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

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## **Key words**

Understorey vegetation; light; growth

## **Abstract**

*Calluna vulgaris*, *Molinia caerulea* and *Pteridium aquilinum* are three forest understorey species that compete with tree seedlings for environmental resources. Forest managers therefore seek to control their growth, which is driven in part by the light available in the forest understorey.

An experiment was set up in a nursery in which the three understorey species *C. vulgaris*, *M. caerulea* and *P. aquilinum* were planted at six light levels (6, 11, 22, 36, 48 and 100% of full sunlight) replicated in three blocks. The different light levels other than 100% were obtained using neutral shading nets. The response of the three species to light availability was estimated after two growing seasons by their cover and height, their morphology, assessed by the foliar tuft height-to-width ratio for *C. vulgaris* and *M. caerulea* and by the frond height-to-length ratio for *P. aquilinum*, and their functional acclimation, assessed by a leaf trait (leaf mass on an area basis, LMA).

Vegetation cover changed with light availability following a bell-shaped curve. By contrast, vegetation height remained approximately the same, irrespective of the light treatment, except for *P. aquilinum*, which grew higher than the other two species at medium and high light levels. As a consequence, 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.

All three species showed a notable acclimation to light availability by their LMA, though in different ways. The LMA of *C. vulgaris* decreased in shaded conditions by an increase in leaf area, whereas decrease in LMA for *P. aquilinum* was due to a decrease in leaf mass. For *M. caerulea*, the LMA remained stable whatever the light conditions by a simultaneous increase in both leaf mass and leaf area in shaded conditions.

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

## 1. Introduction

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

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

As reviewed by Balandier *et al.* (2006a), the traits conferring a high colonisation rate are multiple, e.g. high growth rate and morphology of root system and / or aerial parts, high leaf area index (LAI), capacity to take up resources, etc. Thus it has been shown that some perennial grasses possess a dense root system that can efficiently and rapidly colonise superficial soil zones (Aerts *et al.*, 1991; Coll *et al.*, 2003). Some other species, such as certain ferns, have large, very fast-growing aerial organs (Den Ouden, 2000; Parker *et al.*, 2009; Gaudio *et al.*, 2010). These traits are often linked to a strong effect on resource availability, as defined by Goldberg (1990), and consequently a high competitive ability, 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,  $\text{g cm}^{-2}$ ) 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).

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

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

## 2. Materials and methods

### 2.1. Experimental site

In spring 2008 an experiment was set up in a nursery (Cemagref research centre, Nogent-sur-Vernisson, France, 47°50 N-2°44 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 semi-oceanic 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 same three months in the years 1971-2000.

## 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 light treatments repeated in three randomised blocks were tested: 6, 11, 22, 36, 48 and 100% of full sunlight. Except for the 100% light treatment, the different light levels were obtained using shading nets, the spectral neutrality of which was checked using a spectrometer (USB2000, Ocean Optics, 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, 5×5 vegetation individuals were planted at regular 20 cm intervals.

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

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

## 2.3. Measurements

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

### 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.

### 2.3.2. Light

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

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

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

### 2.3.3. Vegetation characteristics

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

In October 2009, the leaf mass on an area basis (LMA,  $\text{mg cm}^{-2}$ ) 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.

## 2.4. Data analysis

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

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

ANOVAs were also compiled to explore the variation of the transmittance and the SWC according to PAR 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.

## 3. Results

### 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 ( $P < 0.05$ ).

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

The positive influence of PAR on vegetation cover differed among the three species (Table 1). Cover was linked to PAR availability following a bell-shaped curve (Fig. 2) for *C. vulgaris* ( $P < 0.0001$ ,  $R^2 = 90\%$ ), *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* ( $P \leq 0.001$ ). 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 higher than 80%. At the PAR treatment of 100%, *C. vulgaris* cover was higher than *M. caerulea* cover, with *P. aquilinum* intermediate between the two other species ( $P = 0.04$ ).

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 ( $P = 0.008$ ).

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

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

### 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* ( $P < 0.0001$ ,

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

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

#### 3.5.1. Vegetation transmittance

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

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

#### 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 ( $P = 0.09$ ).

## 4. Discussion

### 4.1. Vegetation growth in response to light availability

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

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

At the two lowest PAR treatments, the cover of *P. aquilinum* was significantly higher than that of the other two species and almost at its maximum value, showing that even at very low light levels, this species was well developed with a cover of 75% at only 6% of full sunlight. This explains the weak influence of light on *P. aquilinum* cover, at least with a minimal light value of 6%. Thus *P. aquilinum* is able to grow in shaded forest understoreys. However, foliage development was characterised only by cover in this study, i.e. vertical projection of the foliage on the soil. The same cover can be produced in different ways, with one or many leaf or frond layers, i.e. the same cover percentage can correspond to different leaf area indices (LAI). Thus although cover is certainly a most useful variable 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.

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

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

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

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

with a spreading posture and fronds trailing on the ground. As noticed by Koop and Hilgen (1987) and observed in dark forest understoreys (personal observation), this flexible posture in shaded conditions allows *P. aquilinum* to climb along tree trunks and branches to seek more strongly lit environments.

#### 4.3. Leaf functional trait, LMA

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

Thus although the three understorey species implemented different strategies to resist shade, they all showed a notable acclimation to low light levels.

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

In the study presented here, vegetation transmittance calculated from the Beer-Lambert's law used vegetation cover rather than LAI, which is traditionally used. Two reasons justify this choice: i) cover can be easily measured in the field by forest managers and ii) our results and some other studies found a reliable relationship between cover and transmittance. For example, Stadt and Lieffers (2005), who

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.

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

Compared with the species effect on transmittance, the effect on SWC was low, no clearly marked difference being found among the three species, except that SWC was lower overall in *P. aquilinum*

and *M. caerulea* subplots than in *C. vulgaris* subplots with all plots pooled. However, no difference was recorded among the three species within the same treatment. Thus the three species may have the same behaviour concerning water absorption, although the proximity of the three subplots within a plot may have erased potential differences among the three species.

## 5. Conclusion

### 5.1. Practical implications

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

Conversely, *C. vulgaris* and *M. caerulea* reached high covers only for light levels above 20%. This means that foresters could control the development of both species by decreasing light in the understorey below 20%, which is dependent on adult tree density and identity. However, the possible control of the two species depends mainly on the light requirement of the tree species that the foresters want to regenerate. In acidic temperate forests, these two species are often encountered in the understorey of *Pinus sylvestris*, *P. pinaster* or *Quercus petraea* and *Q. robur* stands. The two pines are classified as light-demanding species and the two oaks as medium light-demanding species (Von Lüpke, 1998; Richardson, 2000). As pointed out by Sonohat *et al.* (2004), transmittance below 20% in *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 found in *P. sylvestris* stands (see e.g. Pérot *et al.*, 2007; Chabaud and Nicolas, 2009), it seems that the two understorey species could be controlled through adult canopy management in these stand types in such a way as to ensure *P. sylvestris* regeneration, considering a light availability of 20% to be sufficient for Scots pine regeneration, at least in temperate acidic forests. Conversely, Berbigier and 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 light arriving in the understorey is always too high to allow *C. vulgaris* and *M. caerulea* control by overstorey management. Concerning oaks, Balandier *et al.* (2006b) showed that a transmittance below

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

## 5.2. Ecological implications

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

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

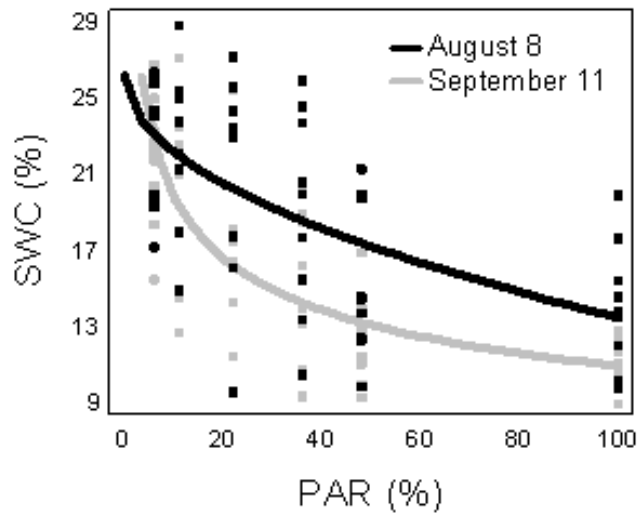


Fig 2: Cover (%) of *Calluna vulgaris*, *Molinia caerulea* and *Pteridium aquilinum* (c) in September 2009 according to light (PAR) in a nursery experiment. Regression equations, Cover =

*C. vulgaris*:  $-80.7458 - 1.10349 \cdot \text{PAR} + 29.0551 \cdot \text{LOG}(\text{PAR}^2)$  ( $R^2 = 90\%$ )

*M. caerulea*:  $-54.3864 - 1.10152 \cdot \text{PAR} + 25.4721 \cdot \text{LOG}(\text{PAR}^2)$  ( $R^2 = 86\%$ )

*P. aquilinum*:  $49.4357 - 0.588658 \cdot \text{PAR} + 9.16872 \cdot \text{LOG}(\text{PAR}^2)$  ( $R^2 = 38\%$ )

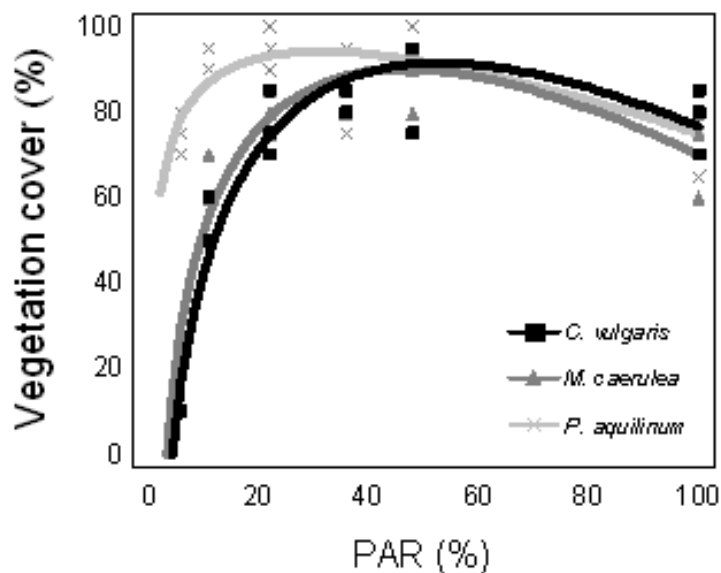


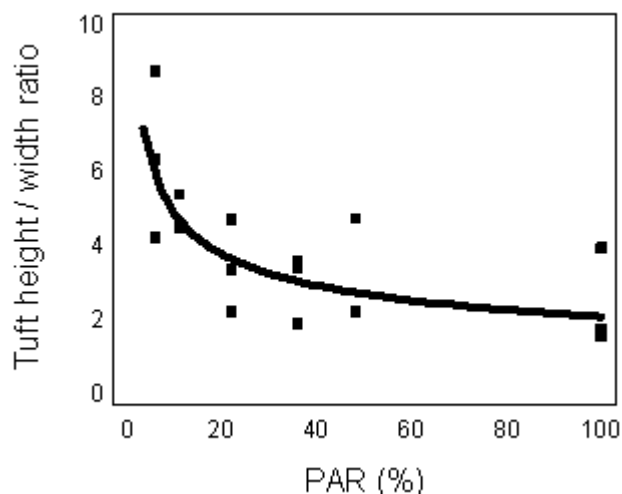
Fig 3: Foliar tuft height / width ratios of *Calluna vulgaris* (a) and *Molinia caerulea* (b) and frond height / length ratio of *Pteridium aquilinum* (c) in September 2009 according to light in a nursery experiment. Regression equations, foliar tuft height / width or frond height / length ratios =

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

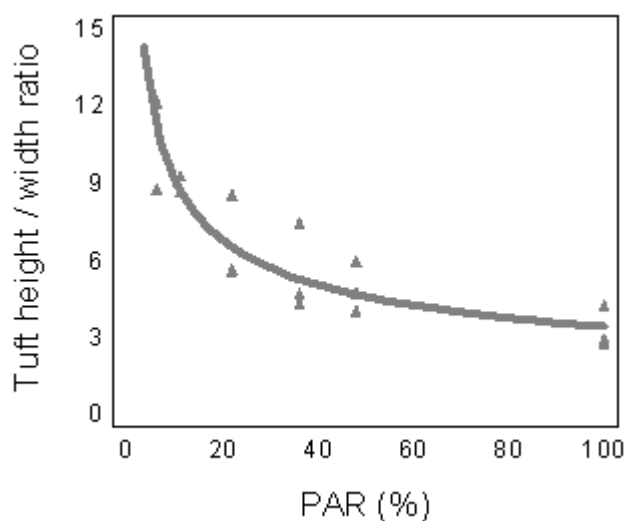
*M. caerulea*:  $24.0746 \cdot \text{PAR}^{-0.424424}$  ( $R^2 = 82\%$ ,  $P < 0.0001$ )

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

a)



b)



c)

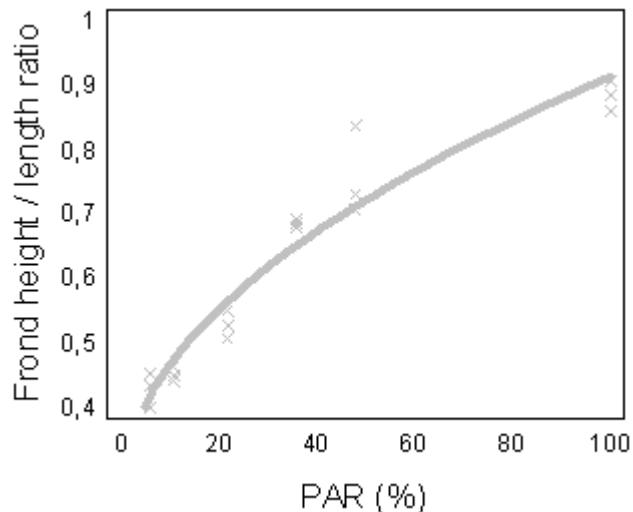


Fig 4: Relationships between the leaf mass on an area basis (LMA) of three understorey species (*Calluna vulgaris*, *Molinia caerulea*, *Pteridium aquilinum*) planted under shading nets in a nursery experiment in spring 2008 and the light availability (PAR) in September 2009. Regression equations, LMA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

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

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

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

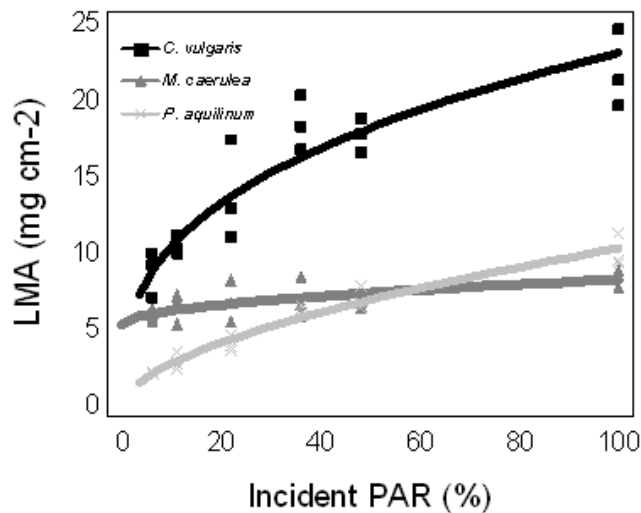


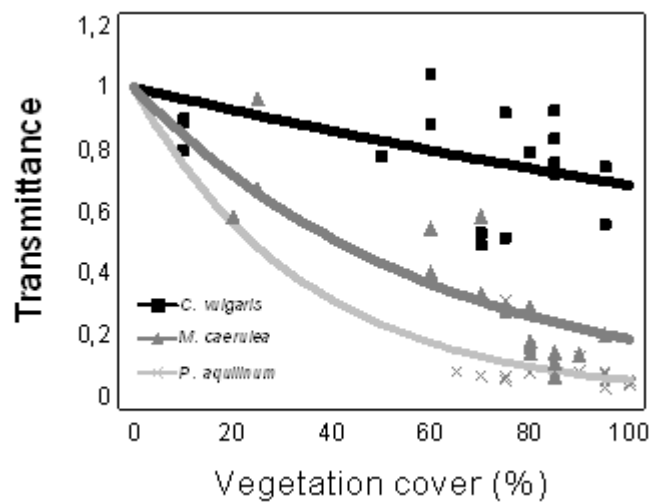
Fig 5: Relationships between vegetation cover of three understorey species (*Calluna vulgaris*, *Molinia caerulea*, *Pteridium aquilinum*) and the light they transmitted (transmittance) in a nursery experiment.

Regression equations, transmittance =

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

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

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



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

			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

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

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

			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

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