



Tree dynamics and co-existence in the montane–sub-alpine ecotone: the role of different light-induced strategies

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Keywords

Abies alba; Forest dynamics; Montane-sub-alpine ecotone; Morphological plasticity; *Pinus sylvestris*; *Pinus uncinata*; Pyrenees; Shade tolerance.

Nomenclature

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Abstract

Questions: Is light availability the main factor driving forest dynamics in Pyrenean sub-alpine forests? Do pines and firs differ in growth, mortality and morphological response to low light availability? Can differences in shade tolerance affect predictions of future biome changes in Pyrenean sub-alpine forests in the absence of thermal limitation?

Location: Montane–sub-alpine ecotones of the Eastern Pyrenees (NE Spain).

Methods: We evaluated morphological plasticity, survival and growth response of saplings of Scots pine, mountain pine and silver fir to light availability in a mixed forest ecotone. For each species, we selected 100 living and 50 dead saplings and measured size, crown morphology and light availability. A wood disk at root collar was then removed for every sapling, and models relating growth and mortality to light were obtained.

Results: Fir had the lowest mortality rate (< 0.1) for any given light condition. Pines had comparable responses to light availability, although in deep shade Scots pine risked higher mortality (0.35) than mountain pine (0.19). Pines and fir developed opposing strategies to light deprivation: fir employed a conservative strategy based on sacrificing height growth, whereas pines enhanced height growth to escape from shade, but at the expense of higher mortality risk. Scots pine showed higher plasticity than mountain pine for all architectural and morphological traits analysed, having higher adaptive capacity to a changing environment.

Conclusions: Our results support the prediction of future biome changes in Pyrenean sub-alpine forests as silver fir and Scots pine may find appropriate conditions for colonizing mountain pine-dominated stands due to land-use change-related forest densification and climate warming-related temperature increases, respectively.

Introduction

Mountain pine (*Pinus uncinata* Ram.) is the dominant species in the sub-alpine belt of the Pyrenees, whereas Scots pine (*Pinus sylvestris* L.) and silver fir (*Abies alba* Mill.) dominate the montane belt. However, these three species co-exist in the ecotone between the upper montane and lower sub-alpine belts, constituting a conifer mixed forest (Mason & Alía 2000; Aunós et al. 2007). The rise in temperatures associated with climate change has prompted predictions of species displacement in mountain areas (Walther et al. 2002; Resco et al. 2006),

meaning an upward encroachment of montane species (silver fir and Scots pine) into the sub-alpine belt can be expected (Walther et al. 2002; Peñuelas & Boada 2003; Resco et al. 2006; Peñuelas et al. 2007). Upward spread of species into existing forests is driven not only by climate but also by interspecific competition for resources and dispersal and establishment patterns (Woodward & Williams 1987; Vetaas 2002), as species-specific adaptive responses to the environment and homeostatic effects may modulate changes in community composition (Neilson 1993; Walther et al. 2002; Valladares et al. 2006). Together with increasing temperatures, mountain forests

in Spain have also experienced a drastic reduction in logging in recent decades, thanks to environmental concerns and the drop in timber profitability. In the absence of large-scale disturbances, this has promoted severe canopy closure and establishment of advanced regeneration of shade-tolerant species such as silver fir (Robakowski et al. 2004; Aunós et al. 2007). In this context, and in the absence of water deficit, interspecific differences in performance under contrasting light conditions can sharply affect the dynamics of these transition areas (Neilson 1993; Delagrange et al. 2004). Light is a highly temporally and spatially heterogeneous resource in the forest (Canham 1988; Gravel et al. 2010), and species have developed different abilities to adjust their morphology and physiology to different sets of light conditions (Messier et al. 1999; Delagrange et al. 2004). The way in which species allocate their resources will determine their ability to perform in sun and shade conditions, the latter ability being traditionally called ‘shade tolerance’ (Canham 1988; Valladares & Niinemets 2008). Early classifications of shade tolerance were constructed as relative rankings among species or discrete classes (Baker 1949; Anderson et al. 1969; Whitmore 1989; Ellenberg 1992). The first attempts at quantification related shade tolerance to ability to maximize carbon gain and growth in shady environments (Bazzaz 1979; Givnish 1988), but more recent studies have reported a trade-off between survival and radial growth under low light (Kobe et al. 1995; Lin et al. 2002; Kunstler et al. 2005). Thus, shade tolerance has been quantified by estimating the relationship between growth and probability of mortality (Kobe 1996; Wyckoff & Clark 2000, 2002), producing quantitative estimates of shade tolerance that generally match the previously accepted ranks (Kneeshaw et al. 2006). Accordingly, in low-light conditions, shade-tolerant species do not necessarily grow faster than shade-intolerants (Canham 1989; Pacala et al. 1994), but will be more likely to survive (Kobe & Coates 1997; Canham et al. 1999). Furthermore, shade tolerance has also been suggested as related to the ability to reduce height growth to avoid the increased respiration and maintenance costs associated with larger size (Messier et al. 1999; Kneeshaw et al. 2006). Overall, ability to grow and survive in the understorey can be achieved by alternative combinations of physiological, morphological, allocational and architectural traits that can be species- and/or environment-specific (Claveau et al. 2002; Delagrange et al. 2004; Valladares & Niinemets 2008) and that are, in turn, affected by ontogenetic effects, i.e. by plant size (Niinemets 2006; Sánchez-Gómez et al. 2006b; Lusk et al. 2008).

This study aimed to advance in the understanding of the different light-induced strategies developed by three conifers (silver fir, mountain pine and Scots pine) in order

to co-exist in the montane–sub-alpine ecotones of the Catalan Pyrenees (NE Spain). In today’s changing climate context, potential structure and composition changes are of major concern in these forests, as they constitute the southern distribution limit of endangered plant and animal species, such as the Western capercaillie (*Tetrao urogallus*) and Tengmalm’s Owl (*Aegolius funereus*), which are particularly sensitive to changes in their habitat (Camprodon 2001; Gracia et al. 2007). We hypothesize that in the absence of thermal limitation, silver fir and Scots pine would develop more efficient strategies than mountain pine to respond to light variations, which if true, would lead to an upward displacement of the montane–sub-alpine transition zone.

Methods

Study area and species

The study area is located in the Pallerols Valley in the Alt Pirineu Natural Park, Catalonia, NE Spain (42°23’N; 1°15’E). Mean annual rainfall at the study site is slightly below 1000 mm, distributed equally among seasons. Mean annual temperature is 6.1 °C and, in general, summers are relatively cool (mean temperature around 15 °C), meaning that there is no summer drought. Winters are long and cold, with a growing period of 173 days and only 150 frost-free days. Forests in the montane belt are occupied by Scots pine (*Pinus sylvestris* L.), a shade-intolerant species with an optimum at about 1500 m, and by silver fir (*Abies alba* Mill.), one of the most shade-tolerant conifers in the Pyrenees, which grows in more humid areas between 1200 and 1900 m. Mountain pine (*Pinus uncinata* Ram.), also traditionally considered as shade-intolerant species, dominates the sub-alpine belt (1700–2400 m), with optimum performance at about 1800 m (Blanco et al. 2005; Ruiz de la Torre 2006). Our study site was located between 1700 and 1850 m, in the montane–sub-alpine ecotone where these three conifer species (silver fir, Scots pine and mountain pine) co-exist. No logging, silvicultural treatments or major disturbances affecting the canopy have occurred in the last decade in the study area. The plots were all located in uneven-aged stands characterized by high horizontal and vertical heterogeneity, therefore presenting gaps alternating with heavily shaded areas.

Data collection

Samples were taken along six transects crossing the montane–sub-alpine ecotone. All transects were located in mixed-conifer stands, with different slopes and aspects. A total of 94 silver fir, 98 Scots pine and 96 mountain pine saplings were sampled, with a sapling defined as a tree above 50 cm in height but below 7.5 cm in diameter at

breast height (DBH) (Camarero et al. 2000). For each sapling, we measured diameter at 10 cm, total sapling height, crown height and crown diameter. Apical growth was determined as the mean value of the length of the last three shoots of the main axis. We also measured lateral growth as the mean length growth of the last 3 years for at least four branches per tree, two in the upper third of the sapling and two in the lower one. A wood disk from the root collar of every sapling was removed, dried, sanded and scanned, and annual radial growth was determined as the mean for the last 3 years according to the method described in Lussier et al. (2004).

Light measurements were taken during September and October 2009, under completely overcast conditions, as suggested by Messier & Puttonen (1995) and Parent & Messier (1996). The percentage of above-canopy light (photosynthetic photon flux density; PPFD) at the top of each sapling was used to describe its light environment. Above-canopy PPFD was measured with a Li-190SA quantum sensor (Li-Cor, Nebraska, USA) placed in an open area adjacent to the study site and connected to a data-logger that recorded readings every 10 sec. A second quantum sensor was used to measure PPFD at the top of each sapling, and time of the measurement was recorded. Light availability for each sapling was then determined as %PPFD.

Growth and mortality as a function of light

To obtain the relationship of growth and mortality with light, we employed the two-step approach originally developed by Kobe et al. (1995) for the SORTIE model. Thus, we first modelled the relationships between growth and light availability and between mortality risk and past growth, and then combined them to determine the relationship between mortality and light. Both radial and apical growth were modelled against light availability (Fig. 1). The relationship between growth and light availability was established using a Michaelis–Menten function, which is widely used for modelling tree growth (Pacala et al. 1994; Wright et al. 1998; Lin et al. 2002; Kunstler et al. 2005). According to this function, growth can be expressed as:

$$G = size^d \frac{a^*L}{a/s + L}, \quad (1)$$

where G is the growth of an individual of a given size at a light level L (%PPFD), while a and s are the parameters of the Michaelis–Menten function, which can be interpreted as asymptotic growth rate and slope at zero light, respectively. Size was defined as radius (in mm) in the case of radial growth and as tree height (in cm) in the case of length growth, and d is a parameter that describes the

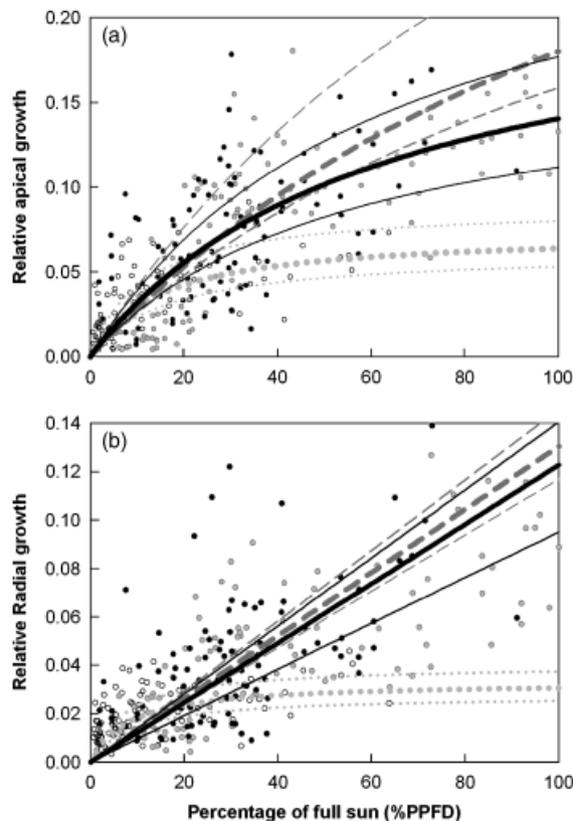


Fig. 1. Response of (a) relative apical growth and (b) relative radial growth to increases in light availability. Dots represent observed values for 94 *Abies alba* (unfilled dots), 98 *Pinus sylvestris* (grey dots) and 96 *Pinus uncinata* (black dots) saplings. Thick lines correspond to the adjusted Michaelis–Menten function for a sapling with average radius (20 mm) and height (180 cm), with the parameters shown in Table 1 for *Pinus uncinata* (black), *Pinus sylvestris* (dark-grey) and *Abies alba* (light-grey). Dashed lines represent upper and lower growth predictions constructed with minimum and maximum values of the two-unit support intervals for parameter estimates.

changes in growth rate with tree size. To estimate the maximum likelihood parameter values, we used simulated annealing (Goffe et al. 1994). A series of alternate models were fitted to each data set. The simplest model (null model) only considered the effect of size on tree growth, and was used to assess the influence of light availability on growth. We also fitted a linear and power model to the data available for each species. The R^2 of the observed versus predicted regression was used as a measure of goodness of fit of each model, and alternative models were compared using $\Delta AICc$, the difference in corrected Akaike information criterion (Burnham & Anderson 2002).

Mortality as a function of radial growth was estimated according to Wyckoff & Clark (2000), who modified the method originally proposed by Kobe et al. (1995). Implementing this method requires the growth rates of live

and recently dead saplings, together with an estimation of annual mortality rate. Growth rates of living saplings were obtained from the sample collected for growth–light relationships. To obtain the growth rate of dead saplings, 50 recently dead saplings of each species were randomly harvested from the transects, and growth rate was obtained using the method given above for living saplings. The criterion used to consider a sapling as ‘recently dead’ was twig suppleness and the maintenance of some needles. We used a parametric option to allow for comparison among species (Kunstler et al. 2005), where the growth–mortality function for each species can be calculated as:

$$p(d|g) = \frac{\theta}{[\theta + (1 - \theta)/Q]}, \quad (2)$$

where $p(d|g)$ is the growth–mortality function, θ is the overall mortality rate, and Q is the ratio of the growth rates (g_i) of living (g_l) and dead (g_d) saplings. These growth rates were estimated by adjusting the data set to a gamma density distribution using the maximum likelihood method, with the likelihood of the gamma density being:

$$L(G_d|\lambda_d, \rho_d) = \prod_{i=1}^D \frac{\lambda_d^{\rho_d}}{\Gamma(\rho_d)} g_i^{(\rho_d-1)} \exp(-\lambda_d g_i), \quad (3)$$

where G_d represents the data set for the growth rates of dead saplings and Γ is the gamma function, while λ_d and ρ_d are *shape* and *scale*, the fitted parameters for the gamma density. The same approach was used for live saplings, but likelihood took parameters λ_l and ρ_l and the data set was G_l . Overall mortality rate θ was estimated for each species from 100×5 -m transects in which all recently dead and living saplings were counted. Parameters were estimated using simulated annealing, as specified above. Mortality as a function of light availability was obtained by combining equations (1) and (2). For a given light availability, growth was estimated from equation (1) for an individual with a radius of 20 mm (the data set average). Then, growth ratio Q was estimated, and annual probability of mortality was obtained from equation (3). To assess sapling performance, the probability of survival as a function of light availability was calculated for an average size sapling and for two situations: i.e. (i) over 5 years and (ii) over the number of years needed to become adult (diameter > 75 mm).

Architecture and crown morphology

For the data set of living saplings, a set of architectural traits was calculated: apical and lateral average growth and slenderness (as the ratio between tree height and diameter). Crown morphology was assessed as crown depth (the ratio between crown height and total tree height), crown slenderness (the ratio between crown

height and crown diameter) and apical dominance, estimated using the plagiotropy index (the ratio between apical and lateral growth). The influence of light availability and ontogenetic effects on these morphological and architectural traits was determined by analysis of covariance, where species was a factor and %PPFD and tree size were covariates. The %PPFD was transformed to its logarithm when necessary to achieve normality of residuals and homoscedasticity. Differences in slope coefficients between species were tested by examining the significance of the interaction term between species and %PPFD or tree size, respectively. Unless otherwise specified, significance was set at a P -value < 0.05.

Results

Growth and mortality as a function of light availability

The key role of light in both apical and radial growth was strongly supported by our data, the full Michaelis–Menten model presenting in all cases a much lower AICc value than the null model, in which no influence of light was considered (Table 1). Furthermore, the Michaelis–Menten model fitted well in all the data sets (R^2 ranging between 0.53 and 0.8; Table 1). At low light levels, the slope of the function relating apical growth and light was similar for the three species. However, fir rapidly reached asymptotic growth and thus both pines outgrew fir as light availability increased above 15% (Fig. 1). In full sun, Scots pine had a higher maximum apical growth rate than mountain pine, the differences between the two species becoming important for light values above 40%. Both pines increased radial growth almost linearly in response to light availability (Table 1; Fig. 1). In contrast, fir reached a maximum growth rate at a light availability of 20%.

In all cases, radial growth over the last 3 years was consistently higher for living saplings than for dead saplings (Table 2). Silver fir had the lowest probability of mortality for any given growth rate or light level, with almost no variation across the entire data range (Fig. 2). Scots pine showed the greatest probability of mortality at low and intermediate growth rates, clearly above that observed for mountain pine, but its mortality rate dropped below mountain pine for growth rates higher than 0.9 mm year^{-1} (Fig. 2).

Among-species trends in mortality for different light levels were similar to those observed for different growth rates (Fig. 3a). Thus, while silver fir consistently showed the highest likelihood of survival (above 0.8) at any given light level, both pines sharply increased their probability of survival as light availability increased. Survival rates for mountain pine and Scots pine reached 50% survival at

Table 1. Parameter estimates for Michaelis–Menten growth–light function for (a) apical growth and (b) radial growth. Note: Parameter estimates for radial growth of *Abies alba* cannot be directly compared with the rest of the species as the dependent variable was multiplied by 100 to avoid abnormal residual behaviour. N is sample size and a , s and d are the fitted parameters of the Michaelis–Menten functions. R^2 is the regression coefficient of the observed versus predicted equation and ΔAICc is the decrease in AICc for the selected Michaelis–Menten model as compared with a null model, in which no light effect on growth is considered. Values in brackets are the two-unit support intervals for the parameter estimates.

Species	N	a	s	d	R^2	ΔAICc
Apical growth						
<i>A. alba</i>	94	0.445 [0.396; 0.498]	0.029 [0.024; 0.035]	0.656 [0.642; 0.668]	0.691	79.17
<i>P. sylvestris</i>	98	6.428 [5.564; 7.486]	0.043 [0.040; 0.046]	0.488 [0.483; 0.493]	0.842	136.89
<i>P. uncinata</i>	96	0.809 [0.669; 0.977]	0.013 [0.011; 0.015]	0.756 [0.741; 0.767]	0.535	35.54
Radial growth						
<i>A. alba</i>	94	17.43 [15.63; 19.41]	2.16 [1.73; 2.70]	0.449 [0.421; 0.473]	0.591	66.10
<i>P. sylvestris</i>	98	4031.8 [40.30; 10 000.0]	0.0071 [0.0068; 0.0076]	0.436 [0.418; 0.449]	0.802	148.49
<i>P. uncinata</i>	96	3069.8 [0.23; 10 000.0]	0.0015 [0.0013; 0.0016]	0.93 [0.90; 0.96]	0.579	88.53

Table 2. Estimated parameters of shape (ρ) and scale (λ) for the adjusted gamma distribution of radial growth for live and dead saplings. Values in brackets are the two-unit support intervals for the parameter estimates.

Species	Live			Dead			Annual mortality rate
	Growth rate (mm year ⁻¹)	λ	ρ	Growth rate (mm year ⁻¹)	λ	ρ	
<i>A. alba</i>	0.30	0.11 [0.09; 0.14]	2.62 [2.17; 3.07]	0.17	0.10 [0.08–0.13]	2.50 [1.89; 3.10]	0.033
<i>P. sylvestris</i>	1.26	1.06 [0.86; 1.26]	1.892 [1.56; 2.22]	0.33	0.60 [0.41–0.79]	1.13 [0.80; 1.46]	0.066
<i>P. uncinata</i>	0.77	0.45 [0.38; 0.53]	1.71 [1.40; 2.03]	0.25	0.39 [0.27–0.50]	1.22 [0.89; 1.55]	0.110

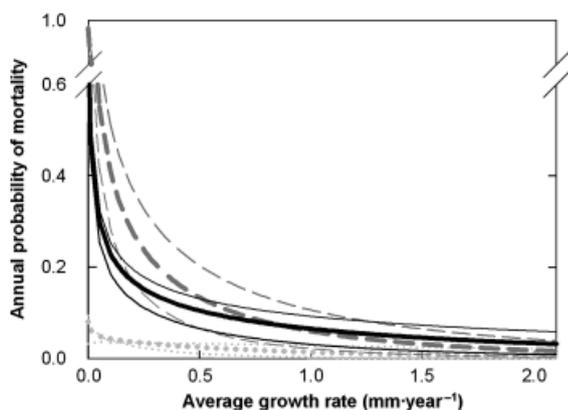


Fig. 2. Annual probability of mortality for a sapling as a function of average radial growth rate. Growth rate was calculated for a sapling with average radius (20 mm). Thick lines represent modelled annual probability of mortality, while dashed lines represent upper and lower growth predictions constructed with minimum and maximum values of the two-unit support intervals for parameter estimates: *Pinus uncinata* (black), *Pinus sylvestris* (dark-grey) and *Abies alba* (light-grey).

12% and 20% of full sun, respectively. However, the Scots pine survival likelihood surpassed that of mountain pine at light levels above 40%. In full light, mountain pine and silver fir showed a similar maximum survival rate of 90% over a period of 5 years (Fig. 3a), whereas the survival rate of Scots pine saplings with no light limitation reached values of up to 99%. Maximum survival probability also differed among species when considering time needed to reach adulthood (defined as a tree with DBH > 7.5 cm), mainly as a consequence of different growth rates (Fig. 3b). At low light levels, fir had the highest survival rate, but as it took more than 25 years for a fir to become adult (data not shown), its survival rate never exceeded 60%, whatever the light level. In the case of pines, their high mortality rate in low light conditions almost prevented them from reaching adulthood at any given light level below 15%. Above this value, their probability of reaching adult size rapidly increased, driven by a lower mortality rate associated with higher radial growth. Both pines showed similar survival trends at light

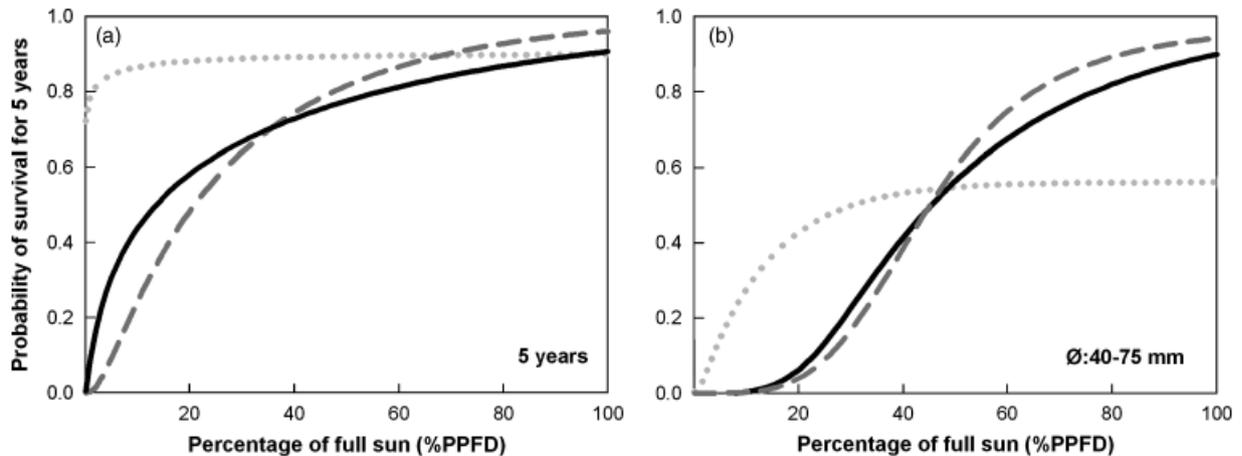


Fig. 3. Probability of survival for an average sapling over (a) a 5-year period; and (b) the time needed to reach a diameter of 75 mm (the average sapling had a diameter of 40 mm). Species are: *Pinus uncinata* (black lines), *Pinus sylvestris* (dark-grey lines) and *Abies alba* (light-grey lines).

levels below 50%. Differences between Scots pine and mountain pine at low light were lower than those observed for a 5-year period due to the accumulated effect of lower mortality for Scots pine at any growth rate above 1 mm year^{-1} (Fig. 3b), but differences in full sun were larger as a consequence of the higher radial growth rate of Scots pine.

Architectural and morphological plasticity in response to light availability

The models explained more than half of total observed variability for all the architectural and morphological variables analysed (R^2 ranging from 0.59 to 0.81), except for slenderness ($R^2 = 0.29$; Fig. 4). All architectural traits significantly changed with variation in light availability and the response was species-specific (Table 3). In effect, response of apical and lateral growth to changes in light environment was significantly higher for Scots pine than the other two species ($P < 0.001$, data not shown), while no significant differences in growth rate variation were observed between mountain pine and silver fir (apical growth: $P = 0.09$; LG: $P = 0.96$; data not shown). Growth curves for Scots pine intersected the x -axis at %PPFD = 10, with almost no apical or lateral growth below that light level (Fig. 4a). In contrast, mountain pine and silver fir showed positive growth values even at very low light levels, but the apical growth of Scots pine rapidly overgrew both of these species (at %PPFD = 9 and 22, respectively). Growth of lateral branches tended to follow the same pattern, but in this case the growth of fir was highest at low light; Scots pine only became the fastest-growing species at light levels above 25%, while mountain pine could not rival fir growth even in full sunlight (Fig. 4a). Slenderness was significantly reduced with increasing

light conditions for all three species (Fig. 4c), but the decrease was significantly sharper for Scots pine, which decreased slenderness by more than 50%, in contrast to the other two species, whose response was not statistically different ($P = 0.270$; data not shown). All three architectural variables increased with tree size (Fig. 4), but species-specific differences in response were only observed for apical growth (Table 3). Silver fir showed a weak response in apical growth with increasing tree size, whereas both pines showed a significantly higher response ($P < 0.01$), but without any significant between-pine differences ($P = 0.237$; data not shown).

Crown morphology also varied among species. Mountain pine and silver fir showed a slight yet significant increase in crown depth as light availability increased, without any difference between the two species ($P = 0.205$; data not shown). However, Scots pine had a significantly higher response slope ($P < 0.001$; data not shown), as its crown depth increased from 0.31 at 10% PPFD to over 0.85 in full sun (Fig. 5a). Both pines had two-fold higher crown slenderness values than silver fir, but no effect of light availability on crown slenderness was observed (Table 3; Fig. 5c). Silver fir presented a significantly lower plagiotropy index than the two pines at any light level. Even though differences were bigger in deep shade as fir reduced its apical dominance to less than 1 (Fig. 5e), no species-specific responses to light variations were observed ($P = 0.089$; Table 3). Size also induced variation in crown morphology variables. Mountain pine and fir increased the depth of their crowns as saplings increased in size, but with no significant difference in their response ($P = 0.101$; data not shown). However, Scots pine showed the opposite trend (Fig. 5b). Crowns also tended to be more slender as tree size increased, whatever the species considered (Fig. 5d). In the case of the plagiotropy index, fir values

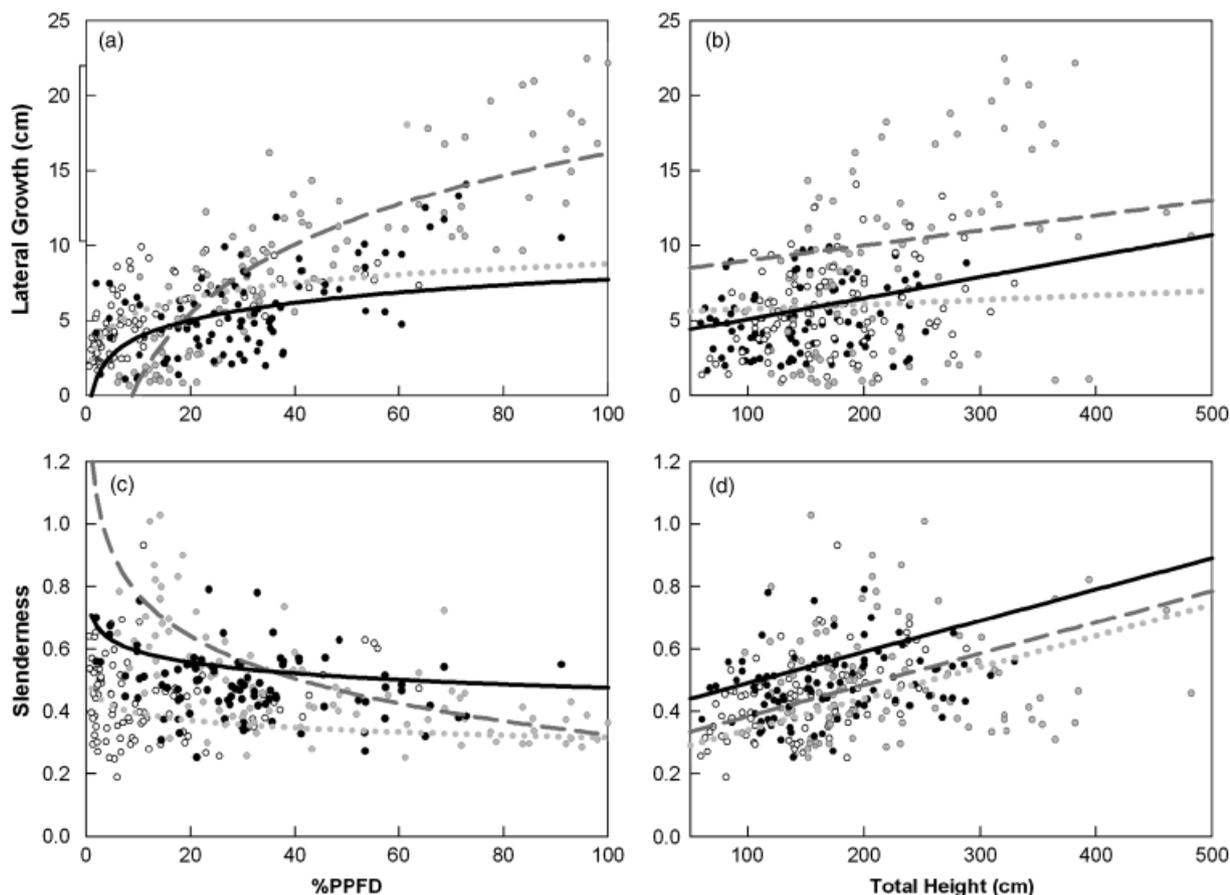


Fig. 4. Effect of light availability and sapling size on sapling architecture. Dots represent observed values, while lines correspond to ANCOVA models. Explanatory variable not indicated in the x-axis is set to the average for each species. Species are: *Pinus uncinata* (black solid dots and black lines), *Pinus sylvestris* (grey dots and dashed lines) and *Abies alba* (unfilled dots and dotted lines).

Table 3. Summary of ANCOVA *P*-values (values in bold indicate significance at $\alpha = 5\%$) for the relationship of plant architecture, crown morphology and tree size (TH), light (L), species (SP) and their interactions.

Variable	SP	L	TH	SPxL	SPxTH
<i>Architecture</i>					
Apical growth	< 0.001	< 0.001	< 0.001	< 0.001	0.002
Lateral growth	< 0.001	< 0.001	< 0.001	< 0.001	0.188
Slenderness	< 0.001	< 0.001	< 0.001	< 0.001	0.172
<i>Crown Morphology</i>					
Plagiotropy index	< 0.001	< 0.001	< 0.001	0.089	0.018
Crown depth	< 0.001	< 0.001	0.201	< 0.001	< 0.001
Crown slenderness	0.001	0.132	< 0.001	0.263	0.002

decreased as saplings increased in size, whereas both pines showed the opposite trend (Fig. 5e).

Discussion

Our results correctly matched previously established classifications of shade tolerance proposed by Ellenberg

(1992), who assigned a value of 3 (shade-tolerant, the minimum value for tree species) to silver fir and 8 (half-light to full-light species) to Scots pine and mountain pine. Radial growth in deep shade (below 10% of full sun) was almost double for silver fir than for the pines, but fir reached maximum growth at around 20% of incident light, as observed by Robakowski et al. (2003). Hence, both pines rapidly outgrew fir as more light became available. However, although differences between fir and pines were especially important in low light conditions, silver fir had the lowest annual mortality rate for any given light level. Therefore, our results confirm that the higher survival ability of silver fir in low light conditions is due to its ability to maintain higher radial growth in light-limiting environments, which has traditionally been considered the main general explanation of shade tolerance (Bazzaz 1979; Givnish 1988; Pacala et al. 1993; Wright et al. 1998; Lin et al. 2002), but also to an intrinsic ability to withstand low radial growth rates, as was more recently suggested for shade-tolerant species (Pacala et al. 1994; Kobe & Coates 1997; Vieilledent et al. 2010). Although

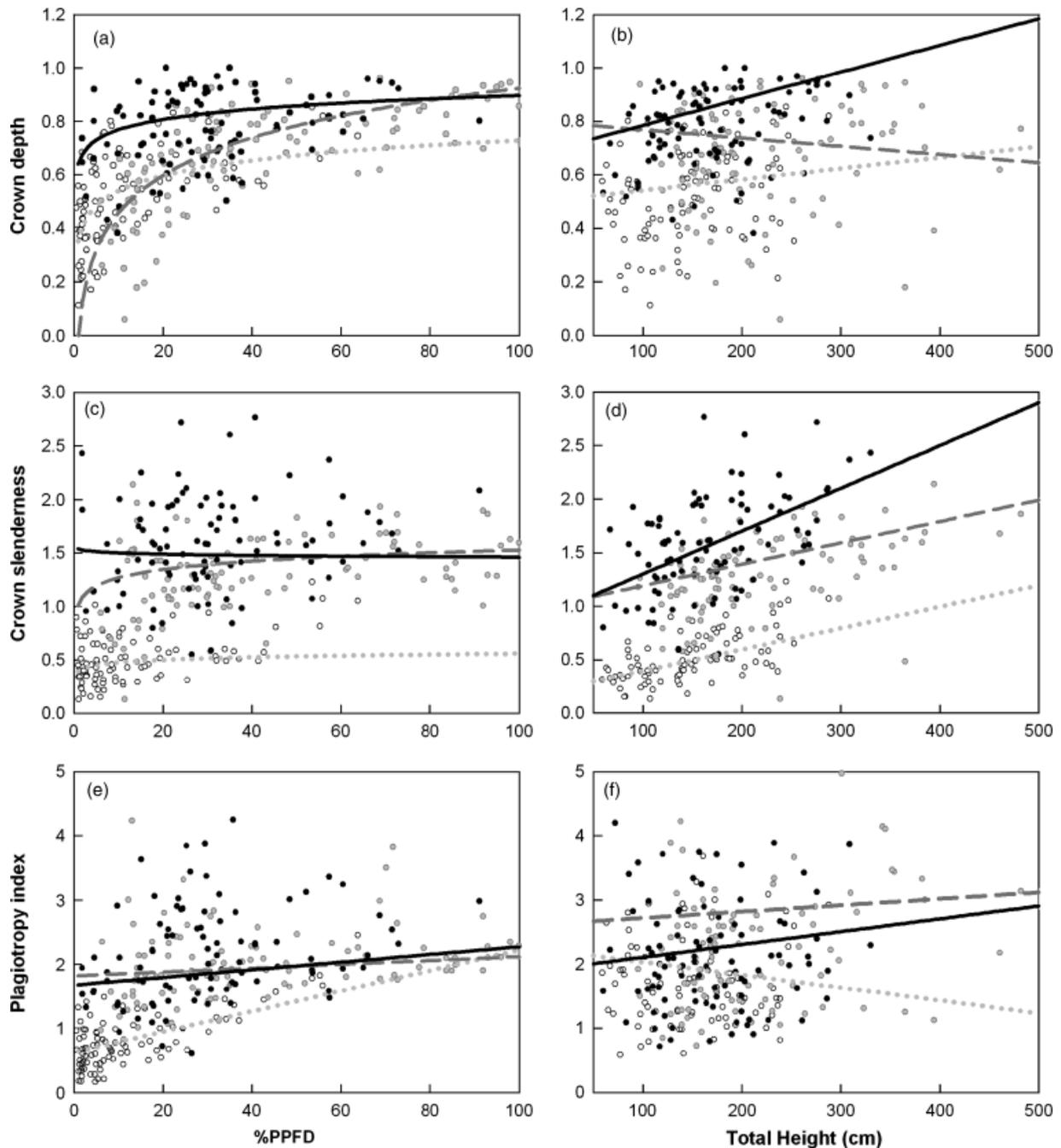


Fig. 5. Effect of light availability and sapling size on crown morphology traits. Dots represent observed values, while lines correspond to ANCOVA models. Explanatory variable not indicated in the x-axis is set to the average for each species. Species are: *Pinus uncinata* (black solid dots and black lines), *Pinus sylvestris* (grey dots and dashed lines) and *Abies alba* (unfilled dots and dotted lines).

differences in tolerance were much smaller between pine species than between genera, Scots pine showed a higher mortality risk in shaded environments than mountain pine, despite no significant differences in relative growth. Therefore, differences in mortality between the two pines are due to lack of ability of Scots pine to survive at low

radial growth rates rather than to enhanced growth ability of mountain pine.

Recently, a series of studies suggested a relationship between shade tolerance (understood as survival in deep shade) and the ability to suppress height growth when faced with shade conditions (Messier et al. 1999; Williams

et al. 1999; Kneeshaw et al. 2006). These studies assert that shade-intolerant species would favour height growth, even in shade conditions. If the enhanced growth results in a greater light availability, for example by rapidly reaching the forest canopy, it will favour sapling performance. Conversely, if it does not result in an advantage in light interception, then the increase in height would cause the saplings to incur higher respiration and maintenance costs that would subsequently increase mortality rate (Givnish 1988; Messier et al. 1999; Claveau et al. 2002). The patterns of maximum height for live and dead saplings observed in our study agree with this hypothesis, and reveal two opposite behaviours when withstanding shade conditions. Both pine species show a ‘shade escape’ strategy, maintaining

enhanced height growth (much higher than silver fir) even in shade. However, only pines not growing above a determined height – slightly above 3 m – are likely to survive (Fig. 6). In contrast, silver fir appears to develop a conservative resource-use strategy, in which growth is reduced to increase the chances of survival, a typical ‘shade-tolerant’ strategy (Canham 1988; Beaudet & Messier 1998; Claveau et al. 2002; Sánchez-Gómez et al. 2006a).

Silver fir showed little variation in its architectural and crown morphological patterns, i.e. low plasticity to changes in available light, except for the plagiotropy index. The observed weak apical dominance in the shade was caused by the ability of fir to reduce height growth and is a common trait in shade-tolerant firs (Fig. 7). Nevertheless, low plasticity in crown depth conflicts with the observed patterns for other *Abies* species, which usually vary in crown shape from conical in full sun to a flat-topped in understory shade (Kohyama 1980; O’Connell & Kelty 1994). If the observed crown depth values at low light match previous findings reported elsewhere (Fig. 7), the scant maximum crown depth reveals a limited ability of *Abies alba* saplings to exploit high light conditions, as observed by Grassi & Bagnaresi (2001). Conversely, *Pinus sylvestris* showed the highest plasticity in apical growth, lateral growth, slenderness and crown depth, conflicting with patterns of low plasticity commonly observed for pines (Fig. 7). High slenderness values were probably a consequence of the ‘shade escape’ strategy of Scots pine, and its sharp reduction of crown depth in shade may be interpreted as an attempt to increase survival chances by reducing maintenance costs

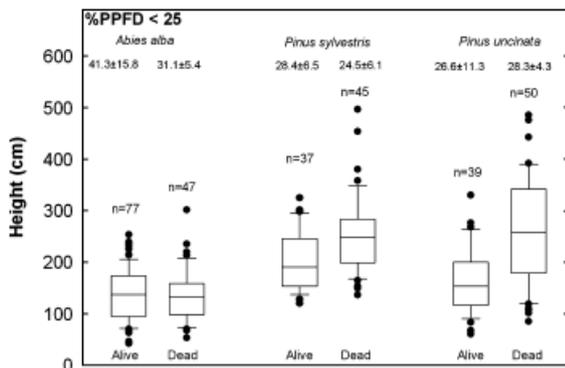


Fig. 6. Box-plots for total height of living and dead saplings of the three studied species in shade conditions (below 25% PPFD). N represents the sample size, while numbers below species name are the mean ± SD of sapling age in years.

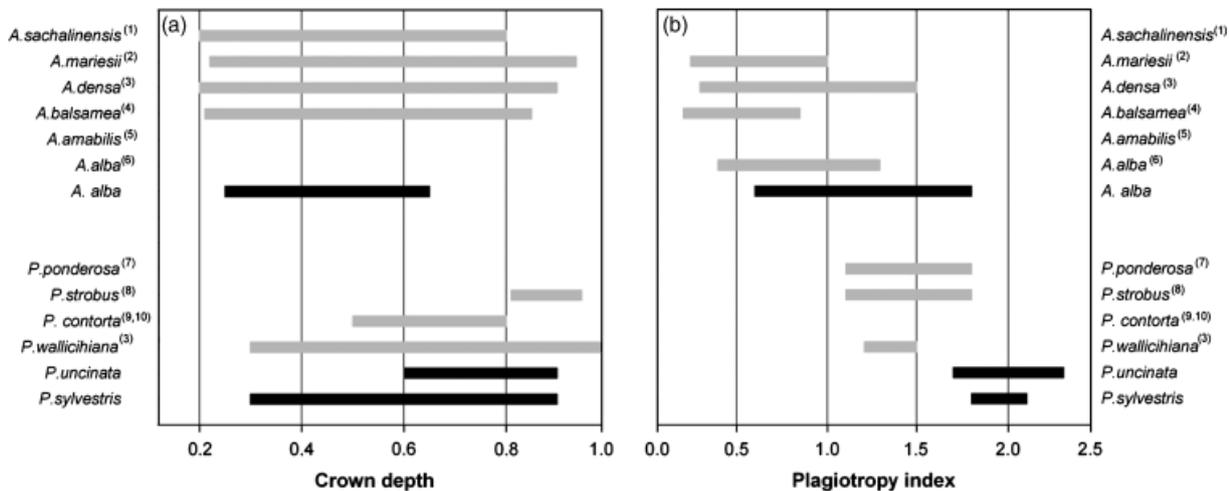


Fig. 7. Minimum (in deep shade) and maximum (in full sunlight) values of (a) crown depth and (b) plagiotropy index for several *Abies* and *Pinus* species. Black bars represent observed values in this study. Grey bars represent values obtained from a literature review: (1) Takahashi (1996); (2) Kohyama (1980); (3) Gratzner et al. (2004); (4) Gilmore & Seymour (1997); (5) Tucker et al. (1987); (6) Robakowski et al. (2004); (7) Chen (1997); (8) O’Connell & Kelty (1994); (9) Chen et al. (1996); (10) Williams et al. (1999).

associated with non-photosynthetic tissues (Givnish 1988; Beaudet & Messier 1998). Finally, mountain pine showed intermediate and moderate behaviour, matching previous results for *Pinus* species (Fig. 7).

The negative correlation between morphological plasticity and survival in deep shade observed in this study has already been linked in Mediterranean areas to the high cost of the 'shade-escape' strategy for intolerant species (Sánchez-Gómez et al. 2006a). Simultaneous adaptation of plants to a combined gradient of different ecological factors requires compromises that can restrict the competitive success of the species (Valladares et al. 2002; Sánchez-Gómez et al. 2008). Since both Scots pine and silver fir have their upper limit of distribution in the studied ecotone, deviations from expected patterns may also correspond to species-specific responses to these compromises. In Mediterranean areas, for example, drought-induced stress caused little change in Scots pine response to light, whereas limited morphological and physiological plasticity in *Abies alba* has been related to its low drought resistance (Grassi & Bagnaresi 2001; Robakowski et al. 2003, 2004).

Sapling size also modulated the architectural response of the three species to changing light conditions. Both pines showed a high response in apical growth as saplings increased in size. This could be related to an existing putative correlation between apical growth and sapling size, but as saplings of all sizes were sampled in every light level, it could also imply higher selective pressure against pines with greater growth, whereas moderate or limited growth for firs would be part of a strategy to avoid growing beyond the maximum sustainable height (Messier et al. 1999; Claveau et al. 2002; Kneeshaw et al. 2006).

Ecological implications

Brokaw & Busing (2000) defined three premises for coexistence through niche partitioning in gaps: (i) existence of a light availability gradient; (ii) specific differential distribution along that transect; and (iii) a species-specific trade-off in performance along the gradient. All three were accomplished in the ecotones studied here. Furthermore, light availability explained a major part of observed variability in growth and mortality for the three studied species, thus emphasizing the important role of light in demographic processes in the studied forests. Pine growth patterns were adapted to maximize performance in high irradiances, yet incurred high mortality in the closed understorey. Conversely, fir optimized performance in shade but cannot compete with pines at light levels above 60%. The generalized densification of mountain forests caused by reduced logging can nevertheless favour the

progressive establishment of advanced regeneration of fir in the understorey (Robakowski et al. 2004; Aunós et al. 2007). Although fir had the lowest annual mortality rate for any given light level, the limited radial growth incurs higher accumulated mortality risk during its life span. Both pines only showed slight differences in growth and mortality, even though the observed differences in plasticity could imply higher adaptive potential of Scots pine to a changing environment. If the minimum temperatures currently acting as a barrier to upward spread of Scots pine were to rise as expected (IPCC 2007), subsequent enhanced growth would mean a competitive advantage for this species. Furthermore, as mountain pine has adapted its morphology and physiology to poor environmental conditions, this could constrain its ability to respond to changes in light availability. In short, if silver fir is the species most favoured by a lack of management (creating shaded understoreys where pine has few opportunities to regenerate), and if temperature no longer limits Scots pine performance (favouring colonization of open areas), the current land-use and climate change context are expected to culminate in a progressive upward shift of the lower distribution limit of *Pinus uncinata* stands.

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