

Contents lists available at [SciVerse ScienceDirect](http://www.sciencedirect.com)

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Understory light predictions in mixed conifer mountain forests: Role of aspect-induced variation in crown geometry and openness

Aitor Ameztegui^{a,*}, Lluís Coll^a, Raquel Benavides^b, Fernando Valladares^b, Alain Paquette^c^a Forest Sciences Center of Catalonia (CTFC), Ctra. Sant Llorenç de Morunys km.2, E-25280 Solsona, Spain^b Museo Nacional de Ciencias Naturales, CSIC, Serrano 115 dpdo, E-28006 Madrid, Spain^c Centre d'Étude de la Forêt, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal (Québec), Canada H3C 3P8

ARTICLE INFO

Article history:

Received 14 December 2011

Received in revised form 16 March 2012

Accepted 21 March 2012

Keywords:

Crown openness

Crown irregularity

Aspect

Pyrenees

SORTIE-ND

Understory light

ABSTRACT

Predicting light availability in forest understory is a key step in the modeling of forest dynamics. Aspect is often the main source of environmental variation in mountain forests, and so aspect-induced differences in crown geometry and transparency can be expected to affect light transmission through the canopy and modify understory light predictions. To gain a better understanding of the effects of aspect on the light interception capacity of forest trees, we determined crown allometry and crown openness (CO) in 120 adult trees of three common conifer species in the Pyrenees (mountain pine, Scots pine and silver fir), sampled in eight montane-subalpine forests that each included two contrasting aspects. CO was calculated from digital photographs and several crown outlines were automatically determined to prevent user bias. We also calculated crown irregularity as the difference between crown surface area for the tightest and loosest outlines. Predictions of understory light availability obtained from a forest dynamics model were compared with actual values obtained from 115 hemispherical photographs. Crown length and CO varied across species following previous rankings of shade tolerance. Both pines had longer and wider crowns in the north aspect, whereas fir crown geometry was not affected by aspect. CO depended largely on the method chosen for determining crown outline, ranging from 0.10 to 0.56, and the tightest outline provided the best predictions of understory light (slope = 0.89, $R^2 = 0.46$). CO was also significantly affected by tree size and plot aspect ($p < 0.001$): crowns in southern-oriented plots were more open for mountain pine and silver fir, whereas Scots pine showed the opposite trend. Predictions of understory light were significantly improved when crown geometry and openness were allowed to vary according to plot aspect (slope of the regression: 0.95, $R^2 = 0.50$). Our results suggest that aspect should be explicitly considered when modeling ecological processes and dynamics in mixed mountain forests given its influence on both abiotic conditions and crown responses to them.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

Understory light plays a crucial role in forest dynamics, often being the most limiting resource for growth and survival of juveniles (Bazzaz, 1979; Kobe et al., 1995; Lefrançois et al., 2008). Also, modifying light regimes is frequently the only way in which managers can intervene in the forest to favor some species over others (Lieffers et al., 1999). Accordingly, the study and modeling of light transmission through the forest canopy has received much attention (Pacala et al., 1993; Brunner, 1998; Stadt and Lieffers, 2000; Groot, 2004). Since the seminal work by Monsi and Saeki (1953), most models of light transmission have been based on Beer's law, and assume that the forest canopy is a homogeneous layer that attenuates light transmission exponentially (Brown and Parker, 1994; Larsen and Kershaw, 1996; Stadt and Lieffers, 2000). These models adduce two important limitations: (i) they require

large amounts of data input (leaf area density, inclination angles, etc.) that is not directly applicable in forest management (Lieffers et al., 1999; Stadt and Lieffers, 2000; Astrup and Larson, 2006); and (ii) they cannot predict light regimes in heterogeneous forests where regeneration dynamics are dependent on small-scale processes (Canham et al., 1994). In this last case, the use of spatially explicit models that include individual representation of crowns are much more appropriate to predict the light transmitted through the canopies (Brunner, 1998; Boivin et al., 2011). Some of these models simulate individual crowns as 3-D objects and estimate light attenuation as a function of the distance traveled by rays through the crowns (Brunner, 1998; Stadt and Lieffers, 2000). Simpler models that reduce light by a given amount for each hit 2-D crown (Canham et al., 1994; Canham et al., 1999) have also been shown to predict understory light levels successfully in very different environments (Pacala et al., 1993; Beaudet et al., 2002; Astrup and Larson, 2006; Uriarte et al., 2009; Thorpe et al., 2010). Spatially explicit 2-D models are easily parameterized and are faster to run, as they only require estimation of the crown size,

* Corresponding author. Tel.: +34 973481752.

E-mail address: aitor.ameztegui@ctfc.cat (A. Ameztegui).

generally determined from allometric relationships and the attenuation factor assigned to each crown, which can be empirically obtained as crown openness (CO), *i.e.* the fraction of sky that on average can be seen through the crown of an individual tree (Boivin et al., 2011).

Crown openness varies substantially among species (see Beaudet et al. (2002), Astrup and Larson (2006)). In general, shade-tolerant species present lower CO than shade-intolerant ones, which in part may explain their reported higher ability to intercept light (Valladares and Niinemets, 2008). Astrup and Larson (2006) and Lefrançois et al. (2008) reported variations in CO along environmental gradients, but Sonohat et al. (2004) and Stadt et al. (2005) could not find a clear relationship, and the effect of these variations on understory light predictions remains unclear. Also, Lefrançois et al. (2008) and Boivin et al. (2011) showed that differences in methodology, *e.g.* angle of transmission through zenith and delimitation of crown outline, can lead to marked differences in CO, therefore affecting light predictions. CO can vary as a result of changes in crown porosity (proportion of hollows inside the crown) and in crown irregularity (understood as the existence of dents and bulges in tree crown profile). The use of different crown outlines can provide information on the role of each of these processes. Moreover, it can be combined with the study of the effect of environmental factors to assess the architectural response of tree crowns to changes in the environment. Crown geometry (crown width and length) also has a marked effect on spatial variation in understory light (Canham et al., 1999), and some models have demonstrated more sensitivity to variation in crown geometry than to variations in crown openness (Beaudet et al., 2002). However, the effect of environmental gradients on crown geometry has received little attention to date. In mountain systems, where most forests are located on hillslopes, aspect is usually one of the main sources of environmental variation. Solar energy regimes differ according to aspect (Hicks and Frank, 1984) and this causes differences in site characteristics such as evapotranspiration and hydrologic regimes (García-Pausas et al., 2007; Navas et al., 2007), soil and nutrient dynamics, species composition and abundance and forest growth and productivity (Verbyla and Fisher, 1989; Bale and Charley, 1994). Hence aspect might also be expected to induce variation in crown morphology and openness, and so differential parameterization of crown characteristics according to aspect may be needed to correctly simulate light transmission through canopies and forest dynamics in mountain systems. To gain a fuller understanding of the potential role of aspect on crown characteristics and light interception we conducted a study in different Pyrenean mixed-conifer forests to (i) estimate crown geometry, openness and irregularity and their variation with aspect for the three main species composing these forests (*Pinus sylvestris* L., *Pinus uncinata* Ram. and *Abies alba* Mill.), (ii) predict understory light in mixed conifer mountain forests using a spatially explicit model of forest dynamics and (iii) assess how aspect-induced differences in the parameterization of the model affected the predictions of understory light levels. Our main hypothesis was that higher evaporative demand on southern aspects would increase crown openness, but would also induce changes in crown geometry, therefore affecting light transmission through forest canopy and the simulations of the SORTIE-ND model (Canham et al., 2005).

2. Materials and methods

2.1. Study area and species

Data were collected from eight montane-subalpine forests in the Catalan Pyrenees (NE Spain; Fig. 1). All the selected stands

were dominated by one or more of the studied species: mountain pine (*P. uncinata*), Scots pine (*P. sylvestris*) and silver fir (*A. alba*). Mountain pine is the dominant species in the Pyrenean subalpine belt, whereas Scots pine and fir dominate the montane areas, although the three species mix in the montane-subalpine ecotone (Ameztegui and Coll, 2011). We used four of the stands to determine the tree allometry and crown openness (sampling sites). The remaining four were physically separate from the sampling sites and were used to validate the model (Fig. 1). Each sampling site included two different, contrasting aspects that were classified either as north-facing (N, NW and NE) or south-facing slopes (SE, S, SW; Table 1) for analysis. In the southern Pyrenees, fir usually grows in the most humid, northern-exposed sites and is absent in full sun-exposed slopes. This caused limitations in the selection of sampling sites, and the two aspects in each site were not as strongly opposed for silver fir as for pines (Table 1). All the stands had been thinned in the previous 3 years, allowing an easier determination of crown openness due to the greater separation between trees, while avoiding the special characteristics of trees grown without competence (Lefrançois et al., 2008).

2.2. Crown geometry

We sampled at least 30 adult trees (diameter at breast height > 75 mm) per species and aspect at each sampling site. Data were collected to ensure a wide range of diameters and a good distribution among diameter classes. For saplings (height > 0.5 m, diameter at breast height < 75 mm), we used data collected from a previous study (Ameztegui and Coll, 2011). For each adult tree, we measured diameter at breast height (DBH), tree height and crown radius and length. Crown radius was defined as the average of two perpendicular crown radii and crown length as the distance from the top of the tree to the base of the living crown. A total of 232 Scots pines, 225 mountain pines and 207 silver firs were sampled, ranging from 1 to 84 cm in DBH and from 0.6 to 27 m in height. We used three allometric equations to define crown geometry for each species: (i) tree height as a function of DBH, (ii) crown length as a function of tree height and (iii) crown radius as a function of DBH. To predict tree height as a function of DBH we used a nonlinear exponential curve that saturates at a maximum height (Canham et al., 1999; Beaudet et al., 2002):

$$\text{Tree height} = 1.3 + (\text{Max. height} - 1.3)[1 - e^{(-b \cdot \text{DBH})}] \quad (1)$$

where DBH is in centimeters and tree height in meters. Maximum height was determined from the Spanish National Forest Inventory in Catalonia (DGCN, 2007) as the average height of the 5% tallest trees for each species. The slope of the curve b was estimated by nonlinear least-square regression (Table 2). We also used nonlinear regression to estimate crown radius and crown length, as saplings usually have wider and longer crowns per unit of DBH than adult trees (Beaudet et al., 2002)

$$\text{Crown radius} = c \cdot \text{DBH}^d \quad (2)$$

$$\text{Crown length} = f \cdot \text{TH}^g \quad (3)$$

where crown radius, crown length and TH (tree height) are expressed in meters and DBH in cm. c , d , f and g are estimated parameters (Table 2). To assess the effect of aspect on crown geometry, we estimated the parameters for northerly and southerly slopes separately, and differences in estimated parameters were determined by examining the significance of the interaction between aspect and the other explanatory variable (DBH or TH).

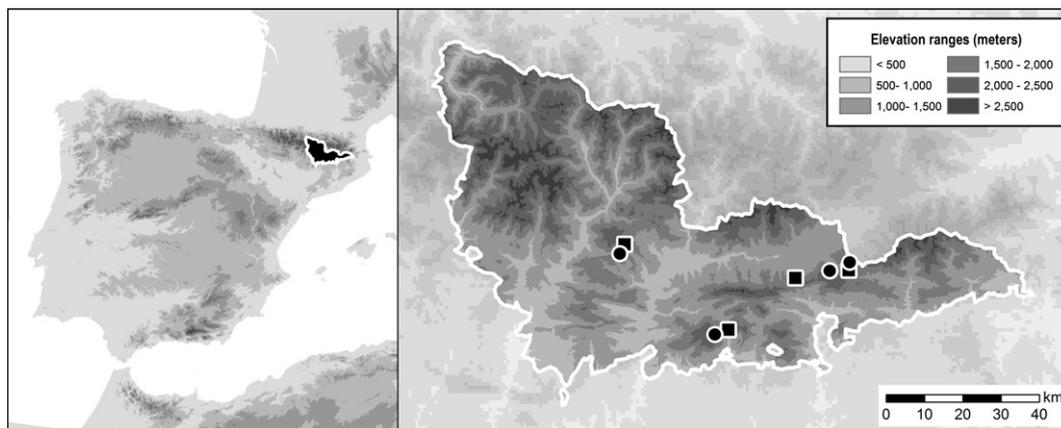


Fig. 1. Location of the study area and the sampling (circles) and validation sites (squares).

Table 1
Summary of site characteristics.

Sites	Site Coordinates	Elevation (m)	Aspects	Species Composition ^a	Mean tree DBH (cm) ±SD
<i>Sampling sites</i>					
Pallerols 1	42°23'N, 1°15'E	1850	NE, SE	Pu, Aa, Ps	34.6 ± 16.3
Riu de Cerdanya	42°19'N, 1°48'E	1800	NW, E	Aa, Pu	27.4 ± 13.0
Serra del Verd	42°12'N, 1°35'E	1770	N, S	Ps	24.6 ± 8.9
Paborde	42°21'N, 1°58'E	1750	NE, SW	Ps, Pu	31.0 ± 11.8
<i>Validation sites</i>					
Pallerols 2	42°23'N, 1°23'E	1940	NE, SE	Pu, Aa, Ps	31.1 ± 14.6
Port del Comte	42°11'N, 1°33'E	1700	NE, S	Ps, Pu	27.0 ± 8.3
Massella	42°20'N, 1°54'E	2000	N, NE	Pu	28.0 ± 9.6
Salteguet	42°21'N, 1°59'E	1750	N	Pu, Aa	23.4 ± 12.5

SD: Standard deviation.

^a Species composition is given in decreasing order of dominance: Pu, mountain pine (*Pinus uncinata*); Aa, silver fir (*Abies alba*); Ps, Scots pine (*Pinus sylvestris*).

Table 2
Parameter estimates by nonlinear least squares regression of tree height, crown radius and crown length as a function of tree size for three conifer species in the Pyrenees: silver fir (*Abies alba*); Scots pine (*Pinus sylvestris*) and mountain pine (*Pinus uncinata*). All regressions were highly significant ($p < 0.001$). Parameters are shown separately for north-facing and sun-exposed slopes except for silver fir, for which no differences were found in the parameters estimated for the two aspects.

Species	Aspect	Tree height			Crown radius			Crown length		
		Max. height ^a (m)	b	R ²	c	d	R ²	f	g	R ²
Silver fir	N,S	29.2	0.020	0.952	0.533	0.488	0.932	0.781	1.056	0.991
Scots pine	N	22.6	0.034	0.872	0.214	0.708	0.889	1.143	0.796	0.867
	S				0.270	0.626	0.891	0.723	0.885	0.848
Mountain pine	N	20.4	0.030	0.897	0.244	0.650	0.911	1.189	0.805	0.927
	S				0.287	0.566	0.912	1.129	0.753	0.863

^a Maximum height was obtained from the Spanish National Forest Inventory in Catalonia (DGCN, 2007) as the average height of the 5% tallest trees for each species.

2.3. Crown openness

We took pictures of the crown of every measured adult tree (120 trees per species) with a Nikon Coolpix 995 digital camera. To eliminate the effect of angle in the determination of crown openness (Lefrançois et al., 2008) we attached a clinometer to the camera to ensure that all photographs were taken at a 45° angle relative to the top of the tree. We selected only undamaged individuals with regular crowns and with no signs of having developed free from competition. Crown openness (CO) was determined as described by Canham et al. (1999). Images were transformed according to a defined threshold, so that all the “shading” elements (trunk, branches and leaves) were set to black and the background to white. Image reclassification was later corrected by hand to eliminate effects of light reflection. CO was determined as the ratio of the surface occupied by white pixels (sky area visible through the crown) to the total surface of the 2D projected silhouette of

the crown. Hence the values estimated with this method are highly dependent on the determination of the crown outline, and due to the fractal nature of the outline projection of a tree crown, large user bias can be expected (Canham et al., 1999; Boivin et al., 2011). To minimize this bias, crown outline was automatically determined using Crown Delineator, a Python script specifically written for this task and developed by Boivin et al. (2011). We used the software to delineate seven different crown outlines: five geometrical buffers with different adjustment sensitivities to crown shape (from tightest to loosest: Out20, Out40, Out80, Out160, Out 320,) together with the smallest convex hull (OutCH) and the smallest rectangle perpendicular to the horizon that includes the entire crown (OutRec; Fig. 2). A thorough description of the functioning of the script and the outlines produced can be found in Boivin et al. (2011). CO was calculated for each of the seven outlines, named accordingly CO20, CO80, CO160, CO320, COCH and COREC. We estimated crown irregularity as the difference in crown

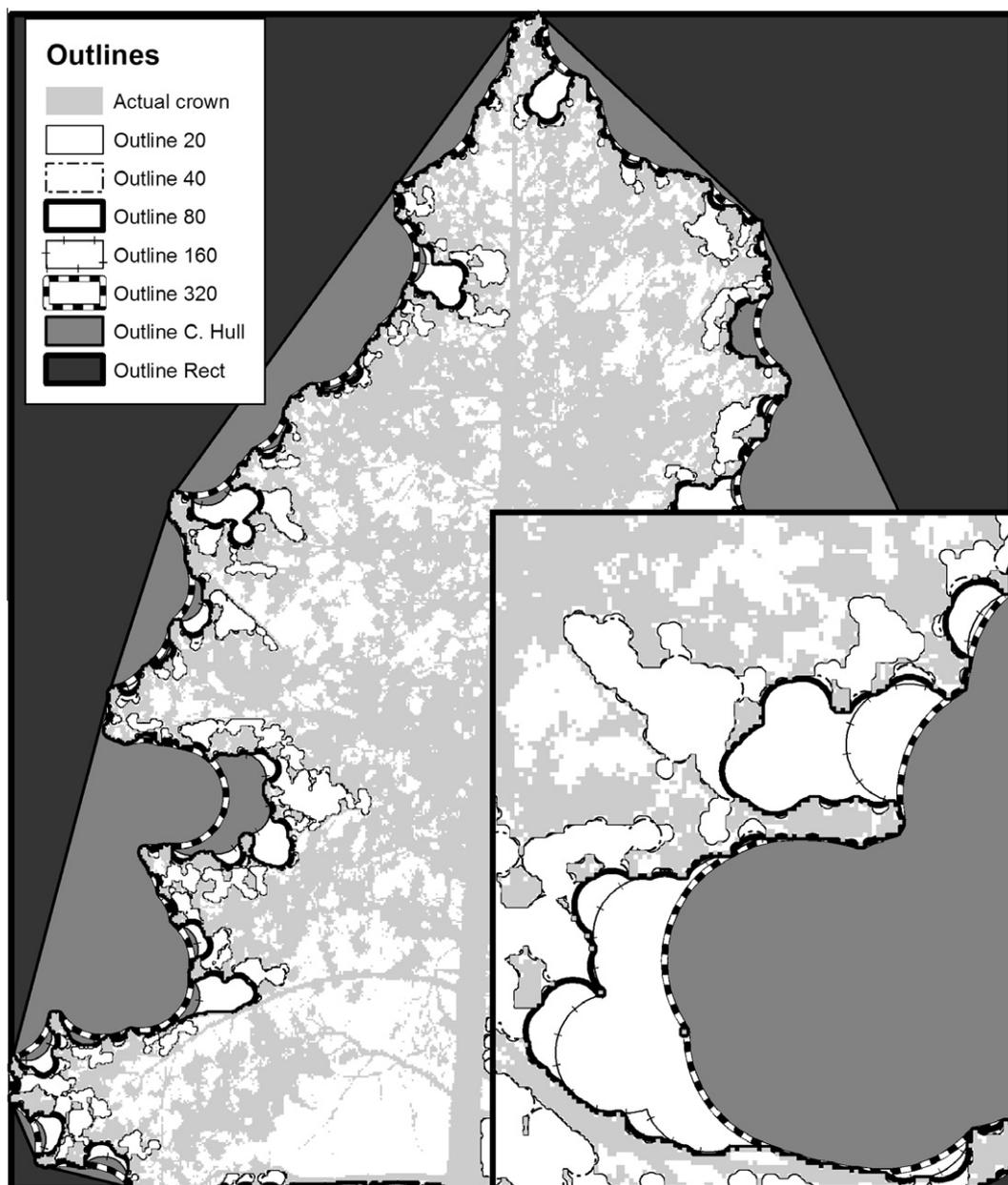


Fig. 2. Example of the different outlines created by the crown delineator for a Scots pine (*Pinus sylvestris*) crown. Tighter outlines produce lower CO values, whereas crown irregularity can be determined as the difference in crown area calculated for the outline 20 and the Convex Hull algorithms, divided by the latter.

area between OutCH and Out20, divided by the former. This crown irregularity index takes values close to 0 for dense, compact conic crowns, and values close to 1 for highly irregular crown shapes that include large void spaces between branches. To assess the variations in CO and irregularity with DBH and aspect we used generalized linear models, setting the seven CO values and irregularity as dependent variables, aspect as a factor (two levels: north- and south-facing) and DBH as covariate. All statistical analyses were performed using R (R Development Core Team, 2010). Unless otherwise specified, the significance level was set to $\alpha = 0.05$.

2.4. Prediction of understory light and role of aspect

Predictions of understory light were carried out using the “GLI light behavior” developed in SORTIE-ND (Canham et al., 2005), a spatially explicit individual tree model where tree growth is mainly driven by light availability, which in turn is determined by shading

of neighboring trees (Pacala et al., 1993, 1996; Canham et al., 2005). The “GLI light behavior” simulates the movement of the sun throughout the growing season to determine the total, seasonally averaged light that reaches a given point expressed as Gap Light Index (GLI), an index equivalent to the percentage of photosynthetically active radiation (PAR) on a horizontal plane compared with above-canopy levels (Canham, 1988; Gendron et al., 1998). For a given point, available light is determined by finding all neighboring trees that shade that point. In SORTIE-ND, calculations are normally restricted to zenith angles within 45° of vertical to optimize computation time, since little illumination comes from angles close to the horizon (Canham et al., 1990; Pacala et al., 1996). In SORTIE-ND, individual crowns of all the neighboring trees are modeled as cylinders and light attenuates by a given factor for each crown it encounters (Boivin et al., 2011). Therefore, each tree must be defined by its location, DBH, crown geometry and CO. We obtained the data to make the predictions from the 24 validation plots (6 plots in 4

validation sites). Each plot was composed of two concentric circles of radius 10 and 20 m, respectively. In the first one, all trees with DBH > 7.5 cm were mapped and measured. In the second one, only those trees with DBH > 20 cm were considered. For every tree measured we determined the species, DBH and its distance and azimuth from the plot center. We created a parameter file for each of the 24 validation plots. For each species, the obtained average values of crown allometry and CO were used (species-specific constants). As SORTIE-ND simulates crowns as cylinders, and because of the conical shape of the crowns of the three species studied, crown radius was set at 50% of the actual values measured in the field (Rautiainen and Stenberg, 2005). This rescale makes the area of the modeled crown closer to the real crown area and has been shown to improve light predictions (Canham et al., 1999; Rautiainen et al., 2008). Simulations were performed eight times for each plot, once for each average CO value obtained from the defined outlines and once assigning a CO of zero to all species (opaque crowns). All the other parameters involved in light calculations (crown geometry, tree location, etc.) were kept constant.

These simulated GLI values were compared with observed values obtained from a series of hemispherical photographs taken at each validation plot: one in the center of the plot, and four at 5 m from the center in each cardinal direction. Photographs were taken on overcast days using a leveled tripod at height 1 m. After discarding all the photographs where branches, leaves or shrubs were too close to the camera we analyzed a total of 114 photographs. Light availability for each photograph was determined by calculating GLI using Gap Light Analyzer v. 2.0 (Frazer et al., 2000), which works in an analogous way to the GLI light behavior in SORTIE. To ensure that observed and simulated GLI values were directly comparable, we set temporal and spatial resolution and the characteristics of the incident radiation in exactly the same way as for the GLI light behavior, and we created a topographic mask that covered the lower 45° from horizon. GLI was thus calculated as the ratio between transmitted and incident light in the area not covered by the mask.

To identify the outline that produced the best fit to observed data we used both the slope of the regression (with a zero intercept) to measure bias and the R^2 value of the regression as a measure of goodness of fit. Once identified, we performed three different simulations. In the first one, we used a single averaged species-specific CO, while two different values of crown allometry were assigned for each species according to the aspect of the validation plots. In the second, crown allometry remained a species-specific constant, but CO varied depending on aspect. Finally, in the third simulation, both crown allometry and CO were allowed to vary for each species according to the aspect of the validation plot. We compared bias and goodness of fit of the models to assess the influence of aspect on predictions of understory light values.

3. Results

3.1. Crown geometry

DBH and TH explained more than 85% of the variability in crown geometry for the three species studied (Table 2). Pine height increased sharply with DBH (high b parameter), and both pines rapidly reached the asymptotic maximum height, whereas fir had a greater maximum height but also a lower slope for the height-DBH relationship (Table 2). We observed that aspect did not affect this relationship (data not shown), so all the data available for each species were modeled together. Average crown ratio ranged from 50% of tree height for Scots pine to more than 90% for silver fir. This ranking in crown ratio matched the observed rankings in shade tolerance for these species in the Pyrenees (Ameztegui and Coll,

2011), with shade-tolerant species having deeper, longer crowns. However, at comparable aspects Scots pine had wider crowns than mountain pine for any given DBH (Fig. 3). Crown geometry of both pines significantly varied with aspect, as pines had wider and longer crowns on north-facing slopes (Fig. 3). Conversely, fir showed the longest and widest crowns all along the size gradient, but no effect of aspect was observed.

3.2. Crown openness

Crown openness ranged from 0.101 to 0.422 for silver fir, from 0.186 to 0.559 for Scots pine and from 0.113 to 0.439 for mountain pine (Fig. 4) depending on the selected outline. CO differed among species for any given outline, but pairwise comparisons indicated that there were no differences in CO between silver fir and mountain pine ($P > 0.12$ for all the outlines). For the tightest outlines (CO20, CO40, CO80), Scots pine CO was almost twice that of the other species, but this difference decreased for looser outlines (Fig. 4). Nevertheless, Scots pine showed a significantly higher CO than the other two species for any outline ($P < 0.001$). For all three species, CO increased as looser outlines were used, as expected. However CO values for a given outline were not much different from the immediately higher and lower outline (data not shown). Hence we selected CO20, CO80, CO320; COCH and CORec to assess the influence of aspect and DBH and to validate the model for light availability in the understory. Mean crown irregularity was 0.172 for silver fir and 0.178 for mountain pine, whereas Scots pine presented a much more irregular crown, with a mean value of 0.275.

CO was significantly affected by DBH and aspect in all cases analyzed except for the tightest outlines for mountain pine (Table 3). The effect of DBH, when significant, was always negative, i.e. CO decreased with increasing DBH. In pines, we found DBH to influence CO for loose outlines but also crown irregularity. For example, CORec in Scots pine decreased from 0.62 for a 10 cm DBH tree to 0.48 for a 60 cm DBH tree, whereas in mountain pine it varied between 0.33 and 0.19 for the same range of tree sizes. Conversely, the effect of DBH on fir CO was only significant for the tightest outlines (Fig. 5). The effect of aspect varied across species: silver fir and mountain pine had higher CO in south-exposed slopes, but the opposite effect was found for Scots pine (Table 3). The same species-specific effect of aspect was also observed for crown irregularity (Table 3, Fig. 6). In the case of DBH, its effect varied across species: it did not have a significant effect on silver fir irregularity, whereas both pines showed more regular crowns for bigger diameters (Table 3).

3.3. Prediction of understory light

The regression between observed and predicted values of light availability in the understory was significant for all the simulations ($P < 0.001$), and the explained variance ranged between 0.43 and 0.50. However, slopes of the regression ranged from 0.69 to 0.89, indicating that predictions of light in the understory overestimated observed values for any outline used (Fig. 7). Predictions using COCH and CORec provided an acceptable fit, but the greatest bias, and so were discarded. Although there were no marked differences in goodness of fit between values obtained using CO320, CO80 and CO20, the latter provided less biased predictions ($y = 0.887x$; $R^2 = 0.46$) and was therefore selected as the reference model. When aspect was explicitly considered, i.e. when CO and allometry were allowed to vary according to plot aspect, regression of observed vs. predicted values produced a better fit and lower bias than the reference model ($y = 0.951x$; $R^2 = 0.50$).

In stands where mountain pine or Scots pine were the dominant species, allowing CO and crown geometry to vary depending on the aspect of the validation plot greatly improved the fit of the models,

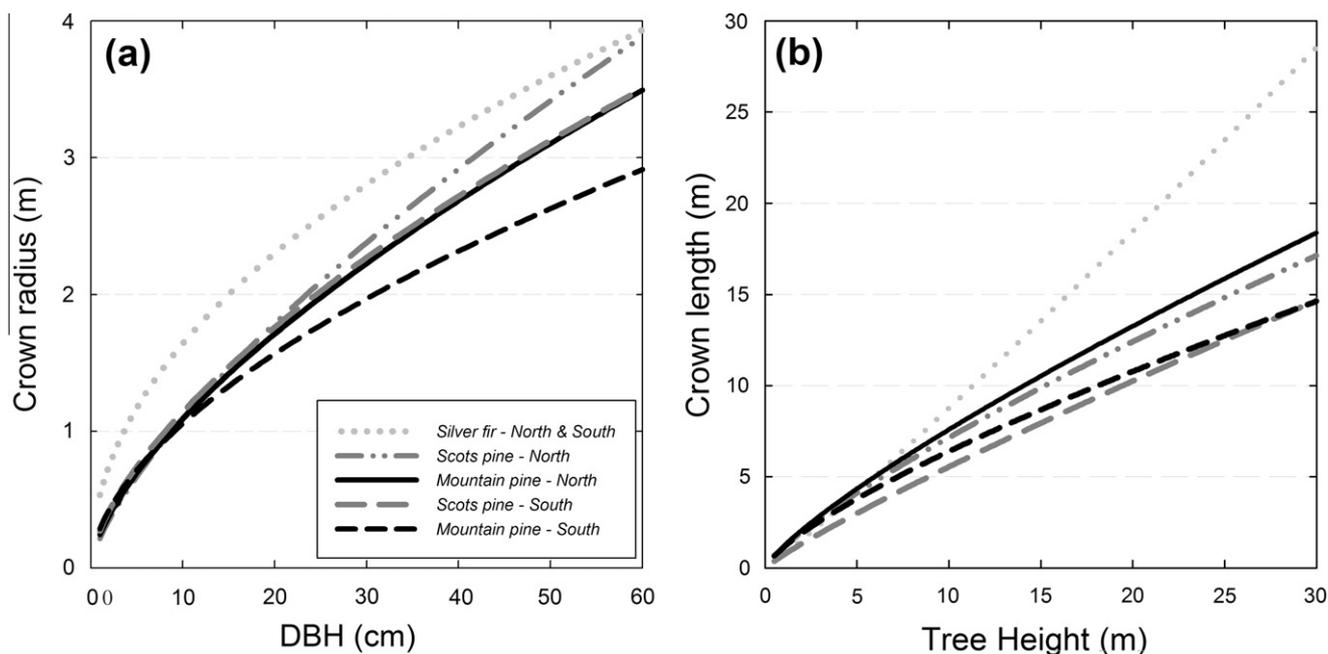


Fig. 3. Allometric relationships for the determination of crown geometry as a function of tree size for three conifer species in the Pyrenees: silver fir (*Abies alba*); Scots pine (*Pinus sylvestris*) and mountain pine (*Pinus uncinata*). (a) Crown radius as a function of DBH. (b) Crown length as a function of tree height. Equations are adjusted separately for north-facing and south-facing slopes except for fir, for which we found no differences in the parameters estimated for the two aspects.

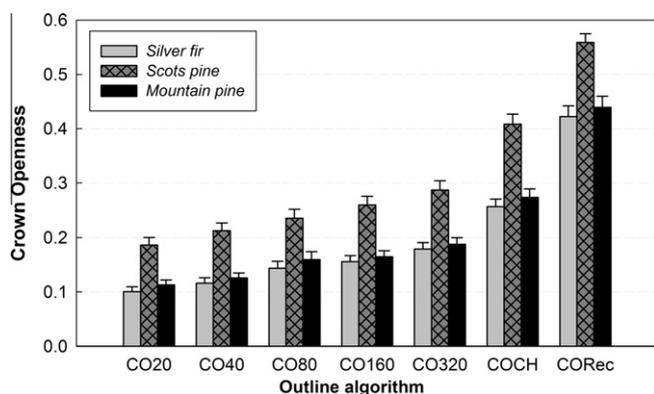


Fig. 4. Values of crown openness (CO) for three conifer species in the Pyrenees as obtained by seven different algorithms included in the Crown Delineator. Bars indicate upper 95% confidence intervals. $N = 104$ for silver fir (*Abies alba*), 119 for Scots pine (*Pinus sylvestris*) and 106 for mountain pine (*Pinus uncinata*).

and the slope of the regression was close to 1. A much poorer fit was obtained in silver fir stands, and variation of parameters according to aspect did not result in substantial improvement of predictions (Fig. 8). Most of the improvement in light predictions when considering the aspect was caused by variation in crown geometry, as variation of crown openness without changing crown geometry caused no or little improvement in predictions compared with the reference model (Table 4).

4. Discussion

4.1. The role of aspect on crown geometry and openness

We hypothesized that aspect would exert a significant influence on the crown architecture and openness of the studied species, thereby affecting light transmission through their canopies. Our results support this hypothesis, but interestingly, we found the effect

of aspect on crown geometry and openness to be highly species-specific. Fir crown allometry was not affected by aspect and showed the largest crown dimensions and little crown rise, so that crowns extended almost the entire length of the tree (Fig. 3). The lack of response of silver fir allometry to aspect may be caused by limited morphological response of the species to changes in environmental conditions, as previously observed for silver fir saplings (Ametegui and Coll, 2011). Its large crown, along with the observed low CO value (0.1) are characteristic of shade-tolerant species, which in general present dense crowns and cast deep shade in the understory (Canham et al., 1999; Valladares and Niinemets, 2008), a strategy that prevents the establishment of pioneer species (Ametegui and Coll, 2011). Scots pine had the shortest and most open crown for any adopted outline (Fig. 3), also matching previous reports (Pettersson, 1997; Rouvinen and Kuuluvainen, 1997; Rautiainen and Stenberg, 2005). Unlike fir, both pine species had wider and longer crowns on northern slopes (Table 3). Better soil quality and higher water availability could explain the observed aspect-related differences in crown geometry (DeLucia et al., 2000; Lang et al., 2010), but changes in architectural traits to optimize light interception can also play a role, as longer and wider crowns allow trees to forage better for light (Falster and Westoby, 2003; Purves et al., 2007).

We observed similar CO values for silver fir and mountain pine (Fig. 4), a species that has been described in the botanic literature as having a narrow, deep, “fir-like” crown (Ruiz de la Torre, 2006). Comparison of the ranking of CO and crown ratio matched shade-tolerance rankings for these species: fir > mountain pine > Scots pine (Ametegui and Coll, 2011) (Fig. 4). Previously reported CO values range between 0.05 for shade tolerant species to more than 0.2 for shade intolerant ones, but CO values derived from crown photographs largely depend on the method chosen for the determination of crown outline (Boivin et al., 2011). The divergence in our results, with CO values ranging from 0.1 to more than 0.5 (Fig. 4), stresses the importance of standardizing the methodology for CO determination. The fractal nature of tree crowns makes the definition of their outline a very uncertain and subjective task (Mandelbrot, 1983;

Table 3
Results of the generalized linear model (GLM) predicting crown openness (CO) as a function of tree size (DBH) and aspect for three montane-subalpine conifers in the Pyrenees: silver fir (*Abies alba*); Scots pine (*Pinus sylvestris*) and mountain pine (*Pinus uncinata*). Parameter estimates and significance of both predictive variables are shown, and model significance is indicated by "Model *p*-value". Positive values of aspect parameter indicate an increase in the dependent variable for south slopes.

	Aspect estimate	<i>p</i> -Value (aspect)	DBH estimate	<i>p</i> -Value (DBH)	Model <i>p</i> -Value
<i>Silver fir</i>					
CO20	0.021	0.026	−7.65 e-04	0.005	<0.001
CO80	0.040	<0.001	−6.47e-04	0.033	<0.001
CO320	0.051	<0.001	−6.85e-04	0.049	<0.001
COCH	0.066	<0.001	−0.77e-04	0.008	<0.001
CORec	0.083	<0.001	n.s.	0.571	<0.001
Irregularity	0.048	<0.001	n.s.	0.416	<0.001
<i>Scots pine</i>					
CO20	−0.047	<0.001	n.s.	0.053	<0.001
CO80	−0.064	<0.001	−2.02 e-03	0.005	<0.001
CO320	−0.072	<0.001	−2.71 e-03	0.001	<0.001
COCH	−0.074	<0.001	−3.05 e-03	<0.001	<0.001
CORec	−0.049	0.001	−2.56 e-03	0.004	<0.001
Irregularity	−0.053	0.001	−2.71 e-03	0.004	<0.001
<i>Mountain pine</i>					
CO20	n.s.	0.806	n.s.	0.149	0.322
CO80	n.s.	0.166	n.s.	0.357	0.378
CO320	n.s.	0.367	n.s.	0.768	0.650
COCH	0.043	0.003	n.s.	0.165	0.003
CORec	0.051	0.011	− 2.56 e-03	0.007	<0.001
Irregularity	0.043	0.001	−1.57 e-03	0.014	<0.001

Zeide and Pfeifer, 1991), but the method chosen can give not merely different numeric results, but also different biological interpretations. If defined by hand, it is common to define a serrated outline following all the cavities and gaps, so that CO is determined by the proportion of leaves and hollows within the crown. However, there is an inherent problem in deciding the smallest cavity that must be taken into account (Zeide, 1998). On the other hand, the use of objective geometrical conventions (convex hull or the circumscribed rectangle) leads to high values of CO where openness is mainly influenced by the existence of dents and bulges in the crown profile, *i.e.* crown irregularity (Mizoue and Dobbertin, 2003). However, the combined study of crown porosity (the value of CO for tight outlines) and irregularity (the difference in CO between tight and loose outlines) can be of interest for assessing the patterns of leaf distribution. This is related to the light interception efficiency, which has commonly been assessed in terms of the silhouette-to-total-area ratio (STAR) (Sinoquet et al., 2005; Delagrange et al., 2006). In turn, STAR depends on crown density (the ratio of leaf area to crown area) and leaf dispersion (Duursma et al., 2011) and can be related to CO as: $STAR = SA \cdot (1 - CO) / LA$, where SA is the projected silhouette leaf area and LA is the crown leaf area. Thus assessment of crown porosity and irregularity can lend insight into the study of leaf distribution throughout the crown and the effect of environmental factors on it.

In our study, the lower CO we observed for bigger trees (Table 3) agrees with previous reports that related this effect to a higher foliage accumulation in the top layer of the canopy and to lower branchiness and sparse display of foliage in smaller trees (Lefrançois et al., 2008; Boivin et al., 2011; Duursma et al., 2011). In pines, we found DBH to influence CO for loose outlines but also crown irregularity (Table 3). Small pines have fewer and less uniformly distributed branches than fir, and so the bigger spaces between branches contribute to higher CO and irregularity. Conversely, the effect of DBH on fir CO was only significant for the tightest outlines, suggesting that differences would be mainly a consequence of changes in the proportion of leaves and hollows within the crown. The rank of crown regularity observed for the three species also matched ranks of shade tolerance (Ameztegui and Coll, 2011). Our results agreed with previous studies that have already found a relationship between shade tolerance and the regularity in the

distribution of foliage, assessed by means of the fractal dimension of the crown (Zeide and Pfeifer, 1991; Osawa, 1995; Boudon et al., 2006).

Crowns in southern-oriented plots were more open for mountain pine and silver fir, while we observed the opposite trend for Scots pine (Table 3). Within-species regional differences in CO have been suggested to vary with water availability, whether from annual precipitation or actual evapotranspiration (Messier et al., 1998; Astrup and Larson, 2006). Lefrançois et al. (2008) showed enhanced CO values in plants growing in drier conditions that were ascribed to a decrease in the quantity of foliage supported by plants. Analyses compiled from 25 studies and including 17 species found that higher vapor pressure deficit (VPD) caused reduction in leaf/sapwood area ratio in pines, but not in other conifer species, including *Abies* (DeLucia et al., 2000). Our observed species-specific changes in CO with aspect cannot be completely explained by either the decrease in the total amount of foliage or by the changes in leaf distribution patterns associated with shade tolerance alone. We found crown regularity to vary with aspect in the same direction as CO (Table 3), suggesting that changes in CO with aspect would be mainly caused by variation in the distribution patterns of branches and foliage.

Increasing light interception efficiency allows plants to increase carbon assimilation, but this can only be achieved at high metabolic cost associated with the construction and maintenance of the woody structures needed (Duursma et al., 2011). Thus the optimal metabolic option is frequently not the one that maximizes light interception, and some degree of leaf clumping is commonly observed (Pearcy et al., 2005). In addition, leaf self-shading prevents leaves warming above air temperature (de Castro and Fetcher, 1999; Falster and Westoby, 2003; Valiente-Banuet et al., 2010), limits evapotranspiration losses and can also help trees to avoid photo-damage caused by excessive radiation (Valladares et al., 2005). This is particularly important in seedlings of plants growing at high altitudes such as mountain pine and silver fir, but has also been observed in adult trees (Germino and Smith, 1999; Grace et al., 2002; Handa et al., 2005). This could explain the observed increase in CO that both species experience in sun-exposed slopes. In the case of Scots pine, its lower crown porosity in southern aspects may be a consequence of its strategy to face higher evaporative

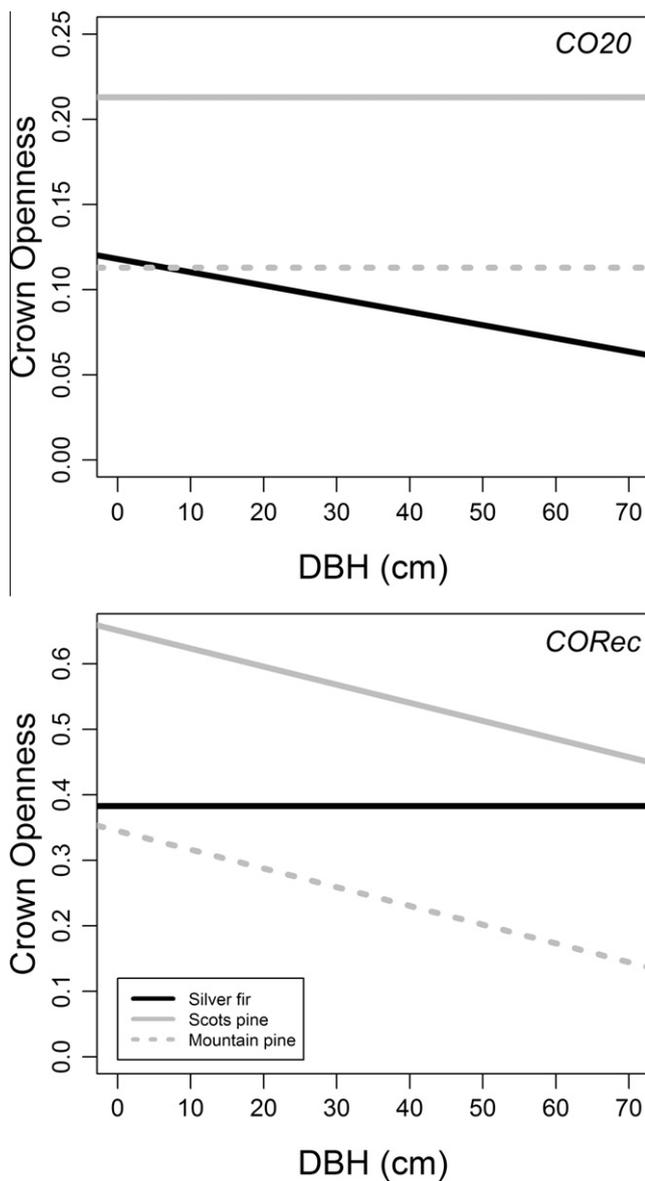


Fig. 5. Effect of DBH on crown openness as determined for the tightest (CO20) and loosest (COREc) outlines using the parameters reported in Table 3. For silver fir, DBH only affected CO for the tightest outlines, denoting variation in crown porosity with DBH. For pines, DBH made CO to decrease only for loosest outlines, thus indicating a major role of crown irregularity. Horizontal lines denote no effect of DBH on CO, and are included only for comparative purposes.

demand. In this species, increased VPD has been observed to cause little variation in the leaf/sapwood area ratio but a marked enhancement of tree branchiness as a strategy to avoid catastrophic cavitation in trees (Berninger et al., 1995; DeLucia et al., 2000).

4.2. Prediction of understory light

Average GLI values in the understory of the forests studied ranged from 7.7 to 97.1%, with an average of 39.7%. In our study area, the SORTIE-ND model slightly overestimated the amount of light reaching the understory. This overestimation may be caused by the effect of slope, which causes a distortion between the actual and the modeled relative position of trees in SORTIE-ND, thus causing changes in shade cast by neighbor trees. However, the potential biasing effect of slope was minimized by restricting

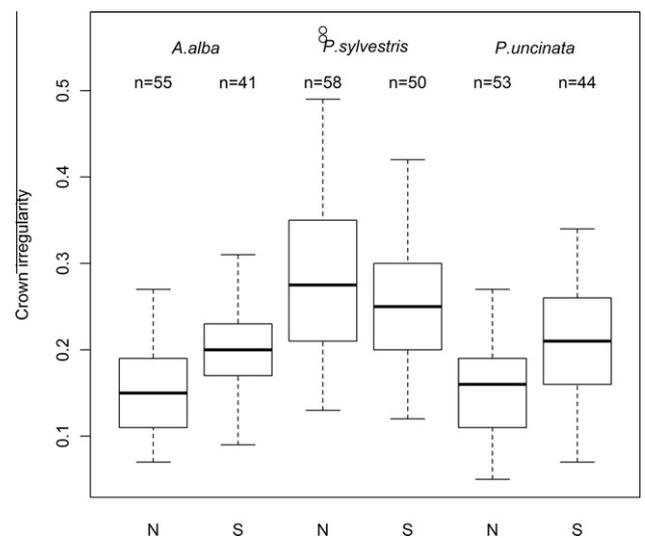


Fig. 6. Boxplot of distribution of crown irregularity determined for the three species: silver fir (*Abies alba*); Scots pine (*Pinus sylvestris*) and mountain pine (*Pinus uncinata*), and two aspects: N: north-facing; S: south-facing slopes.

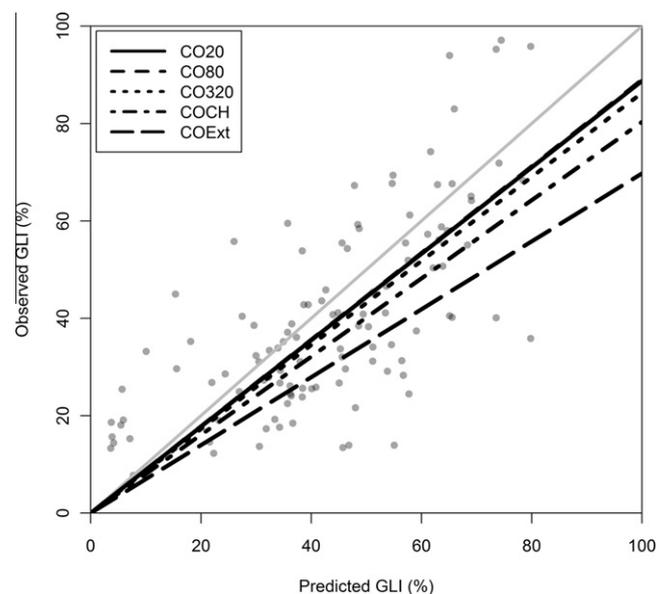


Fig. 7. Test of the model's ability to predict understory light levels in 24 plots in montane-subalpine forests in the Pyrenees. Predicted GLI values are simulated by SORTIE-ND using different crown openness (CO) as calculated from five different outlines, and observed GLI values are obtained from hemispherical photographs. The gray points represent the values obtained for outline CO20, and the gray solid line represents 1:1 relationship.

calculations to the sky region within 45° from vertical. Light predictions can be considered more than acceptable and regression fits were comparable to previously validated forests (Beaudet et al., 2002; Boivin et al., 2011). The least biased predictions of GLI were obtained using CO20, i.e. the tightest crown outline. These results agree with those of Boivin et al. (2011), who also found CO20 to give the best fit in adult poplar plantations. However, we observed few differences in the estimated parameters for different outlines. Only the loosest outlines (COCH and COREc) produced significantly less accurate predictions and slopes different from 1. The weak influence of different crown outlines in predicting GLI suggests a low influence of CO in forest understory light availability. Canham et al. (1999) and Beaudet et al. (2002)

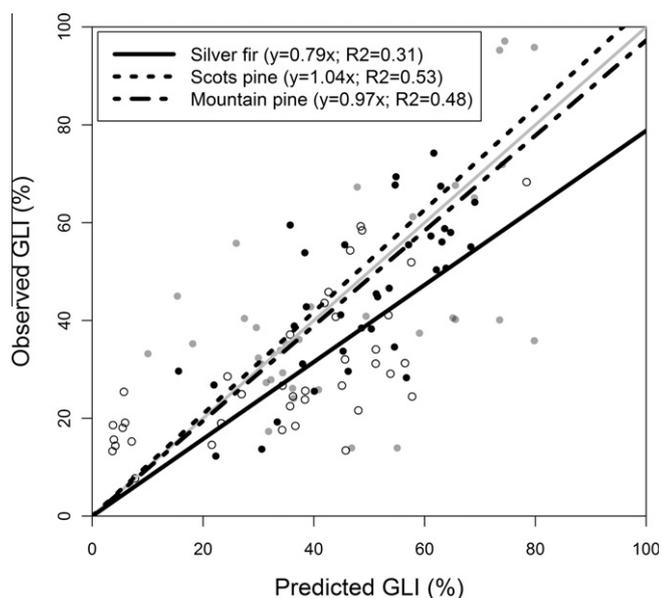


Fig. 8. Test of the model's ability to predict understory light levels in montane-subalpine forests in the Pyrenees depending on the dominant species. Silver fir (*Abies alba*): white dots; Scots pine (*Pinus sylvestris*): grey dots, and mountain pine (*Pinus uncinata*): black dots. Equations and dashed lines correspond to models in which crown openness and crown allometry were allowed to vary as a function of plot aspect. The gray solid line represents 1:1 relationship.

Table 4

Slope and goodness-of-fit of equations relating predicted and observed GLI values in montane-subalpine forests in the Pyrenees. The reference model was adjusted with species-specific constants for crown openness and allometry: silver fir (*Abies alba*); Scots pine (*Pinus sylvestris*) and mountain pine (*Pinus uncinata*). Subsequent models allowed CO, crown geometry and both parameters to vary depending on the species and the aspect of the validation plot.

	Silver fir		Scots pine		Mountain pine	
	Slope	R ²	Slope	R ²	Slope	R ²
Reference model (CO20)	0.767	0.33	0.937	0.32	0.915	0.49
Variable CO	0.773	0.32	1.028	0.48	0.913	0.49
Variable crown geometry	0.781	0.30	1.018	0.53	0.973	0.49
Both	0.788	0.30	1.044	0.54	0.971	0.49

have already suggested that the size, distribution and geometry of tree crowns are the most important factors regulating spatial variation in understory light availability. Our results support these findings, as the marked improvement of light predictions obtained when crown parameters were allowed to vary depending on the aspect of the validation plot was mainly caused by variation in crown geometry (Table 4).

5. Conclusions

In summary, the effect of slope aspect on tree crowns was found to be highly species-specific. Aspect influenced both crown transparency and irregularity of the species studied and, as a consequence, changes in crown openness may be a combined effect of changes in total leaf area and patterns of leaf distribution. The observed species-specific variation in crown geometry and openness with aspect resulted in differences in understory light predictions that were large enough to warrant explicit consideration when studying and modeling the ecological processes driving the dynamics of these forests.

Acknowledgements

This research was primarily supported by the Spanish Ministry of Science and Innovation via the Consolider-Ingenio Montes project (CSD2008-00040) and the DINAMIX project (AGL2009-13270-C02). The Spanish Ministry of Science provided Dr. Lluís Coll with support through a Ramon y Cajal contract (RYC-2009-04985), and the Spanish Ministry of Education provided support to Aitor Ameztegui through a predoctoral grant (FPU Program - AP2007-01663). We also thank F. Boivin for kind help with the script for CO determination; N. Ibañez, L. Ivorra, S. Martín and S. Bastien-Henri for valuable help during field sampling and laboratory processing and F. Cano for advise in finding the plots.

References

Ameztegui, A., Coll, L., 2011. Tree dynamics and co-existence in the montane-subalpine ecotone: the role of different light-induced strategies. *J. Veg. Sci.* 22, 1049–1061.

Astrup, R., Larson, B.C., 2006. Regional variability of species-specific crown openness for aspen and spruce in western boreal Canada. *For. Ecol. Manage.* 228, 241–250.

Bale, C.L., Charley, J.L., 1994. The impact of aspect on forest floor characteristics in some eastern Australian sites. *For. Ecol. Manage.* 67, 305–317.

Bazzaz, F.A., 1979. Physiological Ecology of Plant Succession. *Annu. Rev. Ecol. Syst.* 10, 351–371.

Beaudet, M., Messier, C., Canham, C.D., 2002. Predictions of understory light conditions in northern hardwood forests following parameterization, sensitivity analysis, and tests of the SORTIE light model. *For. Ecol. Manage.* 165, 235–248.

Berninger, F., Mencuccini, M., Nikinmaa, E., Grace, J., Hari, P., 1995. Evaporative demand determines branchiness of Scots pine. *Oecologia*, 164–168.

Boivin, F., Paquette, A., Racine, P., Messier, C., 2011. A fast and reliable method for the delineation of tree crown outlines for the computation of crown openness values and other crown parameters. *Can. J. Forest Res.* 41, 1827–1835.

Boudon, F., Godin, C., Pradal, C., Puech, O., Sinoquet, H., 2006. Estimating the fractal dimension of plants using the two-surface method. An analysis based on 3D-digitized tree foliage. *Fractals* 14, 149–163.

Brown, M.J., Parker, G.G., 1994. Canopy light transmittance in a chronosequence of mixed-species deciduous forests. *Can. J. Forest Res.* 24, 1694–1703.

Brunner, A., 1998. A light model for spatially explicit forest stand models. *For. Ecol. Manage.* 107, 19–46.

Canham, C.D., 1988. An index for understory light levels in and around canopy gaps. *Ecology* 69, 1634–1638.

Canham, C.D., Coates, K.D., Bartemucci, P., Quaglia, S., 1999. Measurement and modeling of spatially explicit variation in light transmission through interior cedar-hemlock forests of British Columbia. *Can. J. Forest Res.* 29, 1775–1783.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., White, P.S., 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. Forest Res.* 20, 620–631.

Canham, C.D., Finzi, A.C., Pacala, S.W., Burbank, D.H., 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Can. J. Forest Res.* 24, 337–349.

Canham, C.D., Murphy, L.E., Papaik, M.J., 2005. SORTIE-ND: Software for Spatially-Explicit Simulation of Forest Dynamics. Institute of Ecosystem Studies, Millbrook (NY).

de Castro, F., Fetcher, N., 1999. The effect of leaf clustering in the interception of light in vegetal canopies: theoretical considerations. *Ecol. Model.* 116, 125–134.

Delagrèze, S., Montpied, P., Dreyer, E., Messier, C., Sinoquet, H., 2006. Does shade improve light interception efficiency? A comparison among seedlings from shade-tolerant and -intolerant temperate deciduous tree species. *New Phytol.* 172, 293–304.

DeLucia, E.H., Maherali, H., Carey, E.V., 2000. Climate-driven changes in biomass allocation in pines. *Global Change Biol.* 6, 587–593.

DGCN, 2007. Tercer Inventario Forestal Nacional (1997–2007): Cataluña. Ministerio de Medio Ambiente, Madrid.

Duursma, R.A., Falster, D.S., Valladares, F., Sterck, F.J., Pearcy, R.W., Lusk, C.H., Sendall, K.M., Nordenstahl, M., Houter, N.C., Atwell, B.J., Kelly, N., Kelly, J.W.G., Liberloo, M., Tissue, D.T., Medlyn, B.E., Ellsworth, D.S., 2011. Light interception efficiency explained by two simple variables: a test using a diversity of small- to medium-sized woody plants. *New Phytol.*

Falster, D.S., Westoby, M., 2003. Leaf size and angle vary widely across species: what consequences for light interception? *New Phytol.* 158, 509–525.

Frazier, G.W., Canham, C.D., Letzmann, K.P., 2000. Gap Light Analyzer, version 2.0. *Bull. Ecol. Soc. Am.* 81, 191–197.

García-Pausas, J., Casals, P., Camarero, L., Huguet, C., Sebastià, M.-T., Thompson, R., Romanyà, J., 2007. Soil organic carbon storage in mountain grasslands of the Pyrenees: effects of climate and topography. *Biogeochemistry* 82, 279–289.

Gendron, F., Messier, C., Comeau, P.G., 1998. Comparison of various methods for estimating the mean growing season percent photosynthetic photon flux density in forests. *Agr. Forest Meteorol.* 92, 55–70.

- Germino, M.J., Smith, W.K., 1999. Sky exposure, crown architecture, and low-temperature photoinhibition in conifer seedlings at alpine treeline. *Plant Cell Environ.* 22, 407–415.
- Grace, J., Berninger, F., Nagy, L., 2002. Impacts of climate change on the tree line. *Ann. Bot.*, 537–544.
- Groot, A., 2004. A model to estimate light interception by tree crowns, applied to black spruce. *Can. J. Forest Res.* 34, 788–799.
- Handa, I.T., Körner, C., Hättenschwiler, S., 2005. A test of the tree-line carbon limitation hypothesis by in situ CO₂ enrichment and defoliation. *Ecology* 86, 1288–1300.
- Hicks, R.R.J., Frank, P.S.J., 1984. Relationship of aspect to soil nutrients, species importance and biomass in a forested watershed in West Virginia. *For. Ecol. Manage.* 8, 281–291.
- Kobe, R.K., Pacala, S.W., Silander, J.A., Canham, C.D., 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* 5, 517–532.
- Lang, A.C., Härdtle, W., Bruehlheide, H., Geißler, C., Nadrowski, K., Schuldt, A., Yu, M., von Oheimb, G., 2010. Tree morphology responds to neighbourhood competition and slope in species-rich forests of subtropical China. *For. Ecol. Manage.* 260, 1708–1715.
- Larsen, D.R., Kershaw, J.A., 1996. Influence of canopy structure assumptions on predictions from Beer's law. A comparison of deterministic and stochastic simulations. *Agr. Forest Meteorol.* 81, 61–77.
- Lefrançois, M.L., Beaudet, M., Messier, C., 2008. Crown openness as influenced by tree and site characteristics for yellow birch, sugar maple, and eastern hemlock. *Can. J. Forest Res.* 38, 488–497.
- Lieffers, V.J., Messier, C., Stadt, K.J., Gendron, F., Comeau, P.G., 1999. Predicting and managing light in the understory of boreal forests. *Can. J. Forest Res.* 29, 796–811.
- Mandelbrot, B.B., 1983. *The Fractal Geometry of Nature*. W.H. Freeman, San Francisco.
- Messier, C., Parent, S., Bergeron, Y., 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. *J. Veg. Sci.* 9, 511–520.
- Mizoue, N., Dobbertin, M., 2003. Detecting differences in crown transparency assessments between countries using the image analysis system CROCO. *Environ. Monit. Assess.* 89, 179–195.
- Monsi, M., Saeki, T., 1953. Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. *Jpn. J. Bot.* 14, 22–52.
- Navas, A., Machín, J., Beguería, S., López-Vicente, M., Gaspar, L., 2007. Soil properties and physiographic factors controlling the natural vegetation re-growth in a disturbed catchment of the Central Spanish Pyrenees. *Agroforest. Syst.* 72, 173–185.
- Osawa, A., 1995. Inverse relationship of crown fractal dimension to self-thinning exponent of tree populations: a hypothesis. *Can. J. Forest Res.* 25, 1608–1617.
- Pacala, S.W., Canham, C.D., Saponara Jr, J., Silander, J.A., Kobe, R.K., Ribbens, E., 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol. Monogr.* 66, 1.
- Pacala, S.W., Canham, C.D., Silander, J.A., 1993. Forest models defined by field-measurements. 1. The design of a northeastern forest simulator. *Can. J. Forest Res.* 23, 1980–1988.
- Pearcy, R.W., Muraoka, H., Valladares, F., 2005. Crown architecture in sun and shade environments: assessing function and trade-offs with a three-dimensional simulation model. *New Phytol.* 166, 791–800.
- Petersson, H., 1997. Functions for predicting crown height of *Pinus sylvestris* and *Picea abies* in Sweden. *Scand. J. For. Res.* 12, 179–188.
- Purves, D.W., Lichstein, J.W., Pacala, S.W., 2007. Crown plasticity and competition for canopy space. a new spatially implicit model parameterized for 250 North American tree species. *PLoS ONE* 2, e870.
- R Development Core Team, 2010. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rautiainen, M., Mõttus, M., Stenberg, P., Ervasti, S., 2008. Crown envelope shape measurements and models. *Silva Fenn.* 42, 19–33.
- Rautiainen, M., Stenberg, P., 2005. Simplified tree crown model using standard forest mensuration data for Scots pine. *Agr. Forest Meteorol.* 128, 123–129.
- Rouvinen, S., Kuuluvainen, T., 1997. Structure and asymmetry of tree crowns in relation to local competition in a natural mature Scots pine forest. *Can. J. Forest Res.* 902, 890–902.
- Ruiz de la Torre, J., 2006. *Flora Mayor. Dirección General para la Biodiversidad. Ministerio de Medio Ambiente, Madrid.*
- Sinoquet, H., Sonohat, G., Phattaralerphong, J., Godin, C., 2005. Foliage randomness and light interception in 3-D digitized trees: an analysis from multiscale discretization of the canopy. *Plant Cell Environ.* 28, 1158–1170.
- Sonohat, G., Balandier, P., Ruchaud, F., 2004. Predicting solar radiation transmittance in the understory of even-aged coniferous stands in temperate forests. *Ann. For. Sci.* 61, 629–641.
- Stadt, K., Lieffers, V.J., 2000. MIXLIGHT: a flexible light transmission model for mixed-species forest stands. *Agr. Forest Meteorol.* 102, 235–252.
- Stadt, K.J., Lieffers, V.J., Hall, R.J., Messier, C., 2005. Spatially explicit modeling of PAR transmission and growth of *Picea glauca* and *Abies balsamea* in the boreal forests of Alberta and Quebec. *Can. J. Forest Res.* 35, 1–12.
- Thorpe, H.C., Vanderwel, M.C., Fuller, M.M., Thomas, S.C., Caspersen, J.P., 2010. Modelling stand development after partial harvests: an empirically based, spatially explicit analysis for lowland black spruce. *Ecol. Model.* 221, 256–267.
- Uriarte, M., Canham, C.D., Thompson, J., Zimmerman, J.K., Murphy, L., Sabat, A.M., Fetcher, N., Haines, B.L., 2009. Natural disturbance and human land use as determinants of tropical forest dynamics: results from a forest simulator. *Ecol. Monogr.* 79, 423–443.
- Valiente-Banuet, A., Verdú, M., Valladares, F., García-Fayos, P., 2010. Functional and evolutionary correlations of steep leaf angles in the mexican shrubland. *Oecologia* 163, 25–33.
- Valladares, F., Dobarro, I., Sánchez-Gómez, D., Pearcy, R.W., 2005. Photoinhibition and drought in Mediterranean woody saplings: scaling effects and interactions in sun and shade phenotypes. *J. Exp. Bot.* 56, 483–494.
- Valladares, F., Niinemets, Ü., 2008. Shade tolerance, a key plant feature of complex nature and consequences. *Annu. Rev. Ecol. Syst.* 39, 237–257.
- Verbyla, D., Fisher, R.F., 1989. Effect of aspect on ponderosa pine height and diameter growth. *For. Ecol. Manage.* 27, 93–98.
- Zeide, B., 1998. Fractal analysis of foliage distribution in loblolly pine crowns. *Can. J. Forest Res.* 28, 106–114.
- Zeide, B., Pfeifer, P., 1991. A method for estimation of fractal dimension of tree crowns. *For. Sci.* 37, 1253–1265.