-to-length ratio of *P. aquilinum* increased with light availability. Thus the fronds  
409 growing in full light conditions were approximately as high as they were long, lending the frond an  
410 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.

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

436 For *M. caerulea*, both leaf mass and area increased in the same proportions when light decreased, so  
437 that LMA did not vary with light availability. In shaded conditions, *M. caerulea* therefore produced  
438 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  
449 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*  
469 exhibited the highest light extinction coefficient ( $k = 0.029$ ) and can be considered as highly  
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*.

476 Differences between the three species concerning light interception are probably due to their foliar  
477 morphological characteristics. *P. aquilinum* forms dense covering foliage even for low light levels of  
478 6% whereas the other two species have sparser foliage. Sonohat *et al.* (2002) compared light  
479 interception by the grass *Festuca arundinacea* and by the legume species *Trifolium repens*. The results  
480 showed that for the same LAI the light interception capacity of the grass was lower than that of the  
481 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 Marris 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 m<sup>2</sup> ha<sup>-1</sup>. 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  
519 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  
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 m<sup>2</sup> ha<sup>-1</sup>, 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

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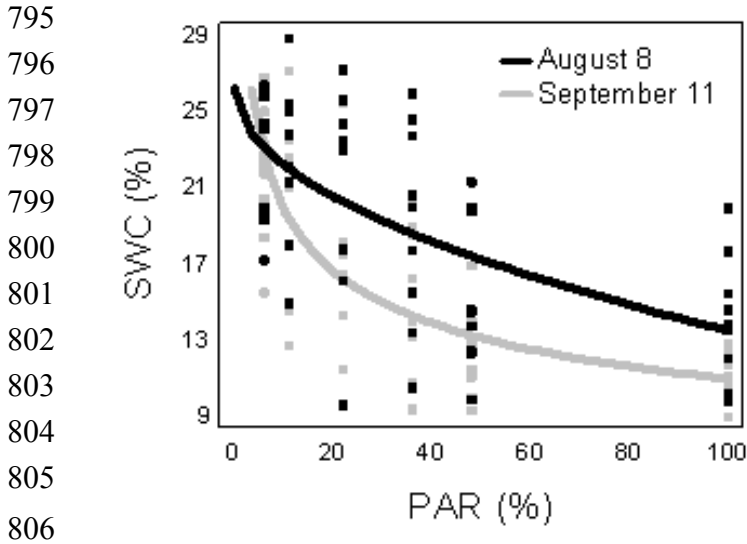
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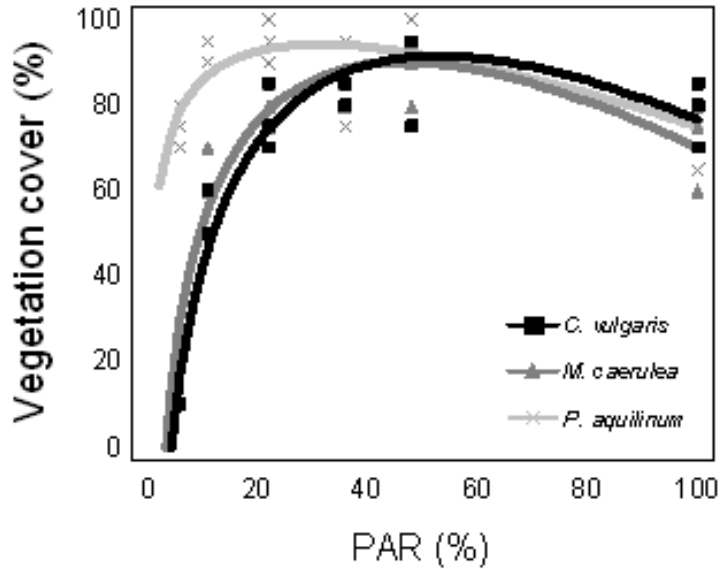
791 Fig 1: Relationships between soil water content (SWC) and light availability (PAR) on August 8 and  
792 September 11, 2009 under shading nets. Regression equations, SWC =

793 August 8:  $26.1736 - 1.2668 \cdot \sqrt{\text{PAR}}$  ( $R^2 = 34\%$ ,  $P < 0.0001$ )

794 September 11:  $35.8645 \cdot \text{PAR}^{-0.25707}$  ( $R^2 = 59\%$ ,  $P < 0.0001$ )



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 =  
 809 *C. vulgaris*:  $-80.7458 - 1.10349*PAR + 29.0551*LOG(PAR^2)$  ( $R^2 = 90\%$ )  
 810 *M. caerulea*:  $-54.3864 - 1.10152*PAR + 25.4721* LOG(PAR^2)$  ( $R^2 = 86\%$ )  
 811 *P. aquilinum*:  $49.4357 - 0.588658*PAR + 9.16872* LOG(PAR^2)$  ( $R^2 = 38\%$ )



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 ratios =

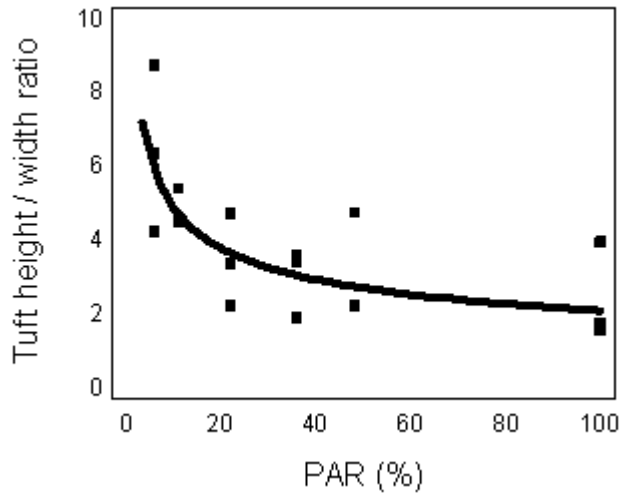
831 *C. vulgaris*:  $11.2784 * PAR^{-0.36508}$  ( $R^2 = 51\%$ ,  $P = 0.0005$ )

832 *M. caerulea*:  $24.0746 * PAR^{-0.424424}$  ( $R^2 = 82\%$ ,  $P < 0.0001$ )

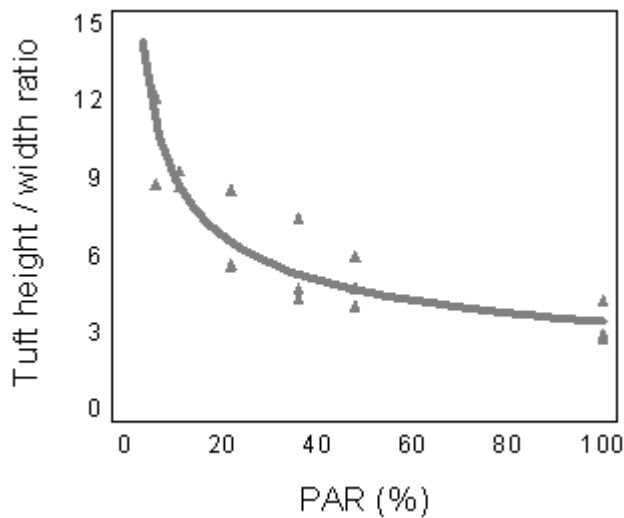
833 *P. aquilinum*:  $0.256794 + 0.0657518 * \sqrt{PAR}$  ( $R^2 = 93\%$ ,  $P < 0.0001$ )

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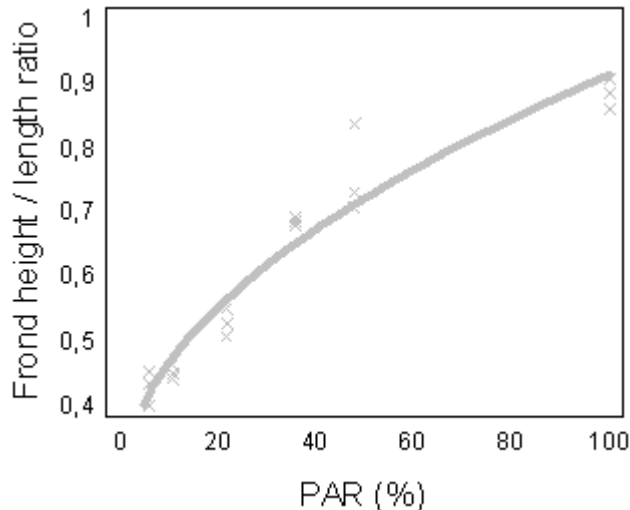
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846 b)



858 c)



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

872 *C. vulgaris*:  $4.70695 * PAR^{0.344563}$  ( $R^2 = 86\%$ ,  $P < 0.0001$ )

873 *M. caerulea*:  $5.25173 + 0.29451 * \sqrt{PAR}$  ( $R^2 = 41\%$ ,  $P = 0.002$ )

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

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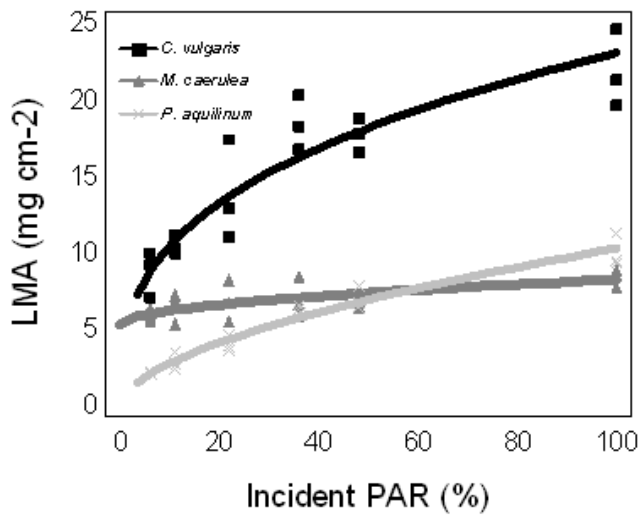
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890 Fig 5: Relationships between vegetation cover of three understorey species (*Calluna vulgaris*, *Molinia*  
891 *caerulea*, *Pteridium aquilinum*) and the light they transmitted (transmittance) in a nursery experiment.

892 Regression equations, transmittance =

893 *C. vulgaris*:  $\exp -(0.00377792 * \text{Cover})$  ( $R^2 = 3\%$ )

894 *M. caerulea*:  $\exp -(0.0167476 * \text{Cover})$  ( $R^2 = 68\%$ )

895 *P. aquilinum*:  $\exp -(0.0288637 * \text{Cover})$  ( $R^2 = 10\%$ )

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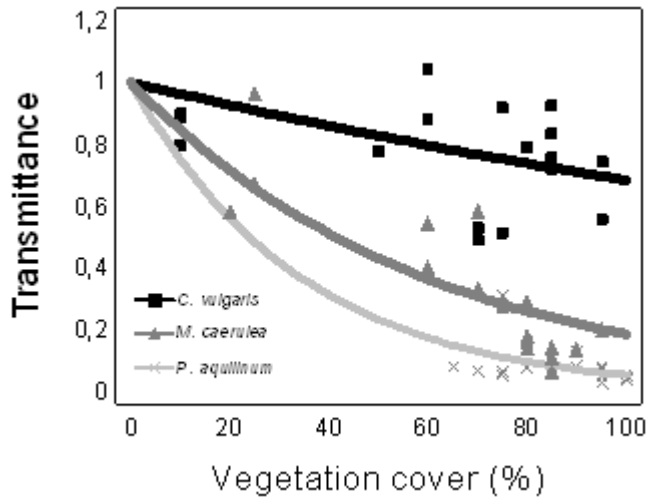
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908 Table 1: Cover, height and leaf mass on an area basis (LMA) in September 2009 of three understorey species  
 909 (*Calluna vulgaris*, *Molinia caerulea*, *Pteridium aquilinum*) planted under six PAR treatments in a nursery in  
 910 spring 2008.

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			Cover (%)	Height (cm)	LMA (mg cm <sup>-2</sup> )
<i>C. vulgaris</i>	PAR (%) =	6	10 ± 0 (c) <sup>C</sup>	20 ± 6 (a) <sup>B</sup>	8.7 ± 1.5 (c) <sup>A</sup>
		11	57 ± 6 (b) <sup>B</sup>	24 ± 5 (a) <sup>A</sup>	10.4 ± 0.6 (bc) <sup>A</sup>
		22	77 ± 8 (a) <sup>B</sup>	32 ± 11 (a) <sup>C</sup>	13.7 ± 3.3 (bc) <sup>A</sup>
		36	83 ± 3 (a) <sup>A</sup>	30 ± 8 (a) <sup>B</sup>	18.4 ± 1.8 (ab) <sup>A</sup>
		48	93 ± 3 (a) <sup>A</sup>	29 ± 6 (a) <sup>C</sup>	17.7 ± 1.1 (ab) <sup>A</sup>
		100	78 ± 8 (a) <sup>A</sup>	27 ± 10 (a) <sup>B</sup>	21.8 ± 2.5 (a) <sup>A</sup>
<i>M. caerulea</i>	PAR (%) =	6	23 ± 3 (c) <sup>B</sup>	31 ± 3 (a) <sup>A</sup>	5.9 ± 0.4 (a) <sup>A</sup>
		11	67 ± 6 (b) <sup>B</sup>	36 ± 6 (a) <sup>A</sup>	6.4 ± 1.0 (a) <sup>B</sup>
		22	80 ± 5 (ab) <sup>AB</sup>	44 ± 14 (a) <sup>B</sup>	6.8 ± 1.4 (a) <sup>B</sup>
		36	83 ± 3 (ab) <sup>A</sup>	43 ± 10 (a) <sup>B</sup>	7.0 ± 1.3 (a) <sup>B</sup>
		48	88 ± 8 (a) <sup>A</sup>	42 ± 6 (a) <sup>B</sup>	6.7 ± 0.2 (a) <sup>B</sup>
		100	71 ± 10 (ab) <sup>B</sup>	30 ± 3 (a) <sup>B</sup>	8.5 ± 0.6 (a) <sup>B</sup>
<i>P. aquilinum</i>	PAR (%) =	6	75 ± 5 (b) <sup>A</sup>	27 ± 5 (c) <sup>A</sup>	2.1 ± 0.1 (d) <sup>C</sup>
		11	93 ± 3 (ab) <sup>A</sup>	37 ± 16 (bc) <sup>A</sup>	2.8 ± 0.6 (cd) <sup>C</sup>
		22	95 ± 5 (ab) <sup>A</sup>	58 ± 11 (abc) <sup>A</sup>	4.0 ± 0.5 (c) <sup>B</sup>
		36	88 ± 10 (ab) <sup>A</sup>	60 ± 18 (ab) <sup>A</sup>	6.2 ± 0.2 (b) <sup>B</sup>
		48	98 ± 3 (a) <sup>A</sup>	69 ± 2 (a) <sup>A</sup>	6.9 ± 0.7 (b) <sup>B</sup>
		100	75 ± 10 (b) <sup>AB</sup>	51 ± 3 (abc) <sup>A</sup>	10.0 ± 1.1 (a) <sup>B</sup>
ANOVA (P)					
Block			NS	0.0001	NS
Species			0.0006	0.0003	<0.0001
PAR			<0.0001	0.009	<0.0001
Species*PAR			<0.0001	0.003	<0.0001

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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.

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923 Table 2: Transmittance and soil water content (SWC) in September 2009 within three understory species  
 924 (*Calluna vulgaris*, *Molinia caerulea*, *Pteridium aquilinum*) planted under six PAR treatments in a nursery in  
 925 spring 2008.

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

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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.

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