

Tree light capture and spatial variability of understory light increase with species mixing and tree size heterogeneity

Gauthier Ligot, Aitor Ameztegui, Benoît Courbaud, Lluís Coll, and Dan Kneeshaw

Abstract: Mixed and multi-layered forest ecosystems are sometimes more productive than monospecific and single-layered ones. It has been suggested that trees of different species and sizes occupy complementary positions in space, which would act as a mechanism to increase canopy light interception and wood production. However, greater canopy light interception reduces the average amount and variability of transmitted radiation, offering fewer opportunities for all species to regenerate and to maintain forest heterogeneity in the long run. We investigated whether increasing overstory heterogeneity indeed results in greater canopy light interception and lower variability in transmittance. We modeled the three-dimensional structure of forest stands with three typical forest structures, 10 mixtures of four tree species, and three different basal areas. We used the forest light interception model *SAMSARALIGHT* and performed three-way analyses of covariance to analyze the effects of the three varied components of forest heterogeneity. We found no evidence that increasing structural heterogeneity increases canopy light interception. However, the light interception by mixed canopies was greater than the weighted average of light interception by the corresponding pure canopies. Variability in transmittance increased in some cases with compositional heterogeneity and, to a lesser extent, with tree size inequalities. The advantage of heterogeneous forests is in opportunities for natural regeneration, as well as in opportunities to enhance canopy light interception.

Key words: understory light, tree species diversity, radiative transfer model, *SAMSARALIGHT*, forest structure.

Résumé : Les écosystèmes forestiers mixtes et multiétages sont parfois plus productifs que les écosystèmes monospécifiques à un seul étage. Il a été suggéré que les arbres de différentes espèces et tailles occupent des positions spatiales complémentaires, ce qui constituerait un mécanisme pour augmenter l'interception de la lumière par le couvert arborescent et la production ligneuse. Cependant, une plus grande interception de la lumière par le couvert arborescent réduit la quantité moyenne et la variabilité du rayonnement transmis, ce qui diminue les occasions de régénérer toutes les espèces et de maintenir l'hétérogénéité forestière à long terme. Nous avons vérifié si l'augmentation de l'hétérogénéité du couvert arborescent augmente effectivement l'interception de la lumière et réduit la variabilité de la transmittance. Nous avons modélisé la structure tridimensionnelle de peuplements forestiers caractérisés par trois structures forestières typiques, 10 mélanges de quatre espèces d'arbre, et trois surfaces terrières différentes. Nous avons utilisé le modèle d'interception de la lumière forestière *SAMSARALIGHT* et avons effectué des analyses de covariance à trois facteurs pour analyser les effets de la variation des trois composantes de l'hétérogénéité forestière. Nous n'avons trouvé aucune preuve qu'une augmentation de l'hétérogénéité de la tailles des arbres augmente l'interception de la lumière par le couvert arborescent. Par contre, les peuplements mélangés interceptent bien une quantité de lumière plus grande que l'interception de la lumière moyenne pondérée des peuplements purs correspondants. Dans certains cas, la variabilité de la transmittance a augmenté avec l'hétérogénéité de la composition et, dans une moindre mesure, avec la diversité de la taille des arbres. L'avantage des forêts hétérogènes tient à la fois au maintien de conditions favorables pour la régénération naturelle qu'en la possibilité d'augmenter l'interception de la lumière par la canopée. [Traduit par la Rédaction]

Mots-clés : lumière sous le couvert, diversité des espèces d'arbre, modèle de transfert radiatif, *SAMSARALIGHT*, structure forestière.

Introduction

It has been advocated that forests with many tree species and a great heterogeneity in tree sizes are more productive (Pretzsch and Schütze 2009; Toigo et al. 2015; Vallet and Pérot 2011), resistant and resilient (Jactel et al. 2005) to future changes, and harbor a greater biodiversity (Huston 1979) than monospecific forests in which all trees have a similar size. Over the last 50–100 years, humans have applied forest management systems over much of

the northern hemisphere that tended to simplify both the structure and composition of many forests (Bengtsson et al. 2000). This simplification resulted in increased production of the targeted product, usually timber of a few species highly valued by the market at the time. However, the advantages of these management systems may have obscured long-term negative impacts such as reductions of genetic and species diversity (Ledig 1992; Noss 1999), rigidity in the face of market and climate variations (Pretzsch et al. 2013), a decrease in forest habitat quality (Franklin

Received 10 February 2016. Accepted 6 May 2016.

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et al. 2000) and soil fertility (Reich et al. 2012), and a loss in overall productivity. Many researchers and forest managers now promote the development of more heterogeneous forests (McElhinny et al. 2005; Puettmann et al. 2009), but our understanding of the sharing and use of resources among species and vegetation strata in heterogeneous forests is limited and impedes our ability to predict the long-term dynamics of such forests.

Researchers have usually hypothesized that forest productivity is greater in mixed forests than in the corresponding pure forests, because species mixtures should capture more resources and, in particular, more solar radiation due to the layering of the forest canopy and the complementarity and overlapping of tree crowns (Bauhus and Schmerbeck 2010; Forrester et al. 2006; Kelty 2006; Pretzsch and Schütze 2009; Vallet and Pérot 2011; Yachi and Loreau 2007). It is also generally assumed that the structural and compositional heterogeneity of the forest overstory directly affects the amount and variability of light available in the understory for tree regeneration (e.g., Kelty 2006). A number of studies have found close relationships between the amount of light transmitted to the understory and canopy density (Comeau and Heineman 2003; Lochhead and Comeau 2012; Sonohat et al. 2004; Vales and Bunnell 1988), stem spatial distribution (i.e., clumped, random, or dispersed; Beaudet et al. 2011; Coates et al. 2003; Drever and Lertzman 2003; Ligot et al. 2014a; Lochhead and Comeau 2012), vertical canopy structure or distribution of tree sizes (Drever and Lertzman 2003; Ligot et al. 2014a; Lochhead and Comeau 2012), and species composition (Lochhead and Comeau 2012; Messier et al. 1998). The effects of these factors on understory light have been tested individually and sometimes in pairs, but their combined effects have been particularly difficult to assess.

Moreover, most studies have focused on the average quantity of light that reaches the forest floor but few have considered spatial variability in light conditions (Puerta-Piñero et al. 2007) even though it is also essential for the sustainability of structurally complex forests. Uneven-aged stands harboring trees of different sizes and ages can only persist if sufficient light reaches seedlings at least in scattered patches in the forest understory. Furthermore, the coexistence of different tree species can only be ensured if the variability in understory light is sufficient for all species to be able to survive, grow, and reproduce (e.g., Ameztegui and Coll 2011; Ligot et al. 2013). The exact needs in terms of variability in light availability ultimately depend on the interspecific range of shade tolerances (Kobe et al. 1995), but the greater the variability in understory light conditions, the greater the opportunities for multiple species to regenerate. However, the variability in understory light is likely positively correlated with the average quantity of light transmitted through the canopy. As canopy openness increases, both the mean and the range of understory light conditions increase (Canham et al. 1990). Because canopy transmittance is hypothesized to decrease with forest heterogeneity, variability in understory light should also decrease with forest heterogeneity. Sustainable management of heterogeneous forests should therefore optimize the capture of solar radiation both by overstory trees and by understory seedlings, i.e., it should both minimize mean light transmittance and maximize the variability of light transmittance.

The main question we address in this paper is how does the structural and compositional heterogeneity of the forest overstory affect light interception and the amount and variability of understory light. In particular, our specific questions are (i) How does overstory structural and compositional heterogeneity affect the total interception of light? and (ii) How does structural and compositional heterogeneity of the overstory affect spatial variability of understory light? We hypothesize that stands composed of trees of multiple species and multiple sizes will intercept more light than uniform stands because canopies would be denser with reduced gap area between crowns. As we expect the variability of light transmittance to be positively correlated with mean light

transmittance, we additionally hypothesize that variability in understory light will be reduced with forest heterogeneity.

Methods

Study species

We selected four species for which allometric relationships required to compute canopy light transmittance with three-dimensional radiative transfer models (Ligot et al. 2014b) have been previously calibrated: sessile oak (*Quercus petraea* (Matt.) Liebl.), European beech (*Fagus sylvatica* L.), mountain pine (*Pinus uncinata* Ram ex. DC), and silver fir (*Abies alba* Mill.). In the first study from which species calibrations were determined, Ligot et al. (2014a) monitored 27 mixed stands of sessile oak and European beech in the Belgian Ardennes (50°15'N, 5°40'E). In a second study, Ameztegui and Coll (2011) monitored 24 mixtures of mountain pine and silver fir in the Spanish Pyrenees (42°20'N, 1°40'E). These study species provided us with a large gradient of species shade tolerance and adult tree crown properties. In particular, the four study species spanned a gradient from shade-tolerant species with very dense and deep ellipsoidal crowns (European beech) to shade-intolerant species with sparse and small parabolic crowns (mountain pine). By increasing order of shade tolerance, the list of the study species is pine, oak, fir, and beech (Niinemets 2006).

Creating virtual stands

To examine how overstory heterogeneity influences the mean and the variability in understory light conditions, we simulated 90 contrasted forest stands including three typical forest structures (single layered, multi-layered with two or three vegetation layers, and reverse J-shaped distribution), 10 mixtures of forest composition based on combinations of the four species (beech, oak, beech-oak, pine, fir, fir-pine, oak-pine, beech-fir, beech-oak-pine, and beech-fir-pine), and three levels of basal area (15, 25, and 35 m²·ha⁻¹) (Fig. 1). Each virtual stand was 50 m × 50 m, and because the position of the trees was randomly drawn from a uniform distribution, each combination was simulated 100 times. We chose a uniform distribution because we found no general evidence of aggregated or regular distributions of trees in stands of the studied species (the values of the aggregation index Clark-Evans were generally close to 1, see Table 1). The resulting tree spatial distribution of most simulated plots was random (Clark-Evans' index close to 1; range, 0.74–1.41).

Tree diameters at breast height (DBHs, 1.3 m) in the virtual stands were drawn from statistical distributions, depending on the stand structure. To create single-layered stands, tree DBHs were drawn from a truncated normal distribution with two parameters, $N(\mu_1 = 30 \text{ cm}, \sigma_1 = 4.5 \text{ cm}, \text{min} = 6 \text{ cm}, \text{max} = 70 \text{ cm})$, and with all species occupying the same canopy layer. In multi-layered stands composed of two species, tree DBHs were drawn from two truncated normal distributions: $N(\mu_1 = 40 \text{ cm}, \sigma_1 = 6 \text{ cm}, \text{min} = 6 \text{ cm}, \text{max} = 70 \text{ cm})$ and $N(\mu_2 = 25 \text{ cm}, \sigma_2 = 3.75 \text{ cm}, \text{min} = 6 \text{ cm}, \text{max} = 70 \text{ cm})$. In multi-layered stands composed of three species, tree DBHs were drawn from the two previous distributions and from a third one: $N(\mu_3 = 35 \text{ cm}, \sigma_3 = 3.75 \text{ cm}, \text{min} = 6 \text{ cm}, \text{max} = 70 \text{ cm})$. The standard deviation of DBHs was set to correspond to a coefficient of variation of 15%. In mixed multi-layered stands, the less shade-tolerant species occupied the upper vegetation strata. To create a reverse J-shape structure, tree DBHs of all species were sampled from a single truncated exponential distribution: $\exp(k)$ with $E(\text{DBH}) = 1/k = 25 \text{ cm}$, $\text{min} = 6 \text{ cm}$, $\text{max} = 70 \text{ cm}$. Altogether, these distribution parameters ensured that the quadratic mean diameter of all simulated stands was relatively similar (about 30 cm). In mixed stands composed of two or three species, each species was assigned 50% or 33% of the total basal area, respectively.

Fig. 1. Examples of three virtual stands with basal area of $25 \text{ m}^2\text{-ha}^{-1}$: (a) a single-layered stand of European beech with a mean DBH of 35 cm, (b) a multi-layered stand of sessile oak and beech with mean DBHs of 15 cm for beech (green) and 35 cm for oak (purple), and (c) a reverse J-shaped stand of mountain pine (blue) and silver fir (gray) with mean DBHs of 25 cm. Understory light was assessed for each cell. Levels of transmittance under the trees are represented by a gradient of color from black (transmittance of 0%–10%) to yellow (90%–100%). DBH, diameter at breast height. Figure is provided in colour online.

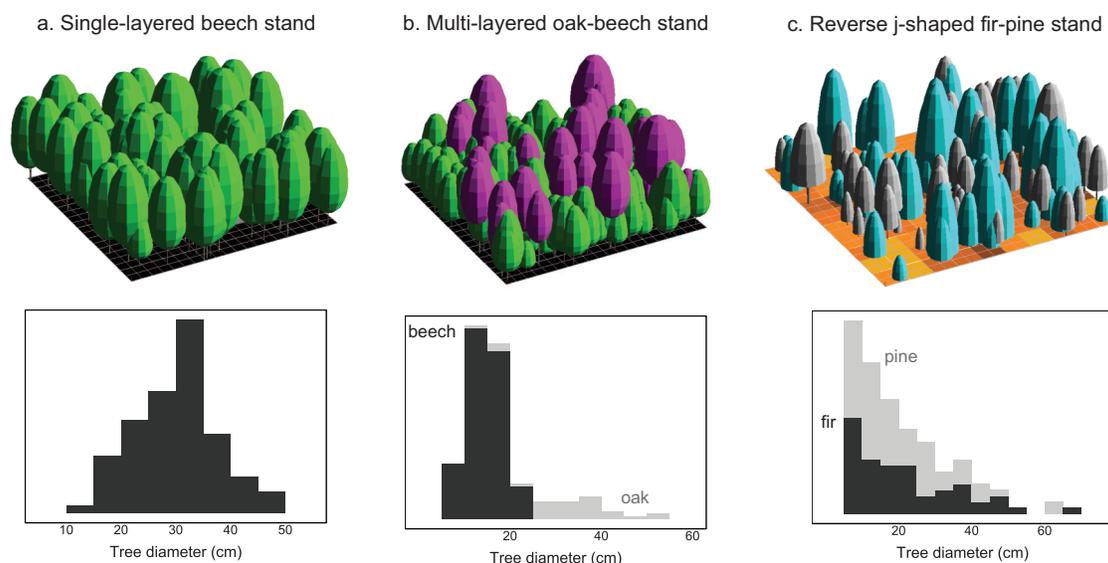


Table 1. A brief description of the plots monitored in oak–beech mixtures by Ligot et al. (2014a) and in fir–pine mixtures by Ameztegui and Coll (2011).

Species	<i>n</i>	Dg (cm)	CV (%)	Basal area ($\text{m}^2\text{-ha}^{-1}$)	Clark–Evans index	Transmittance (%)
Oak–beech ^a	27	42.4 (30.0–54.9)	43 (27–60)	18.0 (7.5–35.0)	1.1 (1.0–1.3)	22.8 (0.8–62.6)
Oak–beech ^b	2773	36.0 (6.9–87.3)	38 (0.0–150.5)	20.0 (1.2–70.4)	—	—
Fir–pine ^c	24	30.6 (19.53–42.0)	36 (15–53)	23.3 (7.6–44.5)	0.9 (0.5–1.2)	36.0 (20.5–71.7)

Note: The table indicates the number of studied plots (*n*) and the average (range from minimum to maximum) of the following: measured quadratic mean diameter (Dg), coefficient of variation of tree diameters (CV), stand basal area, Clark–Evans aggregation index, and transmittance. Regular distributions of trees have Clark–Evans values greater than 1, whereas aggregated distributions have a Clark–Evans value less than 1 (Clark and Evans 1954).

^aData from Ligot et al. (2013).

^bData from the permanent inventory of forest resources in Wallonie (Alderweireld et al. 2015).

^cData from Ameztegui and Coll (2011).

This experimental design crossing levels of canopy density, composition, and structure would not have been possible with field experiments. It would be illusory to search for representative stands of every combination of these three factors without interference with other factors (e.g., canopy gaps, stand edges, site conditions).

The choice of the simulated levels of basal area, shapes and parameters of DBH distributions, and species mixtures was critical as a different choice would have led to different results. Even though most of the simulated stands spanned a realistic range of conditions (Table 1), some of them are rather theoretical (e.g., mixtures of three species). However, the light model we used (see next section) is assumed to synthesize our knowledge of radiative transfer through forest canopies and to be valid for different forest structures and compositions.

Tree height and crown radius were computed using species-specific allometric relationships determined by Ameztegui and Coll (2011) and Ligot et al. (2014a) (Fig. 2). Leaf area density (LAD) was set according to previous measurements (Ligot et al. 2014a) to $0.71 \text{ m}^2\text{-m}^{-3}$ for beech and $0.52 \text{ m}^2\text{-m}^{-3}$ for oak. For both pine and fir, LAD was set to $0.6 \text{ m}^2\text{-m}^{-3}$ based on the literature (Ligot et al. 2014b). Moreover, small variations in LAD around 0.6 have been

shown to have little effect on light interception simulations (Courbaud et al. 2003; Ligot et al. 2014a).

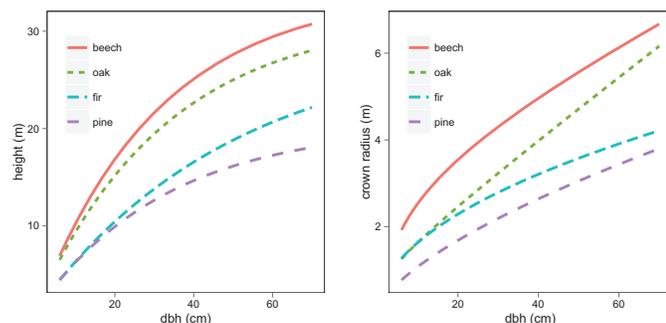
Modeling understory light

The amount of light available in the forest understory of each simulated stand was computed with SAMSARALIGHT (Courbaud et al. 2003; Ligot et al. 2014a), a three-dimensional radiative transfer model¹ implemented in a library of the CAPSIS platform (Dufour-Kowalski et al. 2012). This model has proven to satisfactorily predict understory light in uneven-aged forests of Norway spruce (*Picea abies* (L.) Karst) in the Alps (Courbaud et al. 2003), in Belgian mixtures of oak and beech forests (Ligot et al. 2014a), and in Spanish mixtures of fir and pine in the Pyrenees (Appendix Fig. A1).

For this experiment, SAMSARALIGHT was set to compute light interception using Beer's law (eq. 1). Beer's law describes the attenuation of a monochromatic ray within a turbid medium, i.e., a medium made up of small elements randomly scattered and presenting a homogeneous transparency (Brunner 1998). Briefly, the probability of beam interception ($1-\tau$) by canopy elements is a function of the canopy element density (LAD, in $\text{m}^2\text{-m}^{-3}$), the path

¹A version of this software can freely be downloaded at <http://orbi.ulg.ac.be/handle/2268/187361> (accessed 15 April 2016).

Fig. 2. Allometric relationships of the four study species based on Ligot et al. (2014a) and Ameztegui and Coll (2011). dbh, diameter at breast height. Figure is provided in colour online.



length of a ray through the canopy (l , in m), the extinction coefficient (k), and the clumping factor (Ω). K and Ω depend on canopy element inclination and spatial distribution:

$$(1) \quad \pi(\eta, \gamma) = \exp[-k\Omega LAD(l(\eta, \gamma))]$$

Tree crowns of hardwood and softwood species were modeled with three-dimensional ellipsoidal and parabolic shapes, respectively, using the allometric relationships from Ligot et al. (2014a) and Ameztegui and Coll (2011). In SAMSARALIGHT, individual tree crowns were considered as homogeneous turbid media. For each month of the growing season (from April to October), 130 diffuse and 81 direct light ray directions were sampled. Diffuse ray directions were sampled over the sky hemisphere at regular zenith angles above a starting value of 10° . Similarly, direct ray directions were sampled every hour over the average monthly solar trajectory. For every direction, parallel rays were cast at the centers of each 25 m^2 ground cell. To remove edge effects, SAMSARALIGHT uses an algorithm that considers plots as being wrapped around a torus (Courbaud et al. 2003). The radiation transmitted to a cell by a light beam depended on the radiation absorption of the succession of crowns that are crossed. The amount of radiation available over a vegetation season for each cell was obtained by cumulating the radiation from light coming from every direction. The amount and angular distribution of incident diffuse and direct lights were computed assuming all sites had latitude of 50°N (i.e., the latitude of the Belgian sites). Simulating light interception at the lower latitude of the Spanish sites (42°N) did not alter our conclusions (results not shown). Although latitude affects absolute values of irradiance, the transmittance (i.e., the ratio between the irradiances available above and below forest canopy) is not much affected by latitude.

Statistical analyses

To determine the relative importance of the three studied factors (stand composition, structure, and basal area), two three-way ANCOVAs were carried out. The response variables were the mean and the standard deviation of light transmittance, i.e., the proportion of incident light transmitted to the understory, computed for each simulation run and each cell. The standard deviation of light transmittance was used as an indicator of the variability of light conditions in the understory. Stand composition, structure, and basal area were considered as fixed factors with nine, two, and one degrees of freedom, respectively. As some interactions among factors were significant, multiple one-way ANCOVAs were carried out to further analyze the effect of each factor. To test the differences between the means of factor levels, we used Tukey's honest significant difference method (R Core Team 2013). We graphically examined model residuals to verify that ANCOVA assumptions were fulfilled (i.e., normal distribution of residuals, equal variance among groups, homoscedasticity, and linear relationship). All statistical analyses were performed with R software (R Core Team 2013).

Results

Mean transmittance

Mean light transmittance (m_T) depended on forest composition (62.5% of the total explained variance) and basal area (33.0% of the total explained variance), as indicated by type II sum of squares, whereas the interactions between composition and basal area (2.9% of the total explained variance), forest structure (1.4% of the total explained variance), and the other interactions among factors (0.2% of the total explained variance) had minor effects (Table 1). A gradient of mean transmittance was observed in relation to stand composition. Light transmittance was the lowest (i.e., tree light interception was the greatest) in the most shade-tolerant pure beech stands (on average, $m_T = 4.8\% \pm 4.3\%$ (mean \pm standard deviation)), whereas transmittance in the least shade-tolerant pure pine stands was the greatest ($43.0\% \pm 11.5\%$). As expected, mean transmittance clearly decreased with basal area. For instance, the mean transmittance in oak stands with basal area of 15 and $35 \text{ m}^2\cdot\text{ha}^{-1}$ were $28.7\% \pm 2.36\%$ and $7.6\% \pm 1.31\%$, respectively.

Mean transmittance of mixed stands was always intermediate between the transmittance in corresponding pure stands (Fig. 3) and always lower than the weighted average of transmittance in corresponding pure stands (weighted by species basal area proportion). For example, transmittance in mixtures of oak–pine ($25.9\% \pm 10.8\%$) was intermediate between pure stands of oak (lower light transmitted, $16.9\% \pm 9.0\%$) and pine (higher light transmitted, $43.0\% \pm 11.5\%$) and lower than the weighted average (29.9%). In the case of mixtures of three species, transmittance was intermediate between the transmittance of the corresponding two most shade-tolerant species mixtures, and the transmittance of the pure stand of the most shade-intolerant species although the amount of transmitted light was usually closer to that found in mixtures of the two shade-tolerant species. Again, as an example, in beech–fir–pine mixtures, light transmittance ($14.1\% \pm 8.3\%$) was slightly greater than in beech–fir mixtures (the two more shade-tolerant species in the mix, $9.2\% \pm 6.5\%$). The transmittance values in mixtures of two or three species were on average 3.6% and 9.2% lower than the weighted average, respectively.

Although forest structure had a statistically significant effect on the mean of transmittance, its effect was weaker than that of stand composition or basal area (Table 1). In pure stands, transmittance increased with the number of tree layers, being the lowest in single-layered stands ($18.1\% \pm 13.9\%$) and the highest in reverse J-shaped stands ($21.0\% \pm 14.8\%$). In mixed stands, the mean transmittance of multi-layered stands was in some cases significantly greater than in even-sized stands but in all cases remained lower than in reverse J-shaped stands (Fig. 3).

Transmittance variability

Similar to mean transmittance, the variability in transmittance depended mostly on forest composition (71.5% of total explained variance; Table 2) and basal area (23.9% of total explained variance). Forest structure (1.2% of total explained variance) and interactions among factors (3.4% of total explained variance) had little effect. The variability in transmittance was also lowest in beech stands and increased according to species shade tolerance (beech < fir < oak < pine), with the exception of pine stands, for which the variability in transmittance was lower than in fir stands. The differences between the variability in transmittance of pine and fir stands were significant for basal area values of 15 and $25 \text{ m}^2\cdot\text{ha}^{-1}$. As expected, mean transmittance and standard deviation were positively correlated ($r = 0.759$, $p < 2.2 \times 10^{-16}$). Nevertheless, the relationships between these two variables departed from a linear relationship with a maximum variability in transmittance observed at about a mean transmittance of 40%.

For some combinations of stand structure, composition, and basal area, the variability in transmittance in two-species mixtures was

Fig. 3. Average light transmittance for 90 virtual forest stands as a function of forest composition, forest structure, and basal area. The lowercase letters above the boxplots indicate significantly different groups ($\alpha = 0.05$).

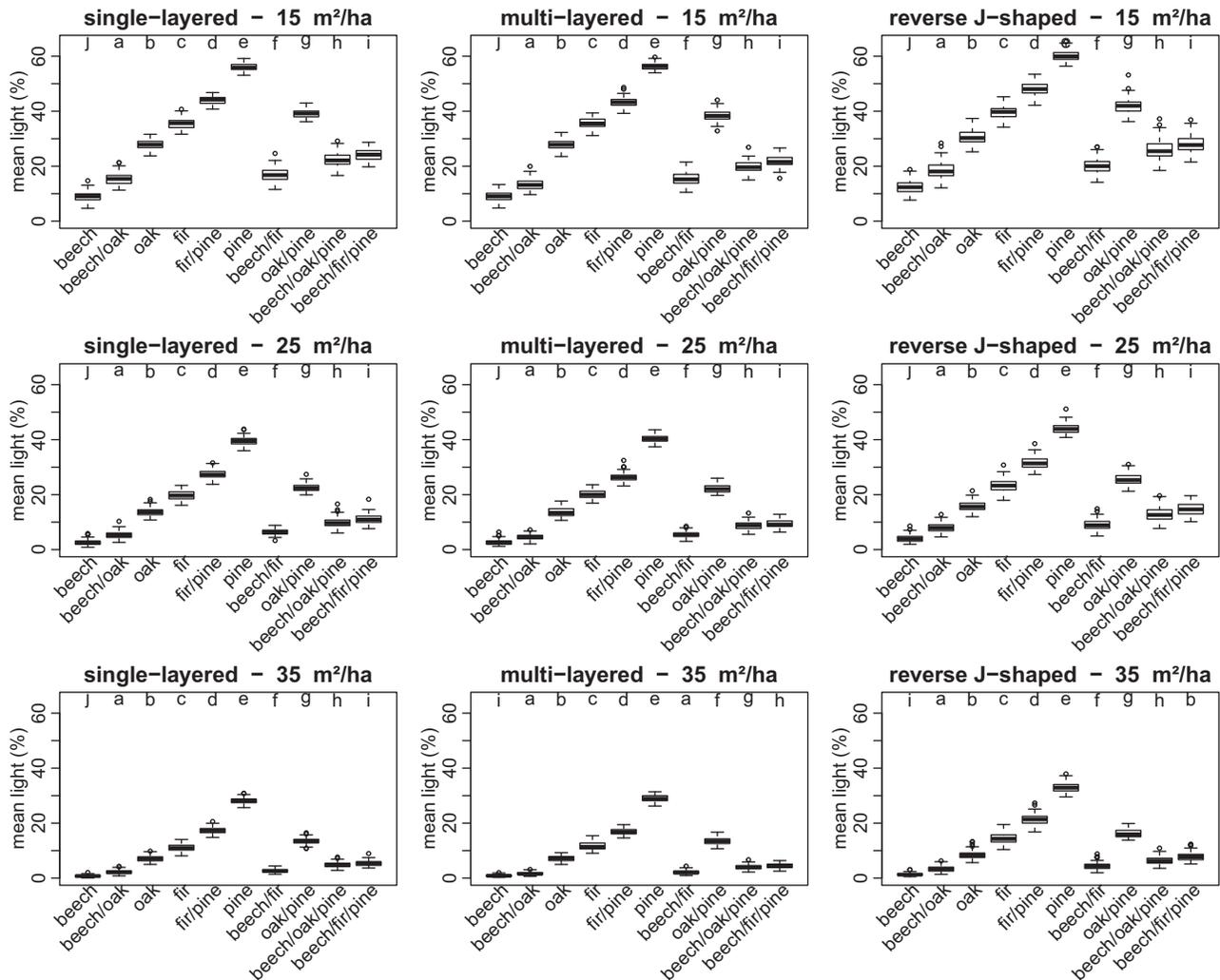


Table 2. ANCOVA table of the mean transmittance (aggregated by simulation run).

	Df.	Sum sq.	Sum sq. %	Mean sq.	F value	P value
Basal area	1	596 270	32.99	596 270	114 564	<0.001
Composition	9	1 129 719	62.50	125 524	24 118	<0.001
Structure	2	24 854	1.37	12 427	2 388	<0.001
Basal area × composition	9	52 436	2.90	5 826	1 119	<0.001
Basal area × structure	2	891	0.05	445	86	1.51×10 ⁻³⁷
Composition × structure	18	2 896	0.16	161	31	3.58×10 ⁻¹⁰³
Basal area × composition × structure	18	550	0.03	31	6	2.54×10 ⁻¹⁴
Residuals	8 940	46 530		5		

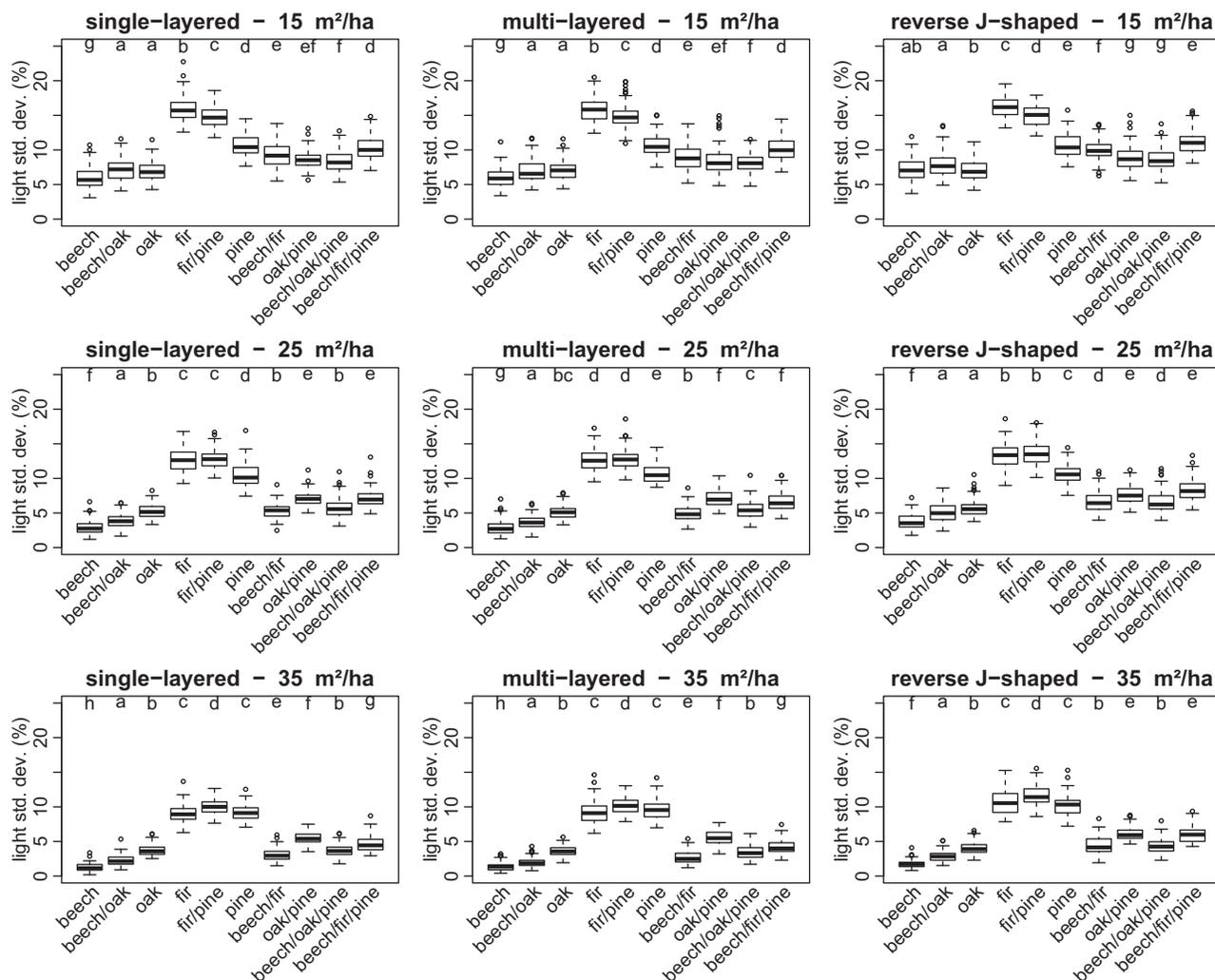
Note: Df., degrees of freedom; Sum sq., the type II sum of squares; Sum sq. %, the percentage of total sum of squares; Mean sq., the mean square. The R^2 of this model is 97%.

Table 3. ANCOVA table of the standard deviation of transmittance predictions.

	Df.	Sum sq.	Sum sq. %	Mean sq.	F value	P value
Basal area	1	28 748	23.91	28 748	16 042	<0.001
Composition	9	85 970	71.51	9 552	5 330	<0.001
Structure	2	1 453	1.21	726	405	3.20×10 ⁻¹⁶⁹
Basal area × composition	9	3 530	2.94	392	219	<0.001
Basal area × structure	2	78	0.07	39	22	3.40×10 ⁻¹⁰
Composition × structure	18	312	0.26	17	10	2.86×10 ⁻²⁷
Basal area × composition × structure	18	133	0.11	7	4	8.52×10 ⁻⁹
Residuals	8 940	16 021		2		

Note: Abbreviations are defined as in Table 2. The R^2 of this model is 88%.

Fig. 4. Light variability in the forest understory of 90 virtual forest stands as a function of forest composition, forest structure, and basal area. The lowercase letters above the boxplots indicates significantly different groups ($\alpha = 0.05$).



greater than the variability in corresponding pure stands (Fig. 4). This happened, for example, in oak and beech mixtures at low basal areas, as well as in the pine and fir mixtures in high-density stands. These relationships were consistent across the three modelled stand structures. However, no additive effect was observed when softwood species were mixed with hardwood species.

Similar to the results of mean transmittance, the variability in transmittance (σ_T) slightly increased with the number of tree layers in pure stands, being the lowest in single-layered stands (on average, $\sigma_T = 7.5\% \pm 3.9\%$) and the highest in stands with a reverse J-shaped structure ($8.2\% \pm 3.8\%$). In mixed stands, in some cases, the variability in transmittance of multi-layered stands was significantly greater than in even-aged stands, but in all cases, it remained lower than in reverse J-shaped structure stands.

The variability in transmittance generally decreased with stand basal area (Fig. 4). Nevertheless, there was a significant interaction between basal area and stand composition (Table 2). The effect of basal area on variability in transmittance was lower in pure stands of shade-intolerant or mid-tolerant species (e.g., pine and oak) than in stands of shade-tolerant species (e.g., beech and fir).

Discussion

Tree light capture and overstory heterogeneity

In contrast to our first hypothesis, we found no evidence that increasing structural heterogeneity reduces forest canopy light

transmittance or increases tree light interception. Light transmittance even slightly increased with increasing forest structural heterogeneity. Stands composed of one homogeneous tree layer transmitted less light than stands with two or more tree layers. These results are in line with the higher productivity of pure stands with low size heterogeneity (Bourdier et al. 2016).

On the other hand, light transmittance in mixed stands was lower than the weighted average of transmittance in corresponding pure stands. This result supports the hypothesis that complementarity of light use could be at the origin of the overyielding that has been observed in some mixed stands (Toigo et al. 2015; Pretzsch and Schütze 2009; Vallet and Pérot 2011). The difference between the observed values of transmittance in mixed stands and weighted averages originates, at least partly, from the nonlinearity of the relationship between light transmittance and stand basal area (Comeau and Heineman 2003; Lochhead and Comeau 2012; Sonohat et al. 2004).

However, other factors likely affect forest productivity as our results are insufficient to explain the absence of overyielding reported for mixtures such as oak–pine and oak–beech mixtures (Toigo et al. 2015). In addition to the interception of light, light use efficiency (Onoda 2014) and belowground resources also influence forest growth conditions (Richards et al. 2010) and the understory (Granhus et al. 2016). Despite receiving less light than taller trees, subordinate trees tend to use intercepted light more efficiently, pro-

ducing a greater amount of biomass per unit of light interception than taller trees (Onoda 2014). In addition, Toigo et al. (2015) found overyielding growth in tree mixtures to increase when soil fertility is low. In a recent review, Forrester (2014) showed that net complementary effects in mixed forests depend on the spatial and temporal variability in both aboveground and belowground resources. They stressed the need for further studies to quantify both the conditions (e.g., environmental gradients) and the processes driving these patterns (i.e., overyielding, complementary effects).

A potential limit of our approach is that the optimization of light capture in our simulated forest stands is restricted by limited crown plasticity, constrained by allometries and a random spatial distribution of trees. Allometries only roughly estimate individual crown development, as they assume that the lateral growth of a tree crown is isotropic and independent of the past and present surrounding canopy. Yet, anisotropic crown growth and crown plasticity have been mentioned to be important in canopy closure (Purves et al. 2007; Vepakomma et al. 2008, 2011). Additionally, because in many regions tree growth and survival depend on light transmittance, the natural spatial distribution of trees might deviate from a random distribution to optimize light capture. Forest management also alters the spatial distribution of trees but often tends to regularize it. Because of our approach to modeling crown dimensions and the spatial distribution of trees, we may thus underestimate the complementarity of light use in heterogeneous forests. Nevertheless, a closed layer of foliage encountered in dense monospecific even-sized stands is sufficient to capture most of the available light, as shown by the lack of ground vegetation and seedlings in dense even-sized stands (e.g., Bailey and Tappeiner 1998).

Our findings also underline the importance of forest composition and density on light transmittance. In contrast to the literature (e.g., Lochhead and Comeau 2012; Messier et al. 1998), stand composition had the strongest influence on understory light in our simulations. Stand density, as measured by basal area, was the second most important factor, whereas the heterogeneity in tree size affected little (approximately 1%) understory light levels in comparison with the two other factors. However, the order of importance of the tested factors may depend on the chosen study species and levels of basal area. We studied species with contrasted crown shapes and sizes. The effect of the overstory composition on understory light availability is usually explained by differences in species morphological traits related to light interception (Coll et al. 2011). In our case, LAD was relatively similar among the studied species (ranged between 0.5 and 0.7 m²·m⁻³), but crown allometries differed greatly (Fig. 2) and these relationships have been shown to critically affect canopy packing (e.g., Beaudet et al. 2002; Ligot et al. 2014a). In our study, the largest differences in average transmittance were observed between the simulated softwood and hardwood stands, with softwood species (pine and fir) having narrower and smaller crowns than hardwood species (oak and beech), thus transmitting more light (Valladares 2003). However, this result is not generalizable, as the studied hardwood and softwood species were species of different shade tolerances (Valladares and Niinemets 2008), with the hardwood species being the most shade-tolerant species. In addition, individuals of the two studied softwood species grow at higher elevations and in colder sites than those of the two studied hardwood species, with consequences both on allometries and on LAD (Astrup and Larson 2006; Lefrançois et al. 2008; Leuschner et al. 2006; López-Serrano et al. 2005).

Variability of understory light and overstory heterogeneity

In contrast to our second hypothesis, we did not find a systematic decrease in the range of understory light conditions with overstory heterogeneity. Instead, increasing tree size heterogeneity and especially species heterogeneity resulted in significantly greater variability of understory light conditions, depending on stand composition and basal area. For example, beech, a very

shade-tolerant species, maintained a very dark understory (low mean and variability of transmittance) even at moderate basal area (e.g., 25 m²·ha⁻¹). Adding beech in mixtures with oak generally limited the variability of understory light except in stands with very low basal area (15 m²·ha⁻¹). In contrast, the variability of understory light in mixtures of pine and fir was greater than in the corresponding pure stands of either pine or fir when basal area was high (≥25 m²·ha⁻¹). Forest structure, i.e., the organization of trees in different vertical strata, little affected the variability in understory light conditions. In pure stands, the variability in transmittance increased with the number of tree strata, but in mixed stands, the lack of difference between single-layered and multi-layered stands was not expected. Although an earlier study in mixed hardwood stands in northeastern North America found little variation in light transmittance with stand age and thus canopy strata complexification (Brown and Parker 1994). However, we acknowledge that this result may be influenced, at least in part, by the approach we used to generate mixed stands: mixed, single-layered stands were composed of two species in one single tree layer, with trees of about the same DBH but varying in height depending on specific allometries. Therefore, the comparable understory light variability observed between single-layered and multi-layered stands may be due to a lack of sufficient differences in the heterogeneity of tree sizes for these two structures.

The variability in understory light and the mean transmittance through the canopy are positively correlated and hence influenced by similar factors. Both the mean and the variability of transmittance increases as the size of canopy gap increases (Canham et al. 1990; Hardy et al. 2004). Nevertheless, our results further suggest that the relationship is not linear. As corroborated by the data of Da Silva et al. (2011), the variability in understory light is presumably maximized for a certain level of canopy openness that corresponds in our study to an approximate mean transmittance of 40%. At low understory light conditions ($m_T < 40\%$), the frequency distribution of transmittance is typically skewed to the right, as most understory patches are in low light conditions and few are in high light conditions (Beaudet et al. 2011). The variability in transmittance then increases with mean transmittance, e.g., increased overstory heterogeneity or decreased overstory density. In contrast, in high light conditions ($m_T > 40\%$), a reduction in mean transmittance could lead to an increase in transmittance variability, e.g., when a shade-tolerant species was mixed in a stand with less shade-tolerant species.

Research perspectives

Our findings were obtained through the simulation of stands with a random spatial distribution of trees, fixed levels of basal area, and constant quadratic mean diameters of 30 cm. Even though the studied stands were constructed with relatively arbitrary parameters (DBH distribution, composition, basal area), the characteristics of most simulated stands spanned typical conditions found in managed forests of the study species (Table 1), and for these stands, the predictions of understory transmittance are well in the range of observed values (Appendix Fig. A2). However, further work remains to be done before generalizing our results especially in stands with varying diameters or particular spatial distributions of trees (Ngo Bieng et al. 2006), e.g., aggregation of tree species or aggregation of understory trees in overstory gaps. The former is presumably a key variable of stand structure on understory light (Bourdier et al. 2016), as understory light should increase with stand quadratic mean diameter for a given level of basal area (Ligot et al. 2014a; Lochhead and Comeau 2012).

In addition, further modeling efforts are required to analyze the impact of even-aged and uneven-aged silviculture on understory light conditions. Uneven-aged silviculture maintains relatively constant basal area (e.g., about 30 m²·ha⁻¹ in spruce stands with periodic removals of 5–10 m²·ha⁻¹), whereas in even-aged silviculture, basal area varies greatly (e.g., from 0 to 60 m²·ha⁻¹) during a rotation (i.e.,

the full cycle from small regeneration to mature stand). A comparison of the effect of these two silviculture regimes on resource acquisition and use by forest stands therefore requires analyses that consider the change of forest structure during a complete rotation.

An investigation of the influence of individual plasticity of crown geometry such as light induced plagiotropy and LAD should also be performed as these traits are known to be affected by openings and stand composition (Mitchell 1975; Piboule 2001; Purves et al. 2007; Strigul et al. 2008; Umeki 1996, 1997). As we repeated our simulation 100 times, this effect has probably been partly minimized. Nonetheless, the extent to which individual crowns can expand in reaction to the local environment and how this affect understory light needs to be further studied.

Conclusion

The advantage of heterogeneous forest stands may lie in opportunities to naturally regenerate various species in the understory, as well as in opportunities to enhance light capture by the overstory. This study has taken a step in the direction of better understanding the effects of forest heterogeneity on light capture and light distribution between the canopy and regeneration layers, which is a necessary step in the current debate on increasing forest heterogeneity as a technique for making forest management more sustainable.

Acknowledgements

We are particularly grateful to François de Coligny (INRA, AMAP) for his help programming the model of forest radiative transfer (SAMSARALIGHT) and Adeline Fayolle (ULG, Gembloux Agro-Bio Tech) for her precious comments on the manuscript.

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Appendix A

Validation of SAMSARALIGHT

Fig. A1. Comparison of prediction and measures with hemispherical photographs of transmittance in Spanish forests composed of mountain pine and silver fir (left panel) and Belgian forests of European beech and oak (right panel). Predictions were computed with two radiative transfer models: SORTIE-ND (in red) and SAMSARALIGHT (in grey). The SAMSARALIGHT model was chosen to perform the simulation of this study, and its performance was further described by Ligot et al. (2014a). Figure is provided in colour online.

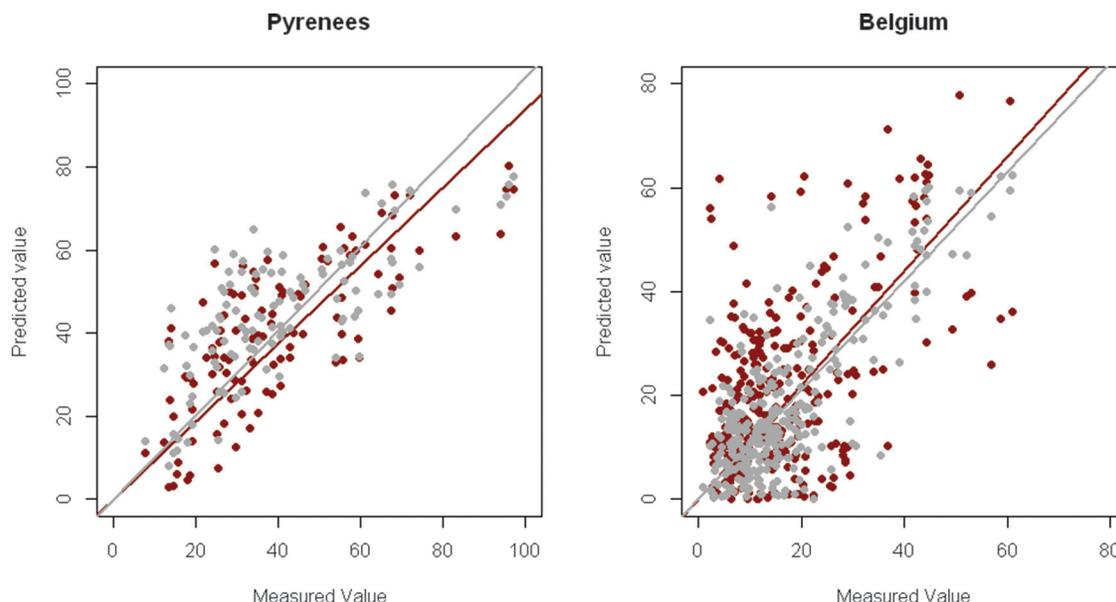


Fig. A2. Comparison of the simulated values of transmittance and values of transmittance recorded in previous studies along a gradient of stand basal area. The two plots on the left show values for beech–oak mixtures (Ligot et al. 2013), whereas the two plots on the right show values for fir–pine mixtures (Ameztegui and Coll 2011). Simulated values are depicted with boxplots, whereas observed values are depicted with empty dots. Ligot et al. (2013) did not sample plots along the whole basal area gradient — even though such stands exist (Table 1) — because their study focused on partially open forests with natural regeneration.

