

Individual variability in tree allometry determines light resource allocation in forest ecosystems: a hierarchical Bayesian approach

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Abstract Tree species differences in crown size and shape are often highlighted as key characteristics determining light interception strategies and successional dynamics. The phenotypic plasticity of species in response to light and space availability suggests that intraspecific variability can have potential consequences on light interception and community dynamics. Species crown size varies depending on site characteristics and other factors at the individual level which

differ from competition for light and space. These factors, such as individual genetic characteristics, past disturbances or environmental micro-site effects, combine with competition-related phenotypic plasticity to determine the individual variability in crown size. Site and individual variability are typically ignored when considering crown size and light interception by trees, and residual variability is relegated to a residual error term, which is then ignored when studying ecological processes. In the present study, we structured and quantified variability at the species, site, and individual levels for three frequently used tree allometric relations using fixed and random effects in a hierarchical Bayesian framework. We focused on two species: *Abies alba* (silver fir) and *Picea abies* (Norway spruce) in nine forest stands of the western Alps. We demonstrated that species had different allometric relations from site to site and that individual variability accounted for a large part of the variation in allometric relations. Using a spatially explicit radiation transmission model on real stands, we showed that individual variability in tree allometry had a substantial impact on light resource allocation in the forest. Individual variability in tree allometry modulates species' light-intercepting ability. It generates heterogeneous light conditions under the canopy, with high light micro-habitats that may promote the regeneration of light-demanding species and slow down successional dynamics.

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Introduction

The size and shape of living organisms directly affect their ability to capture resources (Bonner 2006; Brown et al.

2004; McMahon 1973). Resource acquisition influences not only how populations survive, develop and reproduce, but also how they compete (Tilman 1977, 1982). This is especially true in tree communities, where competition for light is asymmetric (Yokozawa 1999). Large trees capture a disproportionate fraction of resources (Weiner 1990). Such competition has been shown to determine the development of hierarchies, the process of self-thinning, and the development of spatial structure in forest stands (Oliver and Larson 1996). Stand structure determines light allocation, which contributes to growth, mortality and regeneration (Emborg 1998).

Tree species' differences in crown size and allometry (Aarssen 1995; Bohlman and O'Brien 2006; Poorter et al. 2006; Rees et al. 2001) are often highlighted as key characteristics determining species' strategies for light interception and successional dynamics in the forest (Canham et al. 1994; Grubb 1998; King 1996; Parish et al. 2008; Shukla and Ramakrishnan 1986; Yokozawa et al. 1996). Dominant species may be those capable of large size, thereby increasing their light exposure, casting shade on competitors, and increasing reproductive or dispersal organs (Aarssen 1995). Late-successional shade-tolerant species may reach greater heights and develop deeper and larger crowns than early successional shade-intolerant species (Canham 1988; Pacala et al. 1996; Parish et al. 2008). Since they cast more shade, late-successional species promote the regeneration of shade-tolerant species, progressively excluding early successional shade-intolerant species (Canham 1988; Deutschman et al. 1997; Grubb 1998).

For a given species, crown size and shape are highly variable from one individual to another. Numerous studies have analyzed this variability in terms of tree crown response to anisotropic light and space availability through phenotypic plasticity (Canham 1988; Piboule et al. 2005; Purves et al. 2007; Sorrensen-Cothorn et al. 1993; Vincent and Harja 2008). Trees expressing high phenotypic plasticity can form tessellating crown shapes that fill most of the canopy space (Purves et al. 2007). Based on this plasticity some authors have gone as far as assuming a perfect plasticity—crowns filling all the canopy space—resulting in a closed homogeneous canopy (Adams et al. 2007; Purves et al. 2007) and thus simplifying the modeling of tree competition for light. However, such an assumption ignores the high variability in crown shape independent of light-related phenotypic plasticity. Indeed it is well known that soil nutrients and water availability (Deleuze et al. 1996) and climatic conditions such as temperature and air humidity (Geburek et al. 2008) affect the potential maximum size of a tree species and its crown size and shape. Biotic interactions in the stand (e.g., competition between tree species, effects of pathogens and

herbivores) modulate this potential (Oldeman 1990; Parish et al. 2008). Parish et al. (2008) underlined that damage consisting of branch and leader breakage associated with external disturbances (e.g., windthrows, snowfalls) also explained a large part of the intraspecific variability. Multiple external environmental factors combine with intraspecific genetic variability to determine individual growth trajectories (Aarssen 1992), resulting in random individual crown sizes and shapes. Paradoxically, the ecological consequences of the overall individual variability in crown size on light interception and successional dynamics have been poorly studied (Parish et al. 2008).

In order to understand ecological processes related to crown variation and light allocation, one needs to quantify the sources of variation contributed by the species, sites, and individuals. One set of parameters is usually defined for each species because they are assumed to differ from each other (Abe and Yamada 2008; Bohlman and O'Brien 2006; Poorter et al. 2006). Explicit variables such as aspect, slope, elevation, habitat type, location (Wykoff 1990), density (Hummel 2000), species composition and soil (Sterba et al. 2002) may account for site differences. Individual variation in crown size and allometric relations has been associated with individual size [diameter at breast height (DBH) or height or basal area], competition indexes (Monserud and Sterba 1996; Wykoff 1990) or local anisotropic light and space availability when considering plastic asymmetric individual crowns (Purves et al. 2007; Sorrensen-Cothorn et al. 1993; Vincent and Harja 2008). However, much of the intraspecific variability resulting from non-measured environmental and genetic factors is not considered and included as part of a residual error term, so that the potential effect of individual variability in crown size on species' strategies for light interception and on successional dynamics is not assessed.

In this study, a hierarchical Bayesian framework was applied to break down variability into allometric measurements at the individual level. A light interception model was then used to test for the effect of the individual variability in crown size on species' strategies for light interception and regeneration. First, we tested for light- and space-related phenotypic plasticity including competition indexes in allometric models. Second, we quantified individual variability to determine whether this leveled the differences between species in terms of allometry and crown size. Third, we assessed whether individual variation in crown size had an effect on the understory light regime and forest succession. These tests were carried out on two species: a relatively shade-tolerant species *Abies alba* Mill. (silver fir) and a relatively shade-intolerant species *Picea abies* (L.) Karst. (Norway spruce), which coexist spontaneously at the mountain-belt elevation (800–1,800 m) in the western Alps. Three allometric functions were

analyzed: height–DBH, crown height–height, and crown radius–DBH. We used the calibrated allometric measurements to run an explicit radiation transmission model (Courbaud et al. 2003) aiming at analyzing the effect of individual allometric variability on light interception and light penetration in a real forest stand.

Materials and methods

Field measures

Trees were measured on nine plots ranging in size from 0.25 to 1 ha. Plots are located at the mountain-belt elevation (800–1,800 m) in the western Alps: six plots in the French Alps, two in the Italian Alps and one in the Swiss Alps. Stands are uneven-aged with *Abies alba* and *Picea abies* the dominant species. Stand age and stand silvicultural history are different from one plot to another (Appendix S1 in Supplementary Material).

On each plot, we measured DBH (in cm) and mapped all trees taller than 1.3 m. To account for phenotypic plasticity associated with local light and space availability, we computed nine neighborhood competition indexes (NCI) with the basal area of: (1) all the trees, (2) the larger trees, and (3) the smaller trees compared to the target tree, at three different distances: 5, 10 and 15 m from the target tree. Edge effects were taken into account with a torus system. Using a torus, a plot is first wrapped upside down in the vertical plane, which allows the left-hand boundary to join the right-hand boundary. A second wrapping of the plot in the horizontal plane allows the front boundary to join the back boundary. Boundaries disappear and the plot becomes virtually of infinite dimensions (Courbaud et al. 2003).

We measured tree height (in meters), crown base height (“crown height” henceforth, in meters) and crown radius (in meters) for a sample of *A. alba* and *P. abies* trees with height more than or equal to 1.3 m. Crown height was defined as the mean of the distances from the ground to the basal living branches of the crown in four directions: upslope, downslope, left and right. Crown radius was defined as the mean of the lengths of the longest branches of the crown in these four directions. DBH was measured using a metric diameter tape. Tree height and crown height were measured with a Vertex III. Crown radius was measured using a metric tape.

A first census was taken from 1994 to 2005. A second one was taken in 2006 on a sample of four plots previously measured in 1994 (Appendix S1). For the second census, we re-measured all trees which were previously measured in 1994 and which were still alive in 2006. Heights of 794 *P. abies* and 637 *A. alba* trees were measured at the first census with measurements repeated for 148 *P. abies* and 53

A. alba trees at the second census. Crown radius and crown base height were measured for 454 *P. abies* and 513 *A. alba* trees at the first census and measured again for 96 *P. abies* and 53 *A. alba* trees at the second census. Trees that were measured twice allowed us to quantify individual variability.

Model comparison for allometric equations

We calibrated three allometric functions in order to reconstruct each tree in three dimensions from DBH: height as a function of DBH, crown height as a function of total height, and crown radius as a function of DBH. Allometric relations were calibrated independently for each species. We used a log transformation for response variables to restrict them to positive values and to include multiplicative errors.

In the first step, we identified the best function to relate the covariate to the response. Several classic functions (linear, power or asymptotic functions) were compared for each allometric relation. Model parameters were estimated in a Bayesian framework. The model selection was based on various criteria. Firstly, we checked that the fitted models responded to biological criteria. The models giving an implausible range of response were rejected. Secondly, we checked the graphical superposition between the function selected and a nonparametric curve representing the mean of the response for covariate classes (Appendix S2). This was done in order to avoid the bias in the function shape resulting from forest plots containing fewer big trees than small trees. Thirdly, the deviance information criterion (DIC) was used as a crude index to compare models. The DIC is the sum of the mean deviance [deviance = $-2 \log(\text{likelihood})$] and of the effective number of parameters (pD; the posterior mean of the deviance minus the deviance of the posterior means). A difference of more than 10 in DIC was taken as a rough index of difference between two models and ruled out the model with the higher DIC (Spiegelhalter et al. 2002). When the difference in DIC was less than 10, we selected the model with the best goodness of fit, i.e., with the lower deviance. In cases where the deviance difference was less than 10, we chose the model with the lower pD (Appendix S3).

A Gompertz function was selected to describe the height–DBH relation:

$$H = K \exp(-\log(K/1.3) \exp(-r\text{DBH})) \quad (1)$$

A linear function was selected for the crown height (CH)–tree height (H) relation (with CH < H):

$$\text{CH} = (1/(1 + K)) H \quad (2)$$

and a power function was selected for the crown radius (CR)–DBH relation:

$$CR = K(DBH)^b \quad (3)$$

Once the best function was selected, the site effect, the local competition effect and the individual effect were assessed independently for each species. We tested the effect of local competition with six different NCI for height and nine different NCI for crown height and crown radius (in the absence of a plausible ecological interpretation, the basal area of smaller trees were not tested for height). Effects were included through a log-linear relation for parameter K . We denoted K_{ij} the parameter K for tree i of plot j . To test for a local competition effect on allometry, we compared a model for which $\log(K_{ij}) = \mu_j$, where μ_j is the site fixed effect, with several models, each one including a different NCI, for which $\log(K_{ij}) = \mu_j + \alpha NCI_i$, where NCI_i is the neighborhood competition index for tree i and α the local competition effect. Individual effects, δ_i , were considered as random effects drawn in a common normal distribution of mean zero and variance, V_δ . To test for an individual random effect, we compared a model for which $\log(K_{ij}) = \mu_j$ with a model for which $\log(K_{ij}) = \mu_j + \delta_i$. The DIC was again used to compare hierarchical models of increasing complexity (Spiegelhalter et al. 2002).

R 2.4.1 software (Ihaka and Gentleman 1996) was used for data manipulations and graphs, WinBUGS 1.4 (Gilks et al. 1994) for hierarchical Bayes modeling, and R2WinBUGS (Sturtz et al. 2005) to connect R to WinBUGS. We checked the convergence of two Markov Chain Monte Carlo (MCMC) approaches using the potential scale reduction factor Rhat (at convergence, Rhat = 1). We made 300,000 iterations for each MCMC with a burn-in period of 290,000 steps and a thinning of 10 and obtained 2,000 estimations per parameter.

Measurement errors protocol

An independent protocol was applied to evaluate measurement errors made on the four dendrometric variables (DBH, tree height, crown height and crown radius). A substantial part of the variability in allometries can indeed come from measurement errors, especially for crown shape and tree height, which are not easily measured. From a statistical point of view, evaluating measurement error can better separate out the variability observed in data and provide a more accurate inference of parameters (Clark 2005).

To estimate measurement errors, three teams measured the same sample of 50 trees (ten for each 15-cm DBH class from 0–15 to ≥ 60 cm) during a 2-day period, on one plot selected at random. Measurements were independent of the general protocol but were taken under the same conditions and with the same instruments. Differences between the

three teams' measurements were attributed to measurement errors. We denoted z the dendrometric variable considered: DBH, tree height, crown height and crown radius. We used the notation N for normal distribution and LN for log-normal distribution. We assumed that z_{it} , a measurement associated with tree i made by team t , diverged from the "true value" $z_{i,0}$ and that the measurement error term $\exp(\varepsilon_{z,it})$ was multiplicative with $\varepsilon_{z,it}$ drawn in a normal distribution of mean zero and variance σ_z^2 :

$$z_{it} = z_{i,0} \exp(\varepsilon_{z,it}), \varepsilon_{z,it} \sim N(0, \sigma_z^2) \quad (4)$$

equivalent to $z_{it} \sim LN(\log(z_{i,0}), \sigma_z^2)$

Model parameters $z_{i,0}$ and σ_z^2 were estimated in a Bayesian framework (Appendix S4). The mean of the posterior distribution for the parameter σ_z^2 was used as an estimate of the variance associated with measurement errors. The variance estimate was denoted σ_x^2 for the covariate and σ_y^2 for the response variable.

Structure of the best allometric model

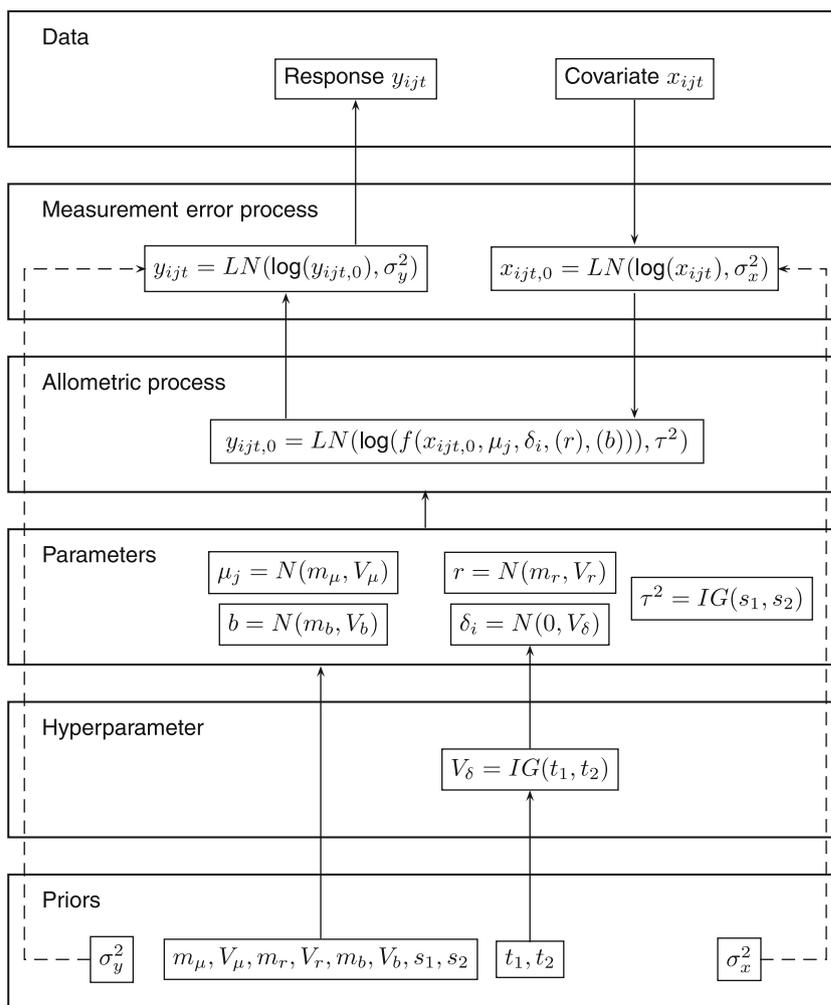
In this part, we present the structure of the model which integrates site effects, individual effects and measurement errors. For the three allometric relations, this model corresponded to the best model that could be obtained basing our choice on the DIC criterion.

The measurement of covariate x for tree i of plot j at time t is denoted x_{ijt} and \mathbf{X} is the vector of observations x_{ijt} . Covariate x is DBH for Eqs. 1 and 3 and height for Eq. 2. The total number of observations for each tree i is T_i ($T = 2$ for trees with two measurements and $T = 1$ otherwise) and the total number of trees is I . The measurement of response y for tree i of plot j at time t is denoted y_{ijt} and \mathbf{Y} is the vector of y_{ijt} . The function relating the covariate to the response is f (see Eqs. 1–3). Parameter K_{ij} , depending on tree i and plot j , is the scale parameter for Eqs. 1 and 3 and is the slope parameter for Eq. 2. We assumed $\log(K_{ij}) = \mu_j + \delta_i$, where μ_j is the site fixed effect and δ_i the individual random effect with $\delta_i \sim N(0, V_\delta)$.

Information on measurement errors was integrated into the allometric model for both the covariate x (e.g., DBH) and the response variable y (e.g., height). For the covariate, we modeled the "true" unobserved value $x_{ijt,0}$ as a realization of a log-normal distribution having parameters $x_{ijt,0}$ (the observed value) and σ_x^2 : $x_{ijt,0} \sim LN(\log(x_{ijt}), \sigma_x^2)$. We denoted \mathbf{X}_0 the vector of $x_{ijt,0}$. Regarding the response variable, we assumed that the observed value y_{ijt} was a realization of a log-normal distribution having parameters $y_{ijt,0}$ and σ_y^2 : $y_{ijt} \sim LN(\log(y_{ijt,0}), \sigma_y^2)$. We denoted \mathbf{Y}_0 the vector of $y_{ijt,0}$. The variance corresponding to unexplained variability was denoted τ^2 .

The model was developed in a hierarchical Bayesian framework (Fig. 1). The likelihood, L , of the model

Fig. 1 Hierarchical Bayesian framework used to model allometric relations. We modeled the response y_{ijt} as a function of the covariate x_{ijt} . The model included: (1) the individual random effects δ_i with variance V_δ , (2) the site fixed effect μ_j , and (3) the measurement errors with: “true” values $x_{ijt,0}$ and $y_{ijt,0}$, variance σ_x^2 for error on the covariate and variance σ_y^2 for error on the response



included both the uncertainty in the data (observation error) and the variability of the process (process error):

$$\begin{aligned}
 L &= p(Y|Y_0, X_0, X, \sigma_x^2, \sigma_y^2, \mu_j, \delta_i, (r), (b), \tau^2) \\
 &= p(Y|Y_0, \sigma_y^2)p(Y_0|X_0, \mu_j, \delta_i, (r), (b), \tau^2)p(X_0|X, \sigma_x^2) \\
 &= \prod_{i=1}^I \prod_{t=1}^{T_i} p\left(y_{ijt}|y_{ijt,0}, \sigma_y^2\right)p\left(y_{ijt,0}|x_{ijt,0}, \mu_j, \delta_i, (r), (b), \tau^2\right) \\
 &\quad \times p\left(x_{ijt,0}|x_{ijt}, \sigma_x^2\right) = \prod_{i=1}^I \prod_{t=1}^{T_i} LN\left(y_{ijt}|\log\left(y_{ijt,0}\right), \sigma_y^2\right) \\
 &\quad \times LN\left(y_{ijt,0}|\log\left(f\left(x_{ijt,0}, \mu_j, \delta_i, (r), (b)\right)\right), \tau^2\right) \\
 &\quad \times LN\left(x_{ijt,0}|\log\left(x_{ijt}\right), \sigma_x^2\right). \tag{5}
 \end{aligned}$$

We used conjugate priors with inverse-gamma distributions (*IG*) for variance parameters and normal distributions for means. The priors for first-level parameters were: $p(\tau^2) = IG(\tau^2|s_1, s_2)$, $p(b) = N(b|m_b, V_b)$ for Eq. 3, $p(r) = N(r|m_r, V_r)$ for Eq. 1 and $p(\mu_j) = N(\mu_j|m_\mu, V_\mu)$. The prior for the second level parameter (hyperparameter) corresponding to the variance of the individual effects was $p(V_\delta) = IG(V_\delta|t_1, t_2)$. For all estimated parameters, we

chose uninformative priors with very large variance. No a priori information enters the model either for the site effect μ_j or for the individual effect variance V_δ (Table 1; Appendix S5).

Computing light intercepted by trees and ground cells

To understand how canopy variation might affect light availability, we used an actualized version of the ‘Sam-saraLight’ light transmission model developed within the ‘Capsis’ simulation platform by Courbaud et al. (2003). Light is divided into direct light rays (rays with high energy, from the sun’s trajectory) and diffuse light rays (rays with low energy, from all other directions in the sky). Light rays arrive at the center of each ground cell. Each time a ray touches a tree, it loses 80% of its energy (Groot 2004). In the light model, crowns of two adjacent trees can overlap, so that a light ray passing through the overlap loses 80% of its energy twice (i.e., 80% of its initial energy then 80% of the remaining energy). If a tree has a bigger crown than the population mean, it casts more shade on the

Table 1 Parameter values for priors and measurement errors

Prior parameter	Description	Allometric relationship		
		$H = f(\text{DBH})$	$\text{CH} = f(H)$	$\text{CR} = f(\text{DBH})$
m_b	Mean	–	–	0.00×10^0
V_b	Variance	–	–	1.00×10^6
m_r	Mean	0.00×10^0	–	–
V_r	Variance	1.00×10^6	–	–
m_μ	Mean	0.00×10^0	0.00×10^0	0.00×10^0
V_μ	Variance	1.00×10^6	1.00×10^6	1.00×10^6
t_1	Shape	1.00×10^{-3}	1.00×10^{-3}	1.00×10^{-3}
t_2	Scale	1.00×10^{-3}	1.00×10^{-3}	1.00×10^{-3}
s_1	Shape	1.00×10^{-3}	1.00×10^{-3}	1.00×10^{-3}
s_2	Scale	1.00×10^{-3}	1.00×10^{-3}	1.00×10^{-3}
σ_x^2	Variance	2.21×10^{-5}	3.97×10^{-3}	2.21×10^{-5}
σ_y^2	Variance	3.97×10^{-3}	7.79×10^{-2}	2.42×10^{-2}

Means of posterior distributions obtained from the measurement error protocol were used for the measurement error variance estimate associated with the covariate (see σ_x^2) and with the response variable (see σ_y^2). Non-informative priors with large variances were used for other parameters. No a priori information enters the model either for the site effect (see m_μ and V_μ) or for the individual effect (see t_1 and t_2). H tree height without major T, f function relating the covariate to the response, DBH diameter at breast height, CH crown height, CR crown radius

ground as it intercepts more rays. We used the light model to compute both the light intercepted by each tree and the light arriving at each 5×5 -m cell on the ground at two selected sites in our data set (the Queige and Teppas sites, see Appendix S1) composed for the most part of *A. alba* and *P. abies* trees (representing more than or equal to 94% of total tree density). These two quantities were studied to see how individual variability in allometries could modify the allocation of the light resource in a forest stand. When considering the amount of light reaching the ground, we focused on the more shaded cells receiving less than 5% of relative light (around 13% of the ground cells). On these cells, regeneration of early successional shade-intolerant species was assumed to be more difficult than on cells receiving more than 5% of relative light.

We used two different approaches to compute light interception. In the first, we used calibrated allometries without individual variability to reconstitute the whole stand in three dimensions from DBH using a conical shape for crowns. Trees that were neither *A. alba* nor *P. abies* (6% of the trees on Teppas) were randomly attributed to one of the two species. In the second approach, we included individual variability in allometries: we randomly drew an additional individual parameter for each tree in the probability distribution corresponding to individual variability. The first approach takes into account uncertainty in parameters since we have a posterior distribution for each parameter obtained from the Bayesian inference. The

second approach takes into account individual variability in allometries in addition to uncertainty in parameters. In our study, we did not assume a deterministic space-filling of the canopy contrary to canopy models proposed by other authors (Adams et al. 2007; Purves et al. 2007). The individual variability we considered is different from phenotypic plasticity in regard to light and space availability. Individual variability is random and includes all possible sources of intra-specific variability in crown size and shape. We carried out 500 different simulations for each approach. Classic approaches usually do not take into account uncertainty in parameters and use only mean parameter estimates for simulations [but see Pacala et al. (1996)]. The comparison in the present study discriminated effects of uncertainty and variability in simulations.

Results

Species and site effects

Species allometries differed from site to site (Fig. 2). Adding a site effect greatly improved models, with a gain in DIC much higher than 10 for the crown radius–DBH relation for both species, the *Picea abies* height–DBH relation and the *Abies alba* crown height–height relation (Table 2). The gain in DIC was lower or slightly greater than 10 for the *A. alba* height–DBH relation and the *P. abies* crown height–height relation, although with a substantial gain in deviance (Table 2). Figure 2 shows that species and site effects were not sufficient to describe all the variability observed in the allometries, which is determined by the dispersion of the data points.

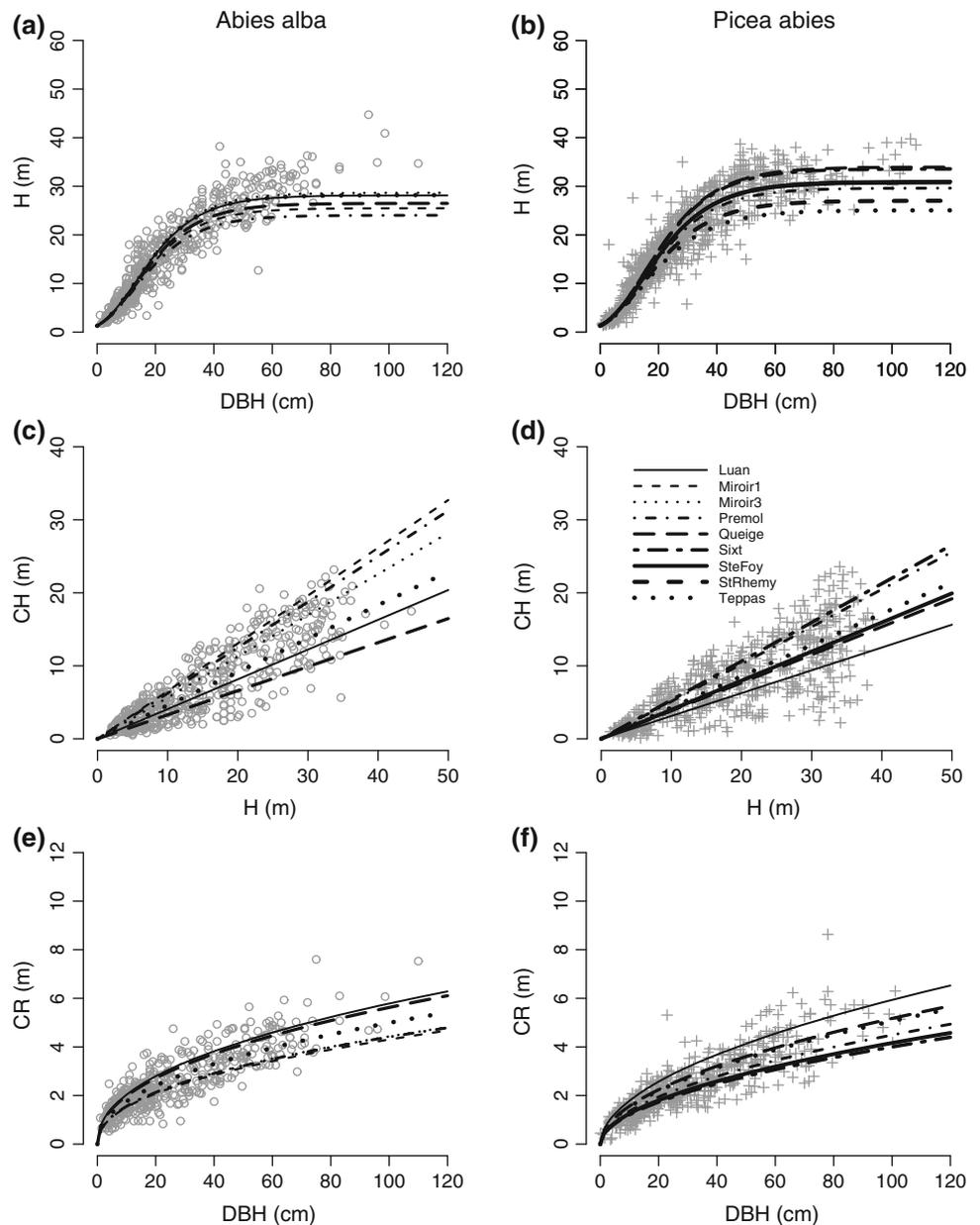
Competition effects and crown plasticity

The remaining variability could not be explained by local competition since we found no local competition effect on allometric relations for our data set, whatever competition index was taken into account (Table 3). These results do not prove that there is no crown plasticity associated with light or space availability for *A. alba* and *P. abies* but that even with nine different competition indexes, we were not able to catch a deterministic crown plasticity associated with the neighborhood.

Individual allometric variability

Individual variability was very high for all the species and all the allometric relations considered. The individual effect led to a high gain in DIC: close to 100 points for all allometric relations except the *P. abies* height–DBH relation. In this case, the high number of effective parameters resulted

Fig. 2 Predicted allometric relations for each species on each site. **a, b** Height (H) as a function of diameter at breast height (DBH), **c, d** crown height (CH) as a function of H and **e, f** crown radius (CR) as a function of DBH . The predictive posterior mean was plotted for each species on each site



in a higher DIC but the model goodness of fit was increased substantially by the addition of individual effects, with a gain in deviance greater than 80 points (Table 2).

For each species on each site, individual variability led to large 95% confidence envelopes, with an overlapping of the confidence envelopes for the two species in our data set (Fig. 3). The remaining variability was partially explained by measurement errors (Table 2). Taking into account measurement errors resulted in a gain in DIC greater than 300 points for the crown height–height relation, for which we demonstrated that measurement error was close to 50% for crown height and nearly 10% for height (Appendix S4). Measurement errors for the two other allometries were smaller but led to a gain in deviance much greater than 10.

Adding an individual effect to the model in addition to species, covariate, site and measurement error effects, we obtained a low variance for unexplained residual errors (see τ^2 of magnitude 1.0×10^2 in Appendix S6), suggesting that the final models for the three allometries explained a major part of the variability observed in the data set.

Impact of individual allometric variability on light allocation

Impact on light intercepted by species

A tree of a given species in a 10-cm DBH class intercepted a variable amount of light because of its size and its

Table 2 Model comparison and effect selection

Function name	Model number	Effects					<i>Abies alba</i>			<i>Picea abies</i>		
		Covariate DBH	Site (fixed)	Comp ^d (fixed)	Individual (random)	Measure errors	Posterior mean of deviance	pD	DIC ^e	Posterior mean of deviance	pD	DIC
H-DBH^a												
Gompertz model	H6	Y	N	N	N	N	-137.6	2.9	-134.7	-95.7	3.0	-92.7
	H7	Y	Y	N	N	N	-152.4	7.9	-144.5	-178.4	9.0	-169.4
	H8	Y	Y	Y	N	N	-156.9	8.9	-148.0	-179.8	9.4	-170.4
	H9	Y	Y	N	Y	N	-395.2	196.1	-199.1	-267.2	116.5	-150.7
	H10	Y	Y	N	Y	Y	-488.9	256.8	-232.1	-368.2	200.8	-167.4
CH-H^b												
Linear model	CH3	Y	N	N	N	N	676.9	1.9	678.8	806.5	2.0	808.5
	CH4	Y	Y	N	N	N	511.2	7.0	518.2	781.1	6.9	788.0
	CH5	Y	Y	Y	N	N	508.3	7.8	516.1	781.3	7.9	789.2
	CH6	Y	Y	N	Y	N	-127.2	338.1	210.9	362.4	243.4	605.8
	CH7	Y	Y	N	Y	Y	-710.7	509.8	-200.9	-163.7	433.3	269.6
CR-DBH^c												
Power model	CR3	Y	N	N	N	N	-2.5	2.9	0.4	120.1	3.0	123.2
	CR4	Y	Y	N	N	N	-115.0	7.9	-107.2	10.9	7.9	18.8
	CR5	Y	Y	Y	N	N	-117.8	9.2	-108.7	8.9	9.1	18.0
	CR6	Y	Y	N	Y	N	-396.3	218.4	-177.9	-357.0	242.1	-114.9
	CR7	Y	Y	N	Y	Y	-859.5	428.4	-431.0	-786.8	424.9	-361.9

pD Posterior mean of the deviance minus deviance of the posterior means, *H-DBH* H as a function of DBH, *CH-H* CH as a function of H, *CR-DBH* CR as a function of DBH, Y Yes, N no; for other abbreviations, see Table 1

^{a,b,c} Effects are progressively included in the model in ascending order to check for their significance

^d Competition (*Comp*) reflects the competition index with the lowest deviance

^e The model with the lower deviance information criterion (*DIC*) was chosen if the difference in *DIC* was > 10. When the difference in *DIC* was < 10, the model with the lower deviance was selected. When the deviance difference was < 10, the model with the lower *pD* was chosen

neighborhood. Species hierarchy was observable on each site. *P. abies* intercepted more light than *A. alba* on the Queige site (Fig. 4a), contrary to the Teppas site, with *A. alba* intercepting more light than *P. abies* (Fig. 4b). Individual allometric variability increased the variance of intercepted light for a tree of a given species and size by fivefold (Fig. 4). The range of intercepted light increased with the size of the tree as the variability in crown shape increased with tree size. On each site, individual variability in crown size totally blurred species differences in terms of light interception (Fig. 4). The maximum amount of light

that can be potentially intercepted by a tree, whatever its size, was also significantly changed, increasing from approximately 2.4 to 3.7 GJ year⁻¹ for *P. abies* on the Queige site (Fig. 4a). The potential number of trees with high light interception increased when individual variability in allometry was taken into account (up to 17 trees intercepting more than 2 GJ year⁻¹ on the Queige site with individual variability against six trees without variability; see Table 4). Individual allometric variability allowed some trees to have a much larger or smaller crown than their mean population so that they intercepted a much

Table 3 Model comparisons with competition index

Model description	Model number	Mathematical function	Competition index	<i>A. alba</i>			<i>P. abies</i>		
				Posterior mean of deviance	pD	DIC	Posterior mean of deviance	pD	DIC
H-DBH									
Gompertz model	H7	$y = Ke^{(-\log(\frac{K}{1.3})e^{(-r)})}$, parameters: K, r	∅	-152.4	7.9	-144.5	-178.4	9.0	-169.4
	H8-1		D5	-151.6	8.9	-142.7	-177.7	9.8	-167.9
	H8-2		D5 bigger	-152.0	8.7	-143.3	-178.0	9.8	-168.2
	H8-3		D10	-156.9	8.9	-148.0	-179.1	9.4	-169.6
	H8-4		D10 bigger	-151.5	8.8	-142.7	-178.4	10.0	-168.4
	H8-5		D15	-152.1	8.7	-143.5	-179.8	9.4	-170.4
	H8-6		D15 bigger	-151.4	8.8	-142.6	-177.7	9.8	-167.9
CH-H									
Linear model	CH4	$y = \frac{1}{1+K}x$, parameter : K	∅	511.2	7.0	518.2	781.1	6.9	788.0
	CH5-1		D5	511.1	7.9	519.0	782.2	8.0	790.1
	CH5-2		D5 bigger	510.9	7.8	518.7	781.4	7.9	789.3
	CH5-3		D5 smaller	512.1	8.0	520.1	781.8	8.0	789.8
	CH5-4		D10	510.8	7.9	518.7	782.0	7.7	789.7
	CH5-5		D10 bigger	510.6	7.9	518.4	782.0	7.9	789.8
	CH5-6		D10 smaller	512.0	8.0	520.0	781.9	8.0	789.8
	CH5-7		D15	511.0	7.9	518.9	781.9	7.7	789.6
	CH5-8		D15 bigger	508.3	7.8	516.1	781.3	7.9	789.2
	CH5-9		D15 smaller	510.7	8.0	518.8	781.5	7.9	789.4
CR-DBH									
Power model	CR4	$y = Kx^b$, parameters : K, b	∅	-115.0	7.9	-107.2	10.9	7.9	18.8
	CR5-1		D5	-115.2	9.4	-105.8	11.8	9.3	21.1
	CR5-2		D5 bigger	-117.3	9.2	-108.0	12.0	9.2	21.2
	CR5-3		D5 smaller	-114.0	9.2	-104.8	10.1	9.0	19.1
	CR5-4		D10	-113.8	9.5	-104.2	8.9	9.1	18.0
	CR5-5		D10 bigger	-114.2	9.1	-105.1	11.1	9.4	20.5
	CR5-6		D10 smaller	-114.9	9.4	-105.5	11.1	9.0	20.1
	CR5-7		D15	-115.8	9.3	-106.6	11.9	9.1	21.0
	CR5-8		D15 bigger	-117.8	9.2	-108.7	10.5	9.2	19.7
	CR5-9		D15 smaller	-114.4	9.2	-105.2	11.2	9.1	20.3

Competition indexes were computed from the basal area of all the trees, of the bigger trees, or of the smaller trees within circles of three different radii: 5, 10 or 15 m from the target tree. Adding a competition index did not improve the model for the three allometric functions studied. For abbreviations, see Tables 1 and 2

higher or lower amount of light. When considering other classes of intercepted light for trees, we observed that the range of the potential number of trees was larger when including individual allometric variability (Table 4).

Impact on light arriving on ground cells

Individual allometric variability influenced the amount of light penetrating the canopy. The variance in the amount of light arriving at ground cells increased eightfold when we included individual variability in allometries for the Queige site (Fig. 5a). Shaded cells that received less than 5% relative light when the canopy was modeled without

individual variation, reached values of up to more than 10% when individual variability was included (Fig. 5a). The light regime on shaded cells was much more heterogeneous when considering individual variability (Fig. 5b). These differences included a small contribution from the estimation error, the bulk of the variation coming from individual variability in tree crowns (Fig. 5a, b). The same results were observed on the Teppas site (not shown here). The increase in the variance of light available on ground cells was twice as large as the increase in variance for light interception by trees. This differs because the light arriving at a cell depends on the shape of all tree crowns surrounding the cell, whereas the amount of light intercepted

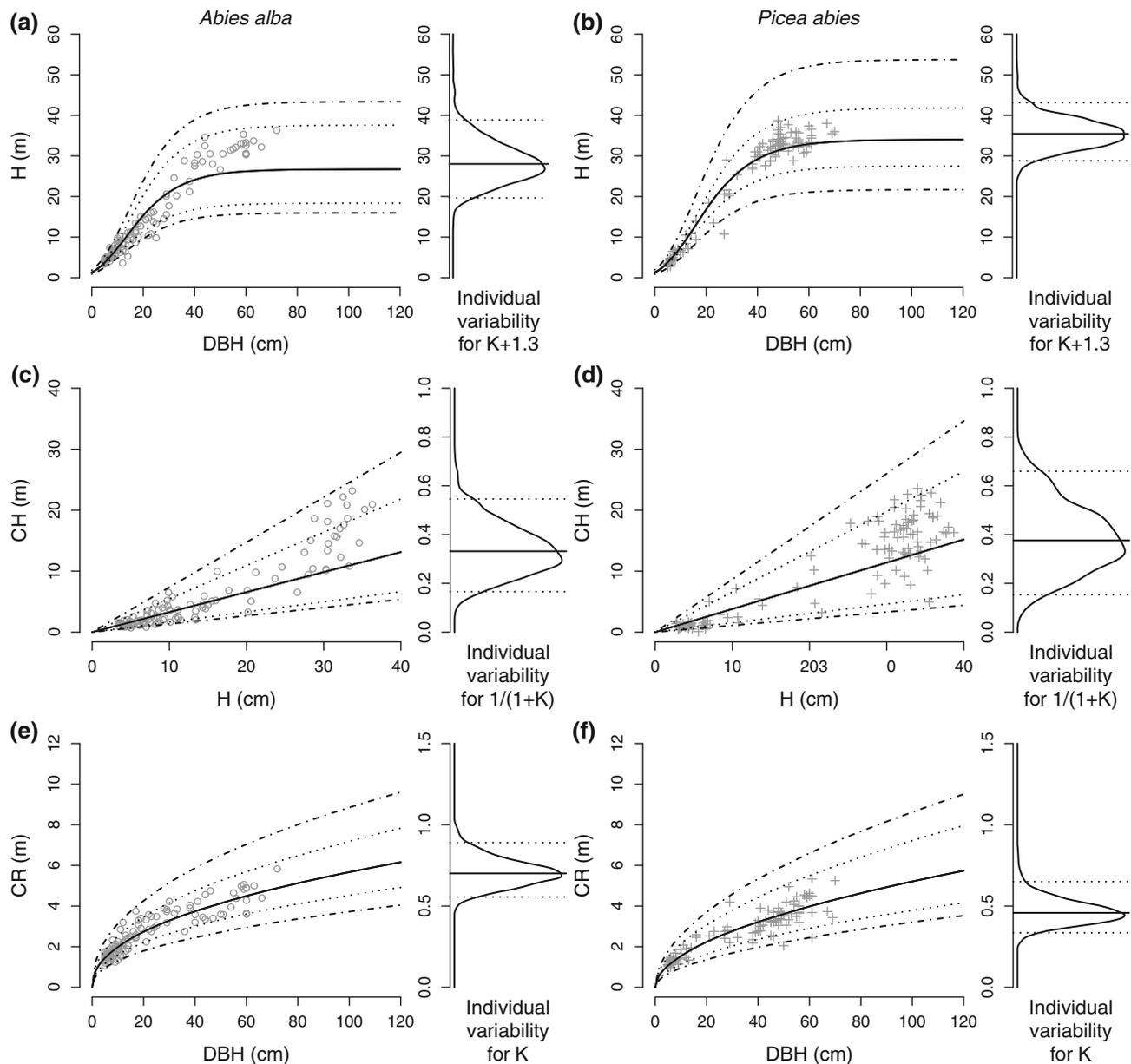


Fig. 3 Individual variability in allometries on the Queige site. **a, b** H as a function of DBH, **c, d** CH as a function of H and **e, f** CR as a function of DBH. We plotted the predictive posterior mean (straight line) and the credible intervals at 95% of the predictive posterior with

individual variance (V_{δ} ; dotted line) and whole variability including V_{δ} , σ_x^2 , σ_y^2 and τ^2 (dashed line). Vertical graphs on the right are marginalized posteriors on individuals that represent the variability of all potential individuals. For abbreviations, see Fig. 2

by a tree depends to a greater degree on its own crown shape.

Discussion

Phenotypic plasticity and individual variability in crown shape

Using a hierarchical Bayesian framework, we quantified individual variability in allometries remaining after having

taken into account species, site, competition, and measurement error effects. We were not able to detect any individual response to local competition (i.e., to local light and space availability); nevertheless, we demonstrated that individual variability in allometries was substantial.

Previous studies have underlined the importance of crown plasticity resulting from local light and space availability to explain individual variability in a deterministic way (Getzin and Wiegand 2007; Kantola and Makela 2004; Purves et al. 2007; Sorrensen-Cothorn et al. 1993; Vincent and Harja 2008). In this study, no crown

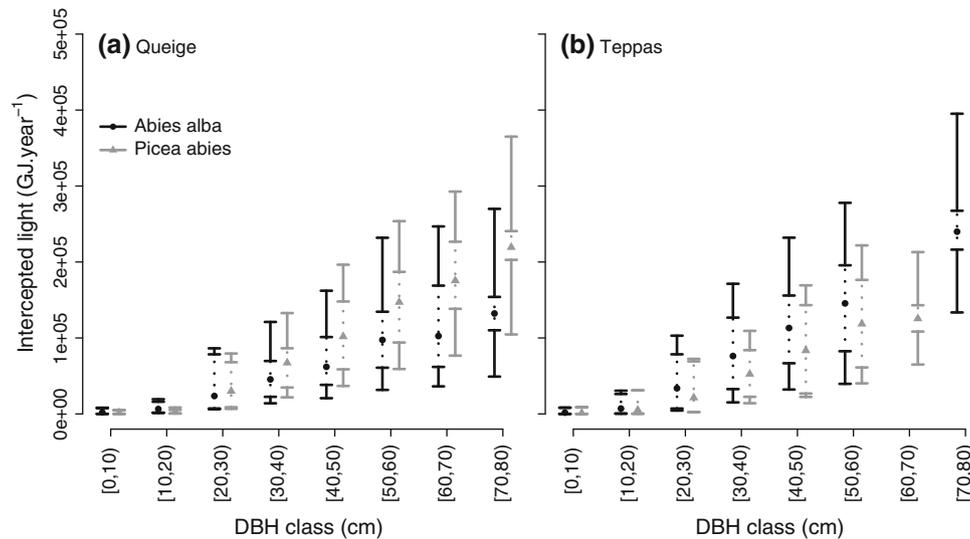


Fig. 4 Effect of individual variability on light interception by both species at the **a** Queige and **b** Teppas site. A light interception model (Courbaud et al. 2003) was used on the two sites which are mixed *Abies alba* and *Picea abies* stands; 95% quantiles (horizontal dashes) and mean (dots or triangles) intercepted light by trees of a given class

of DBH are represented. Vertical dotted lines take into account uncertainty in parameters and neighborhood variability for trees of a given diameter. Vertical solid lines take into account individual allometric variability in addition to uncertainty in parameters and neighborhood variability

Table 4 Distribution of trees by intercepted light class

Class of light for trees ($\times 10^5$ GJ year $^{-1}$)	(0,1)	(1,2)	(2,3)	(3,5)
No individual effect in allometries				
Min	170	46	0	0
Mean	174	52	2	0
Max	178	57	6	0
With individual effect in allometries				
Min	170	24	1	0
Mean	180	42	6	1
Max	192	53	14	3

For the 500 simulations of each approach (with and without individual variability in allometries), for the Queige site, the minimum (*Min*), mean and maximum (*Max*) number of trees for each class of intercepted light were computed

plasticity could be identified even after testing nine different competitive indexes representing the neighborhood. The absence of a significant competitive effect on different tree allometries has already been found by previous authors (Coomes and Grubb 1998; Deleuze et al. 1996; Geburek et al. 2008; Hummel 2000). In these studies, a significant competitive effect may be absent because the competition indexes used are symmetric, whereas phenotypic plasticity is asymmetric (Purves et al. 2007; Vincent and Harja 2008). These results are not a reconsideration of crown plasticity but they demonstrate that crown plasticity is difficult to isolate from other possibly correlated factors in an experimental design including allometric measurements.

In addition, it is recognized that shade-tolerant and coniferous species express much less crown plasticity than shade-intolerant or broad-leaved species (Grubb 1998) and in the present study, *Abies alba* and *Picea abies* are two coniferous species classified as high shade-tolerant species (Ellenberg 1988). Although phenotypic plasticity can result in tessellating crown shapes that fill most of the canopy space in deciduous forest (Purves et al. 2007), this is not always the case in coniferous mountain stands. Indeed, individual variability in crown size can be associated with numerous heterogeneous environmental factors other than light or space availability. In the context of mountain stands, snow damage can be a determining factor of individual crown size variation (Jalkanen and Konopka 1998; Parish et al. 2008), and increasing altitude tends to diminish phenotypic plasticity in comparison to adaptive differentiation associated with temperature or water availability (Geburek et al. 2008). These micro-site environmental factors coalesce with genetic variability to determine intraspecific crown size variability (Aarsen 1992). It is difficult to separate out the deterministic effect of each one of these factors, but taken together they contribute to the estimation of a large random individual variability.

Individual effects describe differences between trees which are conserved throughout their lives. Individual differences in crown size and shape lead to differences in light interception and to individual growth trajectories. Individual effects on allometries may initiate a differentiation between trees and combine with asymmetric

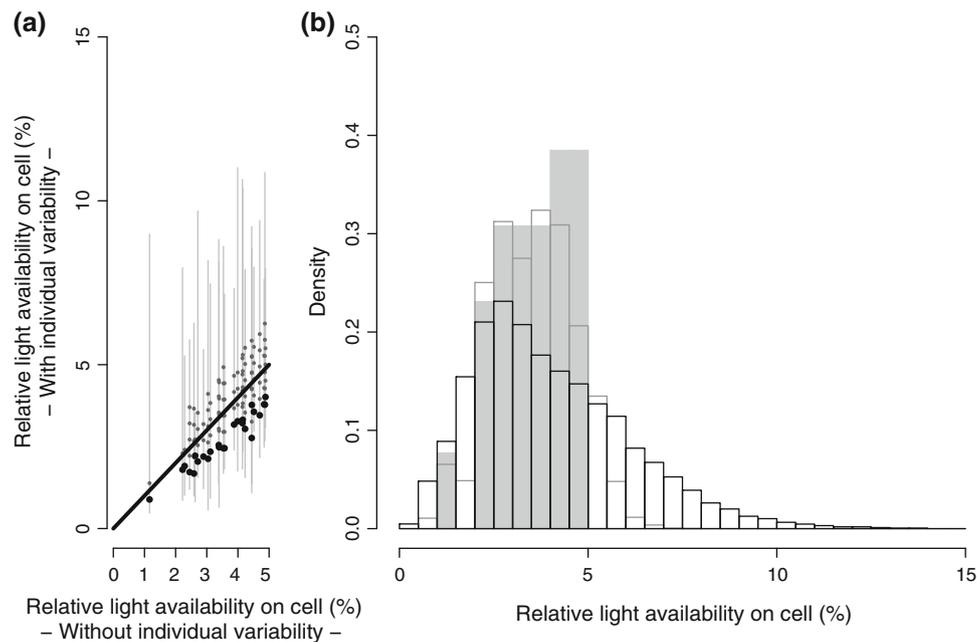


Fig. 5 Effect of individual variability on the light regime under the canopy at the Queige site with **a** potential levels of light on ground cells and **b** ground cells distribution by class of light. A light interception model (Courbaud et al. 2003) was used for the mixed *A. alba* and *P. abies* stand. **a** Horizontal axis Mean intercepted light for each cell receiving less than 5% relative light on the 500 simulations with no individual variability. Vertical axis Mean (black dot) and 95% quantiles (grey vertical lines) of the intercepted light for each

cell on the 500 simulations including individual variability. Dashed vertical lines represent light variability due to uncertainty on parameter estimates. **b** Distribution of cells with less than 5% relative light when considering mean specific allometries (filled grey bars) is compared to the mean distribution of cells on the 500 simulations when including uncertainty in parameters (unfilled grey bars) and to the distribution of cells when including individual variability (unfilled black bars)

competition for light in creating a hierarchy of sizes between trees and a heterogeneous spatial structure.

Individual variability obscures species differences in crown size

The species hierarchy that considers light interception varies spatially. On the Teppas site, the relatively shade-tolerant species *P. abies* had a deeper crown than the relatively shade-intolerant species *A. alba*, whereas on the Queige site, species hierarchy was reversed. Whatever the hierarchy on each site, individual allometric variability was so great that it obscured species differences in crown size and light interception.

Tree species are often classified in terms of architecture and adult stature (Bohlman and O'Brien 2006; Dietze et al. 2010; Pacala et al. 1996; Poorter et al. 2006), which determine species life history and community dynamics (Abe and Yamada 2008; King 1996). Shade-tolerant species are assumed to have a deeper crown than shade-intolerant species, thereby increasing light exposure, casting shade on competitors, and increasing reproductive or dispersal organs (Aarssen 1995; Canham 1988; Grubb 1998; Parish et al. 2008). Our analysis demonstrates that there are limitations to interpretations of average tendencies. Species

differences may be observed when considering the whole population, but they must be put into perspective taking into account site and individual characteristics. Following the niche theory (Hutchinson 1957) and the acclimation mechanism (Korner 1999), species may present different morphological traits depending on local environmental conditions at the site level. As a consequence, species hierarchy for light interception may vary from site to site. Although this result is not new, it does imply the importance of relativizing species classification in terms of architecture and adult stature.

On a given site, the amount of light intercepted by a tree of a specific species and diameter appeared to be much more variable than what is usually assumed. Adding individual variability in allometric relations multiplied the variance of light intercepted by trees of a given species and class of DBH by 5. The phenomenon was amplified because the crown shape of each tree affects light interception of the entire neighborhood. The fact that individual variability can overwhelm species differences locally has previously been demonstrated for growth and fecundity with consequences for species coexistence (Clark et al. 2004; Clark 2003). Light interception determines growth (Clark 2003; Courbaud et al. 2003; Kunstler et al. 2005; Pacala et al. 1996; Wright et al. 1998) and other key

ecological processes such as fecundity (Clark et al. 2004, 2007) and mortality (Bigler and Bugmann 2003; Kobe and Coates 1997; Kunstler et al. 2005; Wyckoff and Clark 2000), which drive community dynamics. As suggested by Parish et al. (2008), the large intraspecific variability resulting in major overlap among species in structural characteristics should greatly reduce the rates or potential for competitive displacement.

Intraspecific variability in crown size and successional dynamics

The variability in light intercepted by trees affects the amount of light reaching the ground. This may have a profound impact on seedling growth and survivorship, which depend on the amount of light available near the ground (Dai 1996; Uriarte et al. 2005; Wright et al. 1998). Seedling response to light is one of the main factors determining succession and species coexistence in forests. The succession niche hypothesis states that early successional species are able to grow rapidly in forest gaps and that late-successional species are able to grow and survive under canopy at low light levels (Pacala and Rees 1998; Rees et al. 2001). Differences in life history traits between late-successional and early successional species explain why, in the absence of disturbance, early successional species cannot regenerate under a closed canopy and are progressively excluded.

When considering the phenotypic plasticity of trees with regard to light and space availability as the main deterministic factor contributing to intraspecific crown variability, it is seen that trees form tessellating crown shapes that fill most of the canopy space (Purves et al. 2007), leading to a potentially rapid exclusion of shade-intolerant early successional species in the absence of disturbances. Our results demonstrated that individual variability in crown size participates significantly in stand structure, leading to high heterogeneity of light conditions in a closed stand and avoidance of homogeneous, low light conditions. Locally, individual variability may decrease light intercepted by big canopy trees, which increases light arriving on the ground. Persistence of individual crown characteristics leads to stable subcanopy light conditions over time. Patches receiving high light levels can provide opportunities for the regeneration of shade-intolerant species that would otherwise be excluded. In our context, the relatively shade-intolerant *P. abies* saplings (Grassi and Bagnaresi 2001) have opportunities to regenerate, leading to a better chance of coexistence with *A. alba* in mixed stands. Competitive exclusion may occur, but individual variability slows down these dynamics, allowing for a transient but long coexistence. In association with other mechanisms such as external perturbations (Connell 1978), intraspecific

variability may partially explain the long-term persistence of shade-intolerant species in ancient mountain forests (Ozenda 1985; Parish et al. 2008).

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