

COMMUNAUTE FRANCAISE DE BELGIQUE  
ACADEMIE UNIVERSITAIRE WALLONIE-EUROPE  
UNIVERSITE DE LIEGE - GEMBLoux AGRO-BIO TECH

# Managing understory light to maintain the coexistence of forest tree species with different shade tolerances

Gauthier LIGOT

Essai présenté en vue de l'obtention du grade  
de docteur en sciences agronomiques et ingénierie biologique

Promoteur : Prof. Philippe LEJEUNE

2014



COMMUNAUTE FRANCAISE DE BELGIQUE  
ACADEMIE UNIVERSITAIRE WALLONIE-EUROPE  
UNIVERSITE DE LIEGE - GEMBLoux AGRO-BIO TECH

# Managing understory light to maintain the coexistence of forest tree species with different shade tolerances

Gauthier LIGOT

Essai présenté en vue de l'obtention du grade  
de docteur en sciences agronomiques et ingénierie biologique

Promoteur : Prof. Philippe LEJEUNE

2014



Gauthier LIGOT (2014) Managing understory light to maintain the coexistence of forest tree species with different shade tolerances (PhD Thesis). Université de Liège – Gembloux Agro-Bio Tech, 112 p., 24 tabl. 25 fig.

## SUMMARY

---

Similar to the management of the other environmental resources, forest management has been questioned and more sustainable practices of forest management are being sought. New close-to-nature practices aim to favor natural processes over human interventions. Particularly, continuous-cover forestry has the goal of relying on natural regeneration, and maintaining irregular stand structure and tree species mixture. However, maintaining mixture of species with different shade tolerances appears arduous with such a silvicultural system. Successfully managing irregular and mixed forests, relying on natural processes, requires a strong knowledge of the ecology of natural regeneration. In particular, strong knowledge is required to predict the result of the interspecific competition in the understory depending upon light availability. The amount of radiation transmitted to the understory is indeed a critical factor determining regeneration dynamics. It determines, at least in part, regeneration composition because of interspecific differences of growth and survival under shade. Moreover, our quantitative understanding of understory light in uneven-aged and mixed stands remains incomplete. A better quantitative understanding of understory light is needed to provide quantitative guidelines for the management of understory light in uneven-aged and mixed stands and, hence, for the management of natural regeneration. The purpose of this thesis is to determine how close-to-nature forest management can maintain mixtures of species with contrasting shade tolerances. I consider ecological conditions with good water and nutrient supplies. In these conditions, partially closed canopy limits the amount of light that reaches the understory, and light is the major factor driving regeneration composition. Consequently, I study the dynamics of natural regeneration with regards to light availability as well as the interception of light by the canopy of heterogeneous stands. Studying the regeneration ecology of two species with contrasting shade tolerances (*Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl.), I find that the shade-tolerant species outgrow the less shade-tolerant species in all light conditions. Even though the control of understory light with continuous-cover silviculture is required to sustain the growth of less shade-tolerant regenerations, it might not be sufficient to maintain the coexistence of species with contrasting shade tolerances. In order to examine the effects of canopy structure and composition on understory light availability, I use a model of light interception by heterogeneous canopies after synthesizing and discussing the approaches reported in the literature. The model predicts satisfactorily measures of transmitted light even though it is a relatively simple radiative transfer model. I next explore how various

silvicultural treatments can be manipulated to provide favorable understory light conditions for natural regeneration. These silvicultural strategies correspond to selective thinnings of five different types, e.g., harvesting preferentially small trees, large trees, or trees of shade-tolerant species or creating circular gaps. The results underline that creating favorable understory light conditions for natural regeneration can be achieved with various regeneration treatments. However, the adequate reduction of stand density depends upon the chosen silvicultural strategies. In particular, creating gaps of about 500 m<sup>2</sup> provides adequate light for small regeneration clumps. Harvesting preferentially small and trees of shade-tolerant species are also appropriate but required higher harvest intensity. Harvesting preferentially large trees slightly increases understory light and promotes more shade-tolerant species than less shade-tolerant species. In order to maintain the coexistence of species with contrasting shade tolerances, forest manager must control understory light and, in some cases, manually suppress the regeneration of the shade-tolerant species. The outcome of this study provides foresters with the necessary tools to evaluate how silvicultural treatments can be manipulated to create or maintain favorable light conditions for the regeneration of species of different shade tolerances. Guidelines are additionally proposed for forest managers wanting to maintain the coexistence of species with contrasting shade tolerances.

Gauthier LIGOT (2014) Gestion de l'éclaircissement dans le sous-bois pour maintenir la coexistence d'essences forestières sciaphiles et semi-héliophiles (Thèse de doctorat en anglais). Université de Liège – Gembloux Agro-Bio Tech, 112 p., 24 tabl. 25 fig.

## RÉSUMÉ

---

Tout comme la gestion des autres ressources environnementales, la gestion des forêts a été remise en question et de nouvelles pratiques, dites plus durables et plus proches de la nature, sont recherchées. Ces dernières minimisent les interventions humaines et préfèrent utiliser les processus naturels. Bien souvent, cela se traduit par le maintien de forêts irrégulières et mélangées avec un couvert continu et en utilisant la régénération naturelle. L'une des principales difficultés est de pouvoir maintenir un mélange d'espèces sciaphiles et semi-héliophiles, c'est-à-dire des espèces avec différents niveaux de tolérance à l'ombre. Réussir à maintenir un tel mélange avec une gestion proche de la nature demande une bonne connaissance de l'écologie de la régénération naturelle, notamment afin de pouvoir prédire l'issue de la compétition interspécifique en fonction de la quantité de lumière disponible dans le sous-bois. La lumière disponible pour la régénération détermine, au moins en partie, la future composition de la régénération puisque les espèces en mélange ont différents niveaux de tolérance à l'ombre et que leur croissance et survie diffèrent en fonction de la quantité de lumière disponible. Cependant, il est difficile de prédire la quantité de lumière disponible pour la régénération en peuplements irréguliers et mélangés. Le but de cette thèse de doctorat est de déterminer comment une gestion proche de la nature peut maintenir un mélange d'essences forestières avec différents niveaux de tolérance à l'ombre. J'étudie cette problématique pour des conditions écologiques avec de bons apports en eau et en nutriments. Dans ces conditions, la lumière est le facteur prédominant de la composition de la régénération car seule une fraction de la lumière disponible au-dessus de la canopée est transmise jusqu'à la régénération dans le sous-bois. J'étudie donc le développement de la régénération naturelle en fonction de la lumière disponible ainsi que l'interception de la lumière par la canopée de peuplements hétérogènes. L'étude de l'écologie de la régénération de deux espèces avec des niveaux de tolérance à l'ombre contrastés (*Fagus sylvatica* L. et *Quercus petraea* (Matt.) Liebl.) montre que l'espèce sciaphile grandit plus vigoureusement que l'espèce semi-héliophile dans toutes les conditions d'éclaircissement. Bien que le contrôle de la lumière transmise à la régénération soit nécessaire pour promouvoir la croissance de la régénération de l'espèce semi-héliophile, ce contrôle est dans certains cas insuffisant pour maintenir la coexistence d'espèces sciaphiles et semi-héliophiles. Dans le but d'examiner la disponibilité de la lumière dans le sous-bois en fonction de la structure et de la composition de forêts irrégulières, j'utilise un modèle d'interception de la lumière par

la canopée après avoir synthétisé et discuté les différentes approches de modélisations proposées dans la littérature. Ce modèle prédit de manière satisfaisante les mesures de l'éclairement disponible dans le sous-bois, bien que ce soit un modèle relativement simple. J'explore l'effet de différentes stratégies sylvicoles visant à contrôler l'éclairement disponible pour la régénération. Ces stratégies correspondent à des éclaircies sélectives de différentes natures prélevant, par exemple, plutôt les gros arbres, les petits arbres, les arbres des espèces les plus tolérantes à l'ombre, ou formant des trouées circulaires. Les résultats soulignent qu'il est possible d'apporter suffisamment de lumière pour la régénération d'espèces semi-héliophiles avec des stratégies sylvicoles très variées. Il convient néanmoins d'ajuster l'intensité des éclaircies en fonction de la stratégie sylvicole choisie. En particulier, l'ouverture de trouées de 500 m<sup>2</sup> apporte suffisamment de lumière pour de petits groupes de régénération. Les éclaircies qui prélèvent préférentiellement les petits arbres et les arbres des espèces tolérantes à l'ombre permettent également d'apporter suffisamment d'éclairement pour la régénération mais demandent une intensité d'éclaircie plus forte. Les coupes qui prélèvent préférentiellement les gros arbres n'augmentent que faiblement l'éclairement disponible pour la régénération et favorisent ainsi la régénération des espèces tolérantes à l'ombre. Afin de maintenir la coexistence de certaines espèces sciaphiles et semi-héliophiles, le gestionnaire forestier doit contrôler l'éclairement disponible pour la régénération et, dans certains cas, réduire manuellement la compétition exercée par la régénération des espèces tolérantes à l'ombre. Cette étude propose un outil permettant de manipuler différentes stratégies sylvicoles pour produire des conditions d'éclairement favorables à la coexistence d'espèces sciaphiles et semi-héliophiles. Des recommandations sylvicoles sont en outre proposées pour les gestionnaires forestiers soucieux de maintenir la coexistence d'espèces sciaphiles et semi-héliophiles.



*Copyright.* Aux termes de la loi belge du 30 juin 1994, sur le droit d'auteur et les droits voisins seul l'auteur a le droit de reproduire partiellement ou complètement cet ouvrage de quelque façon et forme que ce soit ou d'en autoriser la reproduction partielle ou complète de quelque manière et sous quelque forme que ce soit. Toute photocopie ou reproduction sous autre forme est donc faite en violation de la dite loi et des modifications ultérieures.



## REMERCIEMENTS

---

L'ouvrage que vous vous apprêtez à ouvrir, feuilleter ou lire, selon votre ambition et votre courage, se veut être l'aboutissement d'une thèse de doctorat. Mais en réalité, c'est bien plus que cela! C'est l'étude d'un sujet que j'ai trouvé passionnant avec à la fois de réelles implications pratiques pour les gestionnaires forestiers et d'intéressants questionnements scientifiques. Ce sont de nombreuses et agréables journées passées dans des hêtraies-chênaies ardennaises (on peut difficilement espérer mieux comme laboratoire) pour prendre des mesures variées dans un vaste dispositif expérimental. Ce sont de multiples voyages à l'étranger (France, Allemagne, Slovénie, Canada) avec toujours un merveilleux accueil, de très agréables rencontres et d'innombrables découvertes en tous genres. Et, c'est une formation enrichissante qui m'a permis d'approfondir mes compétences en programmation, statistiques, rédaction, écologie et sylviculture.

Pour avoir eu la chance de vivre cette expérience qui a si bien répondu à mes attentes, je remercie chaleureusement l'ensemble des personnes y ayant contribué. Bien que je sois le seul auteur de ce document, il est évident que sans leur aide et leurs encouragements, cet ouvrage n'aurait jamais pu voir le jour.

Merci à Philippe Lejeune et Hugues Claessens de m'avoir offert les ressources nécessaires pour l'élaboration de ce projet avec l'appui financier de l'Accord-Cadre de recherches et de vulgarisation forestière, de ma bourse d'aspirant du Fond de la Recherche Scientifique (F.R.S. - FNRS), des bourses de voyages du Bureau International de la Jeunesse et de l'Université de Liège et de la bourse d'excellence du WBI. Merci également à Daniel Portetelle pour son coup de pouce et le suivi de ces deux dernières bourses. Merci aussi à Jacques Rondeux pour m'avoir initialement proposé ce projet. J'espère avoir appliqué au mieux vos divers enseignements.

Merci, encore une fois, à Philippe Lejeune et Hugues Claessens pour avoir assumé le rôle de promoteur et m'avoir accordé votre confiance, même vis-à-vis de certaines de mes idées parfois loufoques. Avec les autres membres du comité de thèse, Yves Brostaux, Philippe Balandier et Gilles Colinet, votre encadrement m'a permis d'orienter mes travaux dans la bonne voie.

J'ai beaucoup apprécié le travail collaboratif pour la rédaction des différents articles scientifiques et de vulgarisation associée à ce projet. Hugues Claessens, tu auras apporté une touche sylvicole toujours très intéressante.

Mon travail a ainsi gardé une dimension pratique pour le gestionnaire forestier qui m'a particulièrement motivé. Philippe Balandier, tu as su me faire profiter de ta grande connaissance de l'écologie de la régénération et, avec André Marquier, de votre expertise pour la mesure de l'éclairement dans le sous-bois. Sans votre aide et ce dès le début du projet, je n'aurais pas su étudier la régénération en fonction de l'éclairement comme je l'ai fait, les résultats auraient été difficiles à valoriser dans des revues scientifiques et je n'aurais vraisemblablement pas pu terminer cette thèse endéans les délais de ma bourse du FNRS. Benoît Courbaud, ton expertise pour la modélisation de l'interception de la lumière par la canopée m'a également fait gagner beaucoup de temps. Tu as rapidement embarqué dans mon projet de revue de la littérature avec de précieuses propositions pour la rendre la plus intéressante possible. Tes relectures rapides et suggestions ont grandement amélioré la qualité des deux derniers manuscrits. Daniel Kneeshaw, outre de m'avoir si bien accueilli dans ton laboratoire, ton œil particulièrement aiguisé pour mettre en avant les messages clefs d'un texte sans s'encombrer de l'inutile ont certainement permis la publication très rapide des deux derniers articles scientifiques. Merci de m'avoir partagé ce savoir-faire. J'espère signer d'autres futurs papiers avec toi! Adeline Fayolle, merci pour ton aide lorsque je débutais la rédaction de mes premiers résultats. Tu as su me montrer comment mieux structurer mes idées tout en me proposant la lecture de différents articles qui font maintenant partie des principales références de cette thèse. Mathieu Jonard, merci pour tes différentes remarques lors de la rédaction du dernier article et, surtout, pour les brainstormings Louvano-Gembloutois. J'espère que de tels échanges se répéteront. Il a été très intéressant de confronter ta vision de modélisation plutôt orientée sur les processus écophysiologicals avec la vision gembloutoise de tradition plutôt empirique. François Lehaire, merci pour ton aide lors la vulgarisation de mes résultats.

Le travail de modélisation a également été particulièrement agréable. Merci François de Coligny de m'avoir initié au langage de programmation Java et de m'avoir si bien épaulé pour implémenter mon modèle dans la plateforme Capsis. Il a été très précieux de pouvoir, grâce à toi et à tout le travail investi dans Capsis, implémenter mes modèles rapidement et sans grandes connaissances informatiques. Benoît Courbaud, tu avais vu juste en créant une librairie de calcul du bilan radiatif. L'investissement consacré pour créer un module de calcul générique en valait vraiment la peine. Merci encore à vous deux ainsi qu'à Mathieu Jonard, Nicolas Donès et Philippe Balandier pour les réunions et échanges très constructifs. C'était passionnant de développer des outils avec différentes perspectives d'utilisation.

Le travail sur le terrain était la partie la plus ressourçante de ce travail. Merci à tous les acolytes de terrain pour ces si agréables journées. Je pense, pour commencer, à Benoît Mackels et Julien Goijen pour les précieuses réflexions que l'on a eu sur le terrain et pour votre aide pour la gestion des sorties

de terrain et de la paperasse. Benoît Mackels, tu auras été particulièrement efficace pour le traitement des photographies hémisphériques. Pour monsieur tout le monde, il est sans doute impensable de passer des journées entières à quatre pattes au milieu de semis, parfois pleins de tiques, parfois sous la pluie voire sur la neige, et parfois même à partir quatre heures du matin. Avec l'aide de toute l'équipe présente et passée, vous l'avez fait avec le sourire et mesuré, entre autres, 5090 arbres, 58 218 semis et pris 817 photographies hémisphériques. C'est énorme! Merci à Sébastien Delaitte, Régine Borremans, Taziaux Sophie, Edwin Dufays, Frédéric Henrotay, Clémence Teugels, Quentin Nachtergaele, Thomas Baijot, Alain Monseur, Adrien Schot, Cédric Geerts, Coralie Mengal, Amauri André et François Lehaire.

Les mérites relatifs au dispositif expérimental reviennent surtout à Laurence Delahaye qui l'a mis en place et à Matthieu Alderweireld qui l'a temporairement pris en main. Merci en particulier à ce dernier pour son travail méthodique qui m'a permis de prendre la relève facilement et d'avoir toujours pris le temps de répondre à mes questions. Tu retrouveras dans le contexte de cette étude des éléments que tu avais déjà mentionnés dans tes rapports et synthèses. Merci également aux ingénieurs de cantonnement et aux agents forestiers avec qui nous avons collaboré lors de l'installation et du suivi du dispositif expérimental.

Face à certaines difficultés méthodiques, j'ai également toujours pu compter sur diverses aides extérieures. Merci à Benoît Jourez et Céline Vaianopoulos pour avoir mis à ma disposition votre savoir et le matériel nécessaire pour analyser les cernes minuscules de semis au DEMNA. Yves Brostaux et Marc Mazerolle votre aide a été très précieuse pour l'utilisation des modèles mixtes.

La qualité de ce document n'aurait pas non plus eu son pareil sans les révisions attentives des rapporteurs Philippe Balandier et Yves Brostaux, les relectures de Philippe Lejeune, Hugues Claessens et Aitor Ameztegui, ni la correction de l'anglais effectuée par à William F.J. Parsons.

L'ambiance au bureau était également au top que ce soit à Gembloux ou à Montréal. Merci à tous pour vos différents conseils avisés et encouragements, les tartes à 10h, les parties de belotte, les parties d'échec, les verres en terrasse et tout le reste. Grâce à vous, on garde toujours le sourire au boulot.

Last but not least, merci aux proches et amis pour votre soutien durant ces cinq années. Quand le travail s'enlise et que les résultats traînent à montrer le bout de leur nez, il est si précieux de pouvoir se confier, rire et s'évader dans les bois, sur les rochers, sous terre, ou en montagne en si bonne compagnie. Vous avez contribué à maintenir en moi un équilibre

propice à la production d'un travail de qualité.

Merci!

## PUBLICATIONS

---

Some ideas and figures have appeared previously in the following publications.

1. Alderweireld, M., Ligot, G., Latte, N., Claessens, H., 2010. Le chêne en forêt ardennaise, un atout à préserver. *Forêt Wallonne* 109:10-24. [handle: 2268/ 79321](#)
2. Ligot, G., Balandier, P., Fayolle, A., Lejeune, P., Claessens, H., 2013. Height competition between *Quercus petraea* and *Fagus sylvatica* natural regeneration in mixed and uneven-aged stands. *For. Ecol. Manage.* 304:391-398. [handle: 2268/151307](#)
3. Ligot, G., Balandier, P., Mackels, B., Lehaire, F., Claessens, H., 2014. Suivi scientifique de vingt-sept régénérations naturelles de chêne sessile et de hêtre en Ardenne: retour d'expérience. *Forêt Wallonne* 128:3-13. [handle: 2268/151800](#)
4. Ligot, G., Balandier, P., Courbaud, B., Claessens, H., 2014. Forest radiative transfer models: which approach for which application? *Can. J. For. Res.* 44:385-397. [handle: 2268/163600](#)
5. Ligot, G., Balandier, P., Coubraud, B., Jonard, M., Kneeshaw, D., Claessens, H., 2014. Managing understory light to maintain a mixture of species with different shade tolerance. *For. Ecol. Manage.* 327:189-200. [handle: 2268/163600](#)

With the exception of the general introduction and the general discussion, all chapters are the result of a collaborative work with the authors mentioned above. [Chapter 2](#) is a modified translation of paper number 1. [Chapter 3](#) is a slightly modified transcription of paper number 2. The literature review in [Section 4.1](#) is a transcription of paper number 4. [Section 4.2](#) contains elements of paper number 5. [Chapter 5](#) is a slightly modified transcription of the same paper number 5.





# CONTENTS

---

1	GENERAL INTRODUCTION	1
2	STUDY AREA AND SPECIES	7
2.1	Ecological conditions	7
2.2	Reduction of oak population	9
2.3	Why maintain oak?	10
2.3.1	Biodiversity	10
2.3.2	Resilience	10
2.3.3	Productivity	11
2.3.4	Wood quality	12
2.3.5	Climate change	12
2.4	Forest management	13
3	REGENERATION HEIGHT GROWTH	15
3.1	Methods	18
3.1.1	Study sites	18
3.1.2	Regeneration height growth	19
3.1.3	Understory light conditions	21
3.1.4	Statistical analyses	21
3.2	Results	22
3.2.1	Regeneration characteristics	22
3.2.2	Height growth models	23
3.2.3	Diffuse and direct radiation	24
3.2.4	Analyzing site effect	24
3.3	Discussion	25
3.3.1	Height growth ranking	25
3.3.2	Competition	27
3.3.3	Direct radiation	27
3.3.4	Between-site variation	28
3.4	Conclusion	28
4	MODEL OF LIGHT INTERCEPTION	31
4.1	Literature review	32
4.1.1	Classification of FRTMs	34
4.1.2	Input variables	40
4.1.3	Model applications and output variables	44
4.1.4	Model evaluation	46
4.1.5	Model sensitivity	48
4.1.6	Discussion	52
4.2	Implementing a radiative transfer model	57
4.2.1	Crown geometry	57
4.2.2	Crown radius	58

4.2.3	Tree Height . . . . .	59
4.2.4	Height to the base of the crown . . . . .	59
4.2.5	Crown openness and leaf area density . . . . .	59
4.2.6	Model evaluation . . . . .	65
5	MANAGING UNDERSTORY LIGHT . . . . .	69
5.1	Methods . . . . .	70
5.1.1	Study sites . . . . .	70
5.1.2	Light model settings . . . . .	71
5.1.3	Cutting scenarios . . . . .	71
5.1.4	Statistical analyses . . . . .	72
5.2	Results . . . . .	77
5.2.1	Tree inventory . . . . .	77
5.2.2	Cutting scenarios . . . . .	77
5.2.3	Simulation . . . . .	77
5.3	Discussion . . . . .	80
5.3.1	Mean light response . . . . .	80
5.3.2	Optimum cutting scenario . . . . .	83
6	GENERAL DISCUSSION . . . . .	85
6.1	Maintaining species diversity . . . . .	85
6.2	Silvicultural recommendations . . . . .	87
6.3	Study limitations and perspectives . . . . .	88
6.4	Conclusion . . . . .	94
	BIBLIOGRAPHY . . . . .	95

## LIST OF FIGURES

---

Figure 1.1	Examples of mixed forests. . . . .	4
Figure 2.1	Locations of the 27 sites in the study area. . . . .	8
Figure 2.2	Soil conditions in which oaks and beech are found. . . . .	9
Figure 2.3	Frequency histogram of oaks and beech. . . . .	11
Figure 3.1	Plot layout in a site. . . . .	18
Figure 3.2	Model of the height growth of oak and beech. . . . .	25
Figure 4.1	Chart flow of forest radiative models. . . . .	33
Figure 4.2	3D plant mock-up. . . . .	39
Figure 4.3	Overview of the end-uses of FRTMs. . . . .	53
Figure 4.4	Geometric models of tree crown. . . . .	58
Figure 4.5	Measurements required to estimate LAD. . . . .	63
Figure 4.6	Predictions versus measures of PACL. . . . .	67
Figure 4.7	Cumulative distributions of predictions and measures of PACL. . . . .	68
Figure 5.1	Structure of the studied stands. . . . .	73
Figure 5.2	Simulated plot layout. . . . .	74
Figure 5.3	Mean increase of PACL by cutting type and intensity. . . . .	79
Figure 5.4	Post-harvest understory light and cutting intensity. . . . .	81
Figure 5.5	Post-harvest understory light and target basal area. . . . .	82
Figure 6.1	Post-harvest proportion of microsites favorable to less shade-tolerant species. . . . .	87
Figure 6.2	Availability of direct radiation at varying slopes and canopy heights. . . . .	91
Figure 6.3	Light microsites in a canopy gap. . . . .	93

## LIST OF TABLES

---

Table 3.1	Shade tolerance of oak and beech. . . . .	17
Table 3.2	Main characteristics of the study sites. . . . .	20
Table 3.3	Main characteristics of the measured regenerations.	23
Table 3.4	Parameters of the model of regeneration growth. . .	24
Table 4.1	Classification of FRTM modeling approaches. . . .	36
Table 4.2	Examples of 3D-geometric crown models. . . . .	37
Table 4.3	Reported values of leaf area density. . . . .	42
Table 4.4	Reported values of crown openness. . . . .	45
Table 4.5	Summary of the published evaluations of FRTMs. . .	49
Table 4.6	FRTM sensitivity to calibration parameters. . . . .	51
Table 4.7	Synthesis of FRTM advantages and drawbacks. . . .	56
Table 4.8	Parameters of the model of crown radius. . . . .	60
Table 4.9	Parameters of the model of tree height. . . . .	60
Table 4.10	Parameters of the model of the height to the base of the crown. . . . .	61
Table 4.11	Parameters of the power model of the height to the base of the crown. . . . .	61
Table 4.12	Parameters of the polynomial model of LAD. . . . .	64
Table 5.1	Description of the 5 cutting types. . . . .	75
Table 5.2	Stand structure and composition in the studied sites.	78
Table 5.3	Parameters of the model of post-harvest PACL. . . .	79

## ACRONYMS

---

1D	One-dimensional
3D	Three-dimensional
dbh	Diameter at Breast Height (1.3 m)
DIFF	Percentage of Diffuse Above Canopy Light
DIR	Percentage of Direct Above Canopy Light
LAD	Leaf Area Density
LAI	Leaf Area Index
PACL	Percentage of Above Canopy Light
PAR	Photosynthetically Active Radiation
PE	Porous Envelope
RMSE	Root Mean Square Error
TM	Turbid Medium



GENERAL INTRODUCTION

---



*Come forth into the light of things. Let  
nature be your teacher.*

William Wordsworth

Like the management of other environmental resources, forest management has been questioned and more sustainable practices of forest management are being sought. The management of even-aged pure stands with clearcutting has been particularly debated because clearcuts can incur long-lasting environmental damage such as soil mass movement, stream siltation, windthrow, and biodiversity loss (Keenan and Kimmins, 1993). The goal of new forest management practices is to be adaptive and close-to-nature, while sustaining biodiversity and ecosystem services. Forest managers must consider the constantly changing and growing needs of society, take into account climate change, and evaluate of the effects of past management strategies. Attempts are being made to reproduce the structure of old-growth forests in which trees of different sizes and species coexist in the hope of preserving ecosystem values and functions (Touzet, 1996). Natural processes, such as natural regeneration, are being favored over human interventions with the aim of preserving ecosystem services and reducing management costs. More particularly, continuous-cover forestry is being favored. Such silvicultural techniques have the goal of relying on natural regeneration, while maintaining irregular stand structure and tree species mixture (Pommerening and Murphy, 2004; Bruciamacchie and de Turckheim, 2005; Schütz et al., 2012).

Successfully managing irregular and mixed forests by relying upon natural processes requires comprehensive knowledge of the ecology of natu-

ral regeneration. Continuous-cover forestry systems mimic the dynamics of forests without anthropogenic perturbation and where large-scale disturbances are rare. The dynamics of such forests are dominated by small canopy openings, which originate following the death of single or multiple canopy trees. These small-scale disturbances create a mosaic of patches in which vegetation continuously changes through time and space. Regeneration of different tree species can establish within canopy openings, depending upon the size of the openings. Regeneration of late-successional species can colonize small gaps that result, for example, from the death of a single tree. Regeneration of mid-successional species can colonize gaps of moderate size that originate following the death of a small cluster of trees. Regeneration of early-successional species can establish in large gaps that originate, for example, from windthrow. Once the canopy of early- or mid-successional species closes, understory conditions evolve in favor of mid- or late-successional species, respectively (Finegan, 1984; Rameau, 1999). Environmental conditions in partially shaded understories contrast with those that have been observed in clearcut areas. Tree retention creates microclimates with limited light availability, reduced air movement, and modified water and nutrient cycling (Messier et al., 1999). Because species respond differently to these particular conditions, management of the forest canopy can be used, in theory, to manipulate the microclimate and, hence, control understory development and composition (Lieffers et al., 1999). Understanding regeneration ecology is therefore a requirement for predicting ecosystem dynamics and manipulating them.

The amount of radiation transmitted to the understory is a critical factor determining regeneration dynamics wherever nutrient and water availability satisfies regeneration requirements. Solar radiation drives plant photosynthesis and the exchange of mass and energy between soil, vegetation and the atmosphere. As a consequence, the quantity and the spectrum of light that is intercepted by the regeneration greatly affects its survival and growth (Lieffers et al., 1999), as well as stem, branch, leaf and root morphology (Balandier et al., 2006a; Galen et al., 2007; Niinemets, 2010). In temperate and boreal forests that are managed with a continuous-cover forestry system, due to radiation interception by overstory trees, light availability in the understory is often the predominant limiting resource for regeneration and, consequently, drives regeneration dynamics. The amount of transmitted radiation determines, at least in part, regeneration composition because of interspecific differences in growth and survival under shade, i.e., interspecific differences in shade tolerance. Shade-intolerant species are capable of invading open areas, while shade-tolerant species establish under a closed canopy.

Our quantitative understanding of understory light environments in uneven-aged and mixed stands remains incomplete. Due to the complexity of multilayered and mixed canopies, understory light conditions vary greatly in time and space (Pukkala et al., 1991). Measuring and predicting light is complicated under complex canopies (Lieffers et al., 1999). Assessing



understory light requires repeated measurements and specific equipment. In contrast to the situation in even-aged stands, understory light in uneven-aged and mixed stands is poorly predicted by stand density (Lochhead and Comeau, 2012). Understory light also depends upon the vertical and horizontal distribution of gaps and biomass elements. Consequently, new tools need to be developed and validated to predict understory light availability and improve our understanding of the dynamics of heterogeneous forests.

A better quantitative understanding of understory light is required to provide guidelines for the management of understory light regimes in uneven-aged and mixed stands. Forest managers indeed lack quantitative instructions for controlling understory light levels with partial cutting and, thereby control regeneration growth and survival. Using continuous-cover forestry systems, partial cutting reduces the density and modifies the structure of the vegetation that absorbs incoming light. By maintaining a closed canopy or by opening gaps, forest managers can theoretically create distinct regeneration niches (Grubb, 1977) that promote shade-tolerant species or less shade-tolerant species, respectively. Even though these key principles have long been described, important questions remain regarding their practical implementation. How a canopy that is favorable to the regeneration of shade-tolerant species can be distinguished from a canopy that is favorable to the regeneration of less shade-tolerant species? What are the stand characteristics that should be considered apart from stand density to predict understory light? Close-to-nature silviculture can create microclimates that are favorable for the coexistence of species with different shade tolerances, but this requires further scientific investigation.

As a matter of fact, while forest managers maintain complex stand structure with continuous-cover silviculture, they often face difficulties or even fail to maintain some desired species mixtures (Schütz, 1999). Problematic situations occur mostly with mixtures of species with contrasting shade tolerances (Figure 1.1). Such difficulties have been reported worldwide, for example, with the regeneration of valuable and less shade-tolerant species in tree-fall gaps in African rain forests (Hall, 2008; Doucet et al., 2009), the regeneration of yellow birch (*Betula alleghaniensis* Britton) or sugar maple (*Acer saccharum* Marsh.) after partial cutting in stands with, respectively, balsam fir (*Abies balsamea* (L.) Mill.) or American beech (*Fagus grandifolia* Ehrh.) in the province of Quebec (Canada) (Delagrangé et al., 2004; Prévost et al., 2010), or the regeneration of admixed less shade-tolerant species in European beech (*Fagus sylvatica* L.) forests (von Lüpke and Hauskeller-Bullerjahn, 1999; Petrişan et al., 2007; Van Couwenberghe et al., 2013; Petrişan et al., 2014).

The purpose of this thesis is to determine how close-to-nature forest management can maintain mixtures of species with contrasting shade tolerances. I consider ecological conditions in which light is presumably the major factor driving regeneration composition and, hence, I study the ecology of mixed regeneration with respect to light availability, the interception of light by ir-

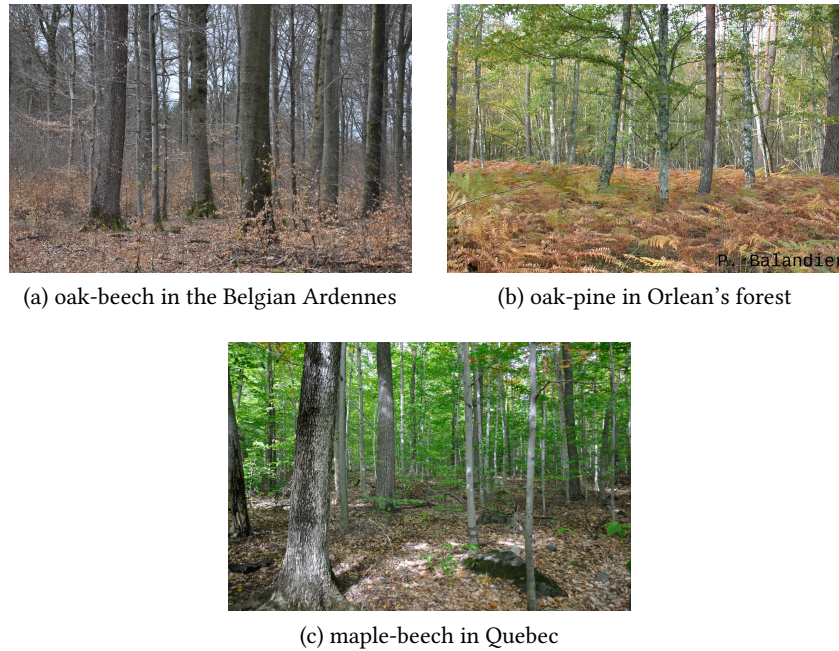


Figure 1.1: Examples of mixed forests with species of contrasting shade tolerances.

regular and mixed canopies, and how forest management affects understory light and regeneration dynamics.

I examine the mixture of sessile oak (*Quercus petraea* (Matt.) Liebl.) and European beech (*Fagus sylvatica* L.) in the Belgian Ardennes (Chapter 2). The mixture of oak and beech is of considerable economic importance in European temperate forests and makes an interesting ecological model for studying the coexistence of species with contrasting shade tolerances. Indeed, the two species are often mixed together and they have contrasting shade tolerances. Beech is a late-successional species that is very shade-tolerant. In contrast, oak is a mid-successional species that is less shade-tolerant. Consequently, the mixture of oak and beech naturally evolves towards pure beech forest, i.e., the climax forest.

First, I study the ecology of advance regeneration of the two species. I study competition between these two species along a gradient of light availability (Chapter 3). Because both species have contrasting shade tolerances, I expect that the shade-tolerant species dominates regeneration in low-light environments, while the opposite situation occurs in high-light environments. In low-light environments, the growth of the less shade-tolerant species is low and the mortality risk is high (Ellenberg, 1974; Pedersen, 1998), whereas in high-light environments the less shade-tolerant species can outgrow the shade-tolerant species (Huston, 1979; Smith and Huston, 1989; Kobe et al., 1995). According to this theory, adequately managing understory light allows regeneration composition to be controlled. However, it hardly explains why forest managers have difficulties in maintaining the mixture of the two species. In modeling competition between the two species, I test whether there is a rank reversal between the height growth

rates of both species in high-light environments or in low-light environments and I seek after the understory light conditions that are favorable for the coexistence of both species.

Second, I attempt to better understand and model light interception by irregular and mixed forest canopies (Chapter 4). Measuring the amount of radiation that is intercepted by the diverse components of a forest canopy is very tedious and time-consuming, especially in heterogeneous forests (Lieffers et al., 1999). Therefore, I investigate how a model of light interception can advantageously replace light measurements. Since several modeling approaches have already been proposed, I synthesize their advantages and drawbacks, and I identify which approaches are the most appropriate to which application. Then, I implement one of these approaches in a simulation model with the goal of exploring understory dynamics regarding the density, structure and composition of heterogeneous canopies. Once implemented, I validate this approach with field measurements of understory light availability.

Third, the implemented model of light interception provides an excellent opportunity for exploring how canopies can be manipulated to maintain mixtures of species with different shade tolerances (Chapter 5). I use the model to explore how modifications to stand density, structure and composition can affect understory light availability. With continuous-cover forestry systems, silvicultural operations mimic small-scale perturbations with group- and single-tree selection cuttings. Cutting aggregated groups of trees opens canopy gaps, substantially increases understory light (Coates et al., 2003; Beaudet et al., 2011), and is often recommended for promoting the regeneration of less shade-tolerant species (von Lüpke, 1998; Bruciamacchie and de Turckheim, 2005). Yet other strategies that harvest scattered trees can also create microsites with sufficient light availability for less shade-tolerant species. I quantify the understory light conditions following the application of 5 selection cutting systems and I identify how these systems can be manipulated to optimize the understory area favorable for either shade-tolerant species or less shade-tolerant species. This work yields new insights into the interception of light by heterogeneous canopies and provides quantitative guidelines for maintaining mixtures of species with contrasting shade tolerances.





*Keep close to Nature's heart... and break clear away, once in awhile, and climb a mountain or spend a week in the woods. Wash your spirit clean.*

John Muir

In the Belgian Ardennes, the mixture of sessile oak (*Quercus petraea* (Matt.) Liebl.) and European beech (*Fagus sylvatica* L.) is of considerable importance as it covers most broadleaf forests. While increasing attention is nowadays being paid to the maintenance of species diversity in forests, oak populations are decreasing in this region. Oak regeneration diminishes, whereas beech regeneration invades the understory.

## 2.1 ECOLOGICAL CONDITIONS

The Belgian Ardennes (50°N, 5°E; [Figure 2.1](#)), is an ecoregion that is characterized by rather homogeneous soil and climate conditions and is fairly representative of medio-European acidophilous beech forests (CORINE classification 41.111). For the period of 1971 to 2000, mean annual rainfall varied between 933 mm year<sup>-1</sup> and 1357 mm year<sup>-1</sup> and precipitation was well distributed throughout the year. Mean annual temperature ranges between 7.4 °C and 9.0 °C<sup>1</sup>. Dominant soils are well drained brown acidic soils (WRB

---

<sup>1</sup> These values were computed by spatial interpolation of climatic data (Tanguy Dejaegere, 2014, Pers. Comm.).

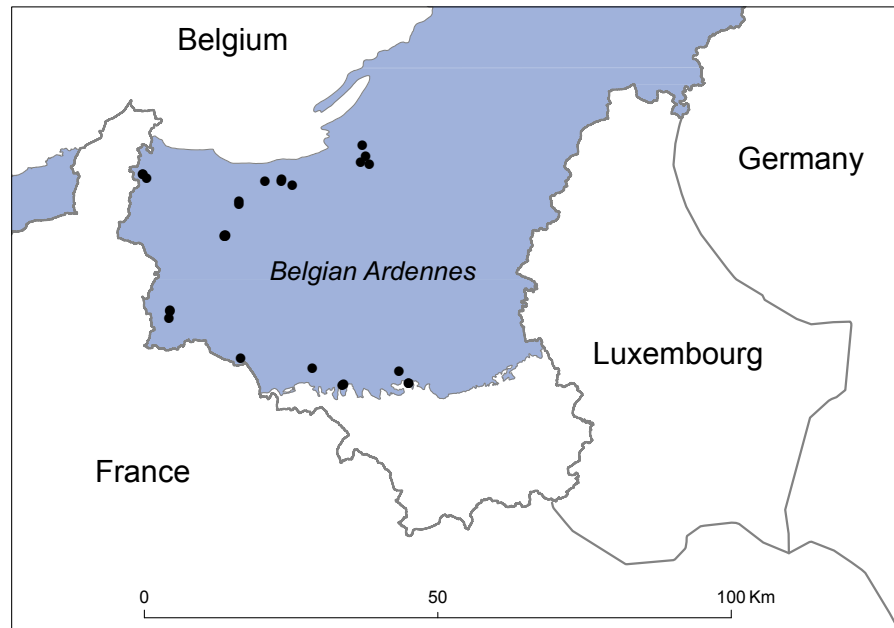


Figure 2.1: Locations of the 27 sites in the study area.

soil classification) of variable depth, which have developed on Hercynian oligotrophic schist and sandstone substrates.

In the Belgian Ardennes, sessile oak (*Quercus petraea* (Matt.) Liebl.) and pedunculate oak (*Quercus robur* L.) are both indigenous species that are frequently mixed with European beech (*Fagus sylvatica* L.). According to the regional forest inventory that does not distinguish pedunculate oak and sessile oak (Lecomte et al., 2003), pure and mixed stands with beech and oaks cover almost three-quarters (71 %) of the broadleaf forests. These stands have varied structures, ranging from secondary oak forests to late-successional beech forest.

In the Belgian Ardennes, oaks and beech have similar requirements regarding soil conditions and most sites are suitable for both species, with few exceptions. They both thrive in acidic soil conditions with good water supplies. Nevertheless, oak thrives better at elevations lower than 500 m above sea level. Sessile oak also thrives better than beech on dry south-facing slopes and pedunculate oak thrives better than beech in valley bottoms (wetter and richer soil conditions). The data that is collected by the regional forest inventory, highlights well that oaks and beech are found in similar soil conditions (Figure 2.2) but the abundance of oaks decreases as elevation increases and oaks are more abundant than beech on well-exposed slopes and valley bottoms.

For the purposes of this study, 27 sites were selected in public forests where European beech and sessile oak grow well (Figure 2.1). Sites at high elevation, valley bottoms, and steep-sloping sites were avoided. The elevation of the sites ranged between 244 m and 514 m above sea level. The average slope was about 9 % with a maximum of 36 %. The soil depth ranged between

15 cm and 110 cm, with an average of 47 cm. No pedunculate oak was found in the sites. Because of the homogeneity of the substrates and topographic positions, water and nutrient supplies were assumed to be similar among sites. The ground flora was indeed homogeneous among sites. The dominant herbaceous species were *Luzula luzuloides* (Lam.) Dandy & Willm, *Vaccinium myrtillus* L., *Deschampsia flexuosa* (L.) Trin, *Dryopteris carthusiana* (Villar) H.P. Fuchs, and *Pteridium aquilinum* (L.) Kuhn.

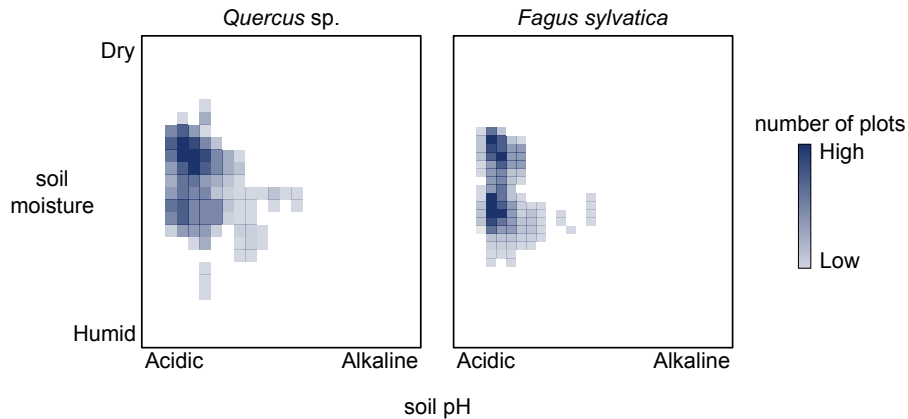


Figure 2.2: Soil conditions in which oaks (sessile oak and pedunculate oak) and beech are found in the Belgian Ardennes. Soil conditions were inferred from Ecoflore indexes (Bartoli et al., 2000) computed from the floristic surveys gathered by the regional forest inventory of Wallonia (2596 plots).

## 2.2 REDUCTION OF OAK POPULATION

The area that is covered by oak is decreasing. According to data that were compiled by the regional forest inventory, there is a shortage of oak trees with diameters less than 60 cm, which clearly indicated that oak regeneration has been deficient (Figure 2.3). Several factors contribute to the decrease in oak abundance. The evolution of social and economic conditions, the contrasted shade tolerances of the two species, and the pressure exerted by wild game are the main contributing factors.

Until the end of the 19<sup>th</sup> century, oak was preferred over beech when the strength, hardness, resistance and tannins of oak wood were needed for the construction of ships, timber-framed buildings, furniture, weapons, plows, and for leather tanning. However, the evolution of social and economic conditions led foresters to stop investing in oak regeneration. The demand for oak wood has decreased and coppicing of oak was abandoned and replaced by the planting of fast-growing species. Harvests in broadleaf stands were limited and oak stands gradually evolved from coppices with standard to well-stocked high forests (Lemaire, 2001).

In the absence of natural and human perturbation, oak regeneration is rapidly suppressed by beech regeneration. Under closed canopies, beech is indeed a strong competitor and a very shade-tolerant species. Beech seedlings usually establish before other less shade-tolerant species and before canopy opening. Once light availability increases, less shade-tolerant species start to develop but beech rapidly suppresses them. This common observation has been reported many times since the beginning of the 20<sup>th</sup> century (Poskin, 1934). Oak, the less shade-tolerant species, has persisted in mixtures with beech mainly because of its longevity and through human intervention. Yet nowadays, the natural succession of mixed stands that are composed of beech and oak toward pure beech stands is clearly observed.

Finally, red deer (*Cervus elaphus* L.) and roe deer (*Capreolus capreolus* L.) preferentially browse oak saplings over beech saplings. The browsing pressure exerted by wild game depends mainly upon the density of game populations and environment carrying capacity. In the Belgian Ardennes, carrying capacity is limited due to the acidic soils, but game populations have increased remarkably over the last decades. Wildlife pressure on regeneration has become dramatically important in some places, ruining the efforts of forest managers to renew their stands and obliging them to fence large areas in the hope of promoting oak regeneration (Licoppe, 2005).

### 2.3 WHY MAINTAIN OAK?

#### 2.3.1 Biodiversity

As a general rule, the coexistence of several tree species promotes forest biodiversity since different sets of organisms are associated with different tree species. Moreover, oak is known to have a large set of associated organisms (Branquart and De Keersmaeker, 2010), with some “charismatic” species such as woodpeckers (Picidae). In contrast, beech tends to suppress the admixed tree species and, consequently, reduce ecosystem diversity.

#### 2.3.2 Resilience

Mixed stands are more resilient and recover faster than pure stands because of interspecific differences in the sensitivity of individual species to biotic and abiotic stressors. The risk of major degradation is therefore weaker in mixed stands than in pure stands. Additionally, trees seem to be less affected by pest damage in mixed stands than in pure stands (Jactel et al., 2005). As a case in point, beech stands are known to be very sensitive to wind storms and drought. Indeed, beech has a superficial root system that is very sensitive to wind storms. Beech stands were among the most affected stands after the wind storm of 1999 in France (Bock et al., 2005). Furthermore, the striking decay of beech trees, that is partly attributable to an outbreak of ambrosia beetles (*Trypodendron domesticum* L. and *Trypodendron signatum* Fabricius, Scolytidae), in the beginning of the current century in the Belgian Ardennes



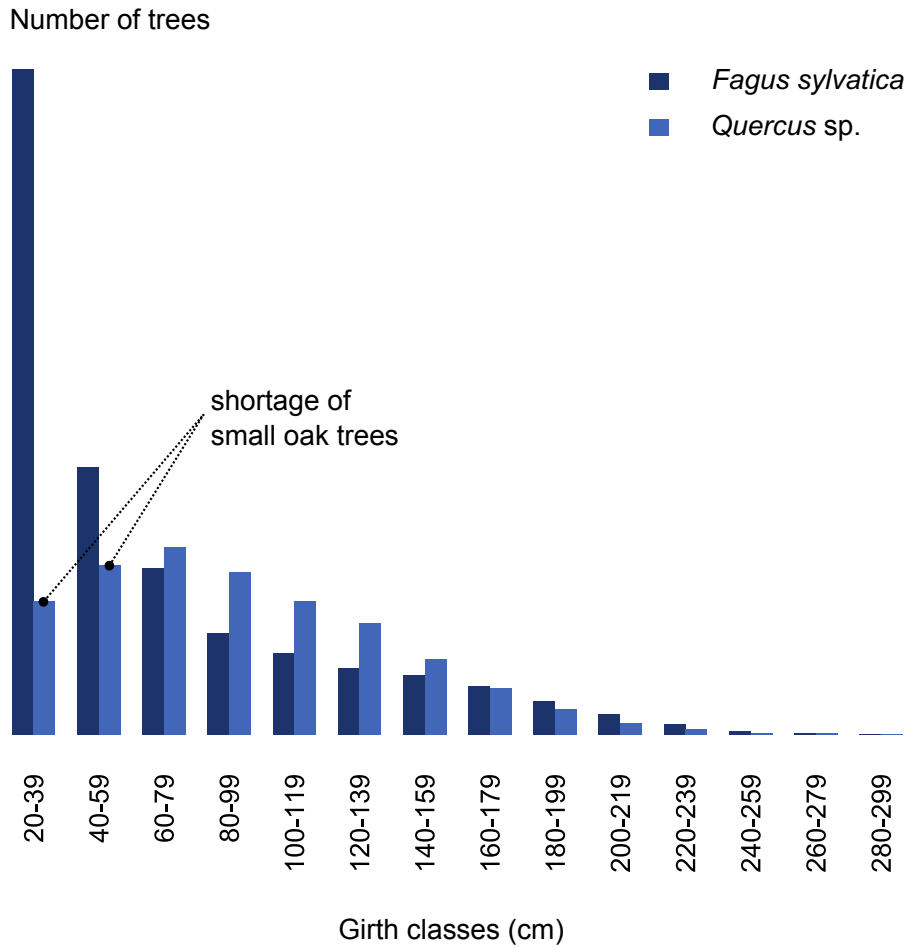


Figure 2.3: The data of the regional forest inventory of Wallonia indicates a shortage of oak (Sessile oak and pedunculate oak) trees with girth of less than 60 cm which underlines the deficiency of oak regeneration.

(Henin et al., 2003) has highlighted the sensitivity of beech stands to pests and pathogens.

### 2.3.3 Productivity

Biomass productivity can be greater in mixed stands than in pure stands because of niche complementarity and positive interspecific interactions (Hector et al., 1999). According to Pretzsch et al. (2013a), mixtures of oak and beech have an average biomass production that is 30 % greater than that of pure stands of oak or beech. Oak and beech have contrasting strategies for aboveground and belowground resource foraging. Due to the complementarity of their strategies, the proportion of captured resources can be higher in mixed stands than in pure stands. Moreover, several facilitation interactions between oak and beech have been reported, such as greater levels of atmospheric deposition (André et al., 2008), higher nutrient contents of leaf litter,

faster litter decomposition (Jonard et al., 2008), and greater mycorrhizal diversity (Tyler, 1992). Recent studies have even shown that beech trees are less sensitive to drought if they grow in mixed stands with oak (Pretzsch et al., 2013b; Mölder and Leuschner, 2014).

#### 2.3.4 *Wood quality*

Oak trees in the high forests of the Belgian Ardennes produce valuable wood for furniture (Plak, 1987; Gruselle, 2002). Although the quality of oak wood in the Belgian Ardennes has a poor reputation, this problem mostly has originated from past management practices in oak stands (oak coppicing). With the exception of sites at high elevations, the ecological conditions in the Belgian Ardennes and, presumably, the continuous-cover forestry management of mixtures of oak and beech, are suitable for producing wood of high quality.

#### 2.3.5 *Climate change*

According to the last report of the IPCC (IPCC Working group I, 2013), climate change is unequivocal, human intervention is clear, and continued greenhouse gas emissions are likely to cause further climate change. By the end of the 21<sup>st</sup> century in the Belgian Ardennes, according to Laurent et al. (2009) and based on IPCC's scenario A1B (IPCC, 2007), mean annual temperature is predicted to increase by about 3 °C. Precipitation is supposed to increase during winter (+18 %) and decrease during summer (−15 %), with more severe drought episodes. Even if the extent of climate change is questionable, scientists agree on the temperature and precipitation trends for this century.

Such climate changes will likely affect forest ecosystems in various ways. Even though most of them are still unpredictable (e.g., species adaptations, community dynamics, pest outbreaks), scientists have agreed that summer drought will probably be one of the major drivers of ecosystem change in Western Europe. The increase in temperatures implies an increase in evapotranspiration, with an increasing demand for water resources. Competition for water resources is likely to increase and trees will suffer from periodic water shortages, depending upon site conditions and species ecology.

Summer drought is already a key factor that contributes to the annual variability of tree growth, as has been highlighted in numerous dendrochronological studies (Scharnweber et al., 2011). From that perspective, oak seems better adapted than beech. The ecological niche of oak with respect to mean annual temperatures (7.3 °C to 13 °C) extends into warmer regions more than that of beech (5 °C to 12 °C) (Piedallu et al., 2009). Oak has a deeper and more efficient root system, a lower vulnerability to cavitation, and is less drought-sensitive than beech (Bréda et al., 1993; Backes and Leuschner, 2000; García-Plazaola and Becerril, 2000; Cavin et al., 2013; Mette et al., 2013).

Furthermore, recent studies have shown that oak competitiveness might increase with climate change. In France, the height growth of beech has recently declined, whereas the height growth of oak has substantially increased (Bontemps et al., 2012). A similar trend has been observed in Central Europe (Mette et al., 2013). In the latter study, researchers even estimated climatic conditions under which oak could become more competitive than beech. They estimated that rank reversal would occur with mean annual temperatures of 11 °C to 12 °C and annual precipitation of 500 mm to 530 mm (with 230 mm during the growing period).

Therefore, there is serious evidence that beech will suffer from climate change to a greater degree than oak. However, the decline of beech in mixed stands will probably be mitigated by positive interspecific interactions. Beech decline in the Belgian Ardennes will likely be observed later than in surrounding areas because the Belgian Ardennes has a relatively cooler and wetter climate than the surrounding areas. Nevertheless, the forecasted 3 °C increase in mean annual temperature endangers beech trees by the end of the 21<sup>st</sup> century, especially in the most xeric conditions, as has already been observed on south-facing slopes.

## 2.4 FOREST MANAGEMENT

With the gradual degradation of the market for small oak timber during the 20<sup>th</sup> century, broadleaf forests of the Belgian Ardennes have been managed with continuous-cover forestry systems to convert oak coppices and oak coppices with standards progressively to high forests. Forest managers have usually maintained high forest stocking of adult trees (Lemaire, 2001), thereby promoting beech regeneration. Nevertheless, during the last decade, the outbreak of ambrosia beetles and the induced beech decay (Henin et al., 2003) has opened the canopy of some of these forests providing opportunities for the regeneration of less shade-tolerant species.

Currently, the management of these forests aims to maintain irregular and mixed stands that rely upon the establishment of natural regeneration under a partially closed canopy. Despite the difficulties of maintaining the coexistence of beech and oak, continuous-cover and close-to-nature silviculture is considered to better fulfill the needs of today's society than the other silvicultural systems (Touzet, 1996) because it is considered to preserve ecosystem values and services (multiple-use management), to offer greater management flexibility (de Turckheim, 2006), and to reduce biotic and abiotic hazards in the context of climate change (Pretzsch et al., 2013a).



## COMPETITION BETWEEN TWO SPECIES WITH CONTRASTING SHADE TOLERANCES

---



*You will find something more in woods  
than in books. Trees and stones will  
teach you that which you can never  
learn from masters.*

Saint Bernard

The management of mixed stands with continuous-cover forestry systems has been increasingly promoted to improve forest biodiversity, resiliency, sustainability, and ecosystem services (Schütz, 1997). However, this approach relies upon the natural regeneration (Pommerening and Murphy, 2004) of species that can have contrasting shade tolerances.

Light availability in the understory determines competitive outcomes between species with different shade tolerances; light availability can be controlled by forest managers through adequate control of canopy closure. Maintaining a closed canopy promotes regeneration of shade-tolerant species, whereas opening canopy gaps promotes the regeneration of less shade-tolerant species. According to Kobe et al. (1995), light-demanding species are characterized by fast growth, allowing them to outcompete neighboring trees in high-light environments, whereas shade-tolerant species are characterized by slow growth and low mortality, which allows their persistence in low-light environments.

However, these assumptions can be questioned as they hardly explain why forest managers rarely succeed in promoting sessile oak (*Quercus petraea* (Matt.) Liebl.) regeneration beneath canopies that also contain European

beech (*Fagus sylvatica* L.) in Europe (von Lüpke and Hauskeller-Bullerjahn, 1999).

The regeneration of oak and beech has been intensively studied in European forests. In particular, many studies have detailed the shade tolerance of both species (Table 3.1). Beech juveniles have greater abilities to survive and grow in shade than oak juveniles. They have greater morphological plasticity, which can presumably enable them to maintain a positive carbon balance in low-light environments. Oak juveniles have greater light requirements than beech juveniles (Collet et al., 1997; Emborg, 1998; Collet et al., 2001; Collet and Chenost, 2006; Stancioiu and O'Hara, 2006; Balandier et al., 2007; Petriřan et al., 2007, 2009; Wagner et al., 2010). According to the definition of shade tolerance that was proposed by Kobe et al. (1995) and from greenhouse experiments (Dreyer et al., 2005), in high-light understories, the most light-demanding species, oak, is expected to outgrow the shade-tolerant beech.

Little information has been published concerning the *in situ* dynamics of advanced and well-established natural regeneration of the two species in mixed stands. Indeed, both species have mostly been studied separately, at the seedling stage, and under controlled conditions. Our understanding of interspecific competition is therefore largely inferred by extrapolating information on the autoecology of the two species (Table 3.1). Consequently, scientific investigation is required to better explain the difficulties that are faced by forest managers who want to maintain the coexistence of oak and beech.

Additionally, modeling the growth of natural regeneration has raised two methodological issues. First, it requires assessing a relevant indicator of understory light conditions, which depend upon the interception of diffuse and direct radiation by trees. The percentage of transmitted diffuse radiation has often been considered to represent accurately the percentage of total transmitted radiation (Petriřan et al., 2007, 2009). Nevertheless, direct radiation carries more energy than does diffuse radiation, but direct radiation that is transmitted under the canopy is limited in time and space (sunflecks) due to canopy irregularities and constant change of sunlight direction (Bonhomme, 1993). Second, *in situ* experiments cannot control all the different factors that influence sapling growth. The growth of beech and oak regeneration is expected to vary from site to site due to both biotic and abiotic factors. In particular, different herbaceous species are known to compete with the saplings for supplies of nutrients, water and light (Collet and Frochot, 1996; Coll et al., 2003, 2004; Wagner et al., 2010), or to produce allelochemicals (Timbal et al., 1990; Dolling, 1996; Jaderlund et al., 1996). Local variations in climate and soil (Turbang, 1954) are additional factors that could influence regeneration development.

Within this context, the growth of natural oak and beech regeneration was monitored and modeled to test that:

- The less shade-tolerant oak grows faster in high-light environments than the shade-tolerant beech;

Table 3.1: Literature review of the shade tolerance of sessile oak and European beech. The columns titled beech and oak provide indications regarding the variable of interest and development stage (if specified) for beech and oak, respectively.

VARIABLE OF INTEREST	DEVELOPMENT STAGE	BEECH	OAK	REFERENCES
Transmittance at light compensation point	1 <sup>st</sup> -year seedling	very low	very low	Turbang (1954), Welander and Ottosson (1998), Chaar and Colin (1999), Nicolini et al. (2000)
	Young seedling	2–5 %	10 %	Madsen and Larsen (1997), Le Duc and Havill (1998), von Lüpke and Hauskeller-Bullerjahn (1999), Emborg et al. (2000), Collet et al. (2001), Collet and Chenost (2006), Petrișan et al. (2007)
Transmittance at saturating growth	young seedling	10 %	20 %	Dineur (1951), Emborg (1998), von Lüpke (1998), Stancioiu and O'Hara (2006b)
	old seedling (>10 years)	20 %	30 %	Jarret (2004), Petrișan et al. (2009)
Morphological plasticity to different light conditions		high	low	Farque et al. (2001), Collet and Frochot (1996), Stancioiu and O'Hara (2006b), Wagner et al. (2010)
Sensitivity to ground vegetation competition		medium	low	Newbold et al. (1981), Collet and Frochot (1996), Coll et al. (2004), Löff and Welander (2004), Wagner et al. (2010)

- Regeneration growth is reduced by interspecific competition between saplings;
- Regeneration growth responds better to the availability of diffuse radiation than to the availability of direct radiation;
- Regeneration growth varies from site to site and this “site effect” is correlated with the local climate and soil conditions.

### 3.1 METHODS

#### 3.1.1 Study sites

We selected 23 sites within the study area (Figure 2.1 and ??). The sites had well-established regeneration (10–300 cm high) that spanned a wide range of stand structures and compositions in mixed stands of the Belgian Ardennes forests. In spring 2007, regeneration areas (100–6500 m<sup>2</sup>) were fenced off to protect them from browsing by wildlife. Inside each fence, we sampled the saplings within 5–31 square plots of 4 m<sup>2</sup> (total of 242 plots). The plots were laid out every 4 m following a square grid (Figure 3.1). Inside the fences and within 20 m outside the fences, we measured and mapped every tree with a diameter at breast height (dbh) greater than 13 cm.

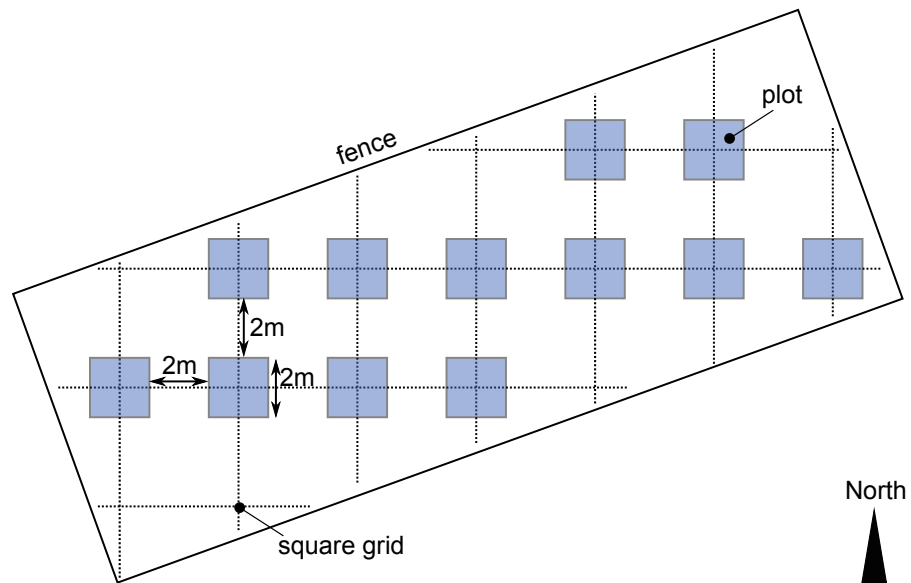


Figure 3.1: Plot layout in a site. Experimental plots were laid out following North-South and West-East transects inside a 2-m tall fence.

We performed a soil and humus description (Jabiol et al., 1995) as well as floristic surveys (Braun-Blanquet method), in order to compute levels of the supply of nutrients and water at every site (Bartoli et al., 2000). Similarly to Ellenberg’s method, every species indicates a range of nutrient and water



conditions, and site values correspond to a weighted average of the indexes of found species. The variation of soil richness between the sites appeared limited with index values ranging between 0.8 and 2 on a scale of 0 (very acid soils) to 6 (calcareous soil). The local variations of climate between sites were also assessed using a regional climate model and computing approximately 30 indexes of temperature, precipitation, and evapotranspiration (Tychon, 2000). They corresponded to averages, standard deviations, minimums, and maximums computed either per season or per year.

Studied stands had complex vertical and horizontal structures and included a wide range of dbh and height classes. Stand composition was also diverse, varying from monospecific beech stands to stands almost completely dominated by oak (Table 3.2). Other species (mainly *Carpinus betulus* L., *Betula pendula* Roth, *Betula pubescens* Ehrh., *Acer pseudoplatanus* L., and *Acer pseudoplatanus* L.) accounted for up to 20 % of stand composition. The percentage of above canopy light measured in the understory (PACL) ranged between 1 % and 61 % for plots dominated by oak, and between 2 % and 43 % for plots dominated by beech. This encompassed a wide gradient ranging from a close canopy to a canopy with a gap size varying up to approximately 1200 m<sup>2</sup> (area without overtopping crown).

### 3.1.2 Regeneration height growth

In this study, we monitored sapling height growth between 2009 and 2011. In 2009 and 2011, we measured sapling height using a telescopic meter stick to the nearest centimeter of the 3 tallest saplings of oak and beech in each plot. Saplings measured in 2009 were not tagged and therefore the saplings measured in 2011 could have been different. The mean annual height increment in site  $i$  and plot  $j$  ( $iH_{ijs}$ ) was computed for each species  $s$  (Equation 3.1).

$$iH_{ijs} = \frac{\overline{H11}_{ijs} - \overline{H09}_{ijs}}{2} \quad (3.1)$$

where  $\overline{H09}_{ijs}$  and  $\overline{H11}_{ijs}$  are, respectively, the average height of the three tallest saplings of species  $s$  in site  $i$  and plot  $j$  measured during year 2009 and 2011.  $iH_{ijs}$  therefore corresponds to the annual height growth of oak or beech saplings two years after the installation of fences.

We counted the sapling in every 4 m<sup>2</sup> plot for every species in 2007 and 2012. In 2009, the sapling density was computed as the average of these two counts.

Up to five different species (beech, oak with mainly *Carpinus betulus* L., *Betula* sp., *Acer pseudoplatanus* L. and *Coryllus avellana* L.) were found to coexist in the plots. In order to take into account the effects of the potential competition between species, we identified the species dominance, i.e., whether  $\overline{H11}_{ijs}$  was the greatest for the species  $s$  in plot  $ij$ .

In 2011, we selected five representative saplings of oak and beech within each site, inside the fences but outside the 4 m<sup>2</sup> plots, to determine sapling

Table 3.2: Main characteristics of the study sites. The number of sites and the number of plots per site ( $n$ ) are given in the two first columns. The structure and composition of the study stands is shown by the minimum and maximum tree diameter (dbh), the average basal area and the average proportion of oak. Regeneration is characterized by the minimum and maximum height, age and total sapling density. The last column contains the minimum and maximum of the percentage of above canopy light (PACL). The table is sorted by average PACL.

Site	$n$	OVERSTORY			OAK SAPLINGS		BEECH SAPLINGS		ALL SAPLINGS	LIGHT
		dbh cm	basal area $\text{m}^2 \text{ha}^{-1}$	oak basal area %	height cm	age year	height cm	age year	density $\text{m}^{-2}$	PACL %
17	6	9 - 74	25	80	26 - 39	4 - 8	49 - 127	4 - 12	10 - 36	6 - 10
22	18	12 - 78	16	74	105 - 209	7 - 12			6 - 13	3 - 14
25	20	13 - 81	22	0			28 - 248	5 - 16	3 - 110	2 - 25
12	10	13 - 81	22	68	16 - 171	5 - 12	39 - 220	5 - 10	12 - 39	5 - 23
15	31	6 - 72	23	80	18 - 58	3 - 6	29 - 145	5 - 13	3 - 25	1 - 26
19	12	8 - 84	15	0			176 - 252	9 - 14	4 - 52	2 - 13
26	6	7 - 80	14	6			133 - 265	7 - 12	4 - 14	2 - 43
3	7	7 - 66	18	17	23 - 80	3 - 6	42 - 210	4 - 21	21 - 94	10 - 19
2	6	6 - 74	17	25	73 - 186	6 - 17	155 - 245	10 - 15	5 - 19	8 - 23
10	9	6 - 60	23	85	123 - 249	12 - 13			10 - 29	10 - 22
29	15	7 - 67	20	51	25 - 204	4 - 12	105 - 264	6 - 17	10 - 43	10 - 21
8	11	6 - 63	19	89	76 - 243	1 - 13			6 - 69	9 - 27
20	5	7 - 92	19	37			159 - 231	11 - 18	14 - 19	10 - 27
4	7	6 - 74	25	73	168 - 255	13 - 18			4 - 95	13 - 20
14	7	7 - 73	20	41	74 - 134	7 - 17	174 - 274	10 - 19	5 - 30	16 - 22
24	11	6 - 55	11	93	166 - 273	10 - 15			17 - 75	10 - 34
28	18	14 - 65	10	6			122 - 246	9 - 12	6 - 15	14 - 32
23	15	6 - 77	21	58	80 - 245	7 - 13	196 - 277	7 - 11	4 - 28	7 - 29
13	2	7 - 73	14	51	21 - 111	7 - 14	203 - 248	12 - 17	8 - 45	12 - 13
1	3	6 - 67	11	28	13 - 43	3 - 5	99 - 152	4 - 11	25 - 67	20 - 26
18	5	6 - 80	7	19	47 - 234	8 - 14	208 - 272	9 - 14	3 - 12	4 - 35
11	9	7 - 68	14	91	165 - 236	11 - 17			7 - 13	42 - 45
9	8	7 - 50	11	95	175 - 240.3	12 - 13			3 - 53	14 - 61

age. Sapling age was determined by counting the number of bud scars and growth rings (Collet et al., 1997). The rings were counted on stem sections at a height of 5 cm using a binocular microscope. The sections were carefully sanded beforehand with sandpaper with a grit designation of up to 2000.

### 3.1.3 Understory light conditions

To estimate light availability just above the saplings, hemispherical photographs were taken before sunrise during mid-summer 2010 or 2011 above the regeneration at the center of the plot. The photographs were used to compute three indexes of light availability for the whole growing season (from 1<sup>st</sup> April to 31<sup>st</sup> October): the percentage of total above canopy light (PACL), the percentage of diffuse above canopy light (DIFF) and the percentage of direct above canopy light (DIR). Photographs were thresholded with PfiPhotem software (Adam et al., 2006) and light was calculated with GLA software (Frazer et al., 1999). Additional details are provided in ??.

We validated our PACL estimates by comparing them with measures of the Photosynthetically Active Radiation (PAR) carried out with sensors (Solem S.A., Palaiseau, France) in five sites during one day in July 2010. The relationship between the estimates and the measures was highly significant ( $r = 0.91$ ,  $P < 0.001$ ,  $n = 70$ ) with a slope not significantly different from 1.

### 3.1.4 Statistical analyses

We modeled the height growth of saplings ( $iH$ ) in relation to the initial height ( $H$ ), understory light (PACL) and species dominance ( $SDOM$ ). Similarly to other studies (Pacala et al., 1994; Kunstler et al., 2005; Stancioiu and O'Hara, 2006; Petriřan et al., 2007; Wagner et al., 2010), height growth of saplings ( $iH$ ) was modeled with a nonlinear saturated relationship with PACL, which meant that growth increased at an increasing rate with PACL up to a certain point (inflection point) and then saturated progressively (asymptote). We attempted to add additional explanatory variables such as regeneration age and sapling density. Nevertheless, adding these latter variables did not improve significantly the models (??). We used mixed models to take into account that the observed growth depended upon a random site factor and a set of explanatory variables ( $H$ , PACL and  $SDOM$ ). Site characteristics were not included in the model as fixed factors because we did not sample the sites across a gradient of environmental conditions. The sites were thus considered as random repetitions of the experiment within the Belgian Ardennes. The mixed modeling approach enabled to quantify and explain the between-site variation. Based on Akaike's Information Criterion (AIC) and residual dispersal (??), we selected the logistic model

among others. For beech (Equation 3.2), it was a function of both the initial height ( $H_{ij}$ ) and the percentage of above canopy light (PACL). For oak, the selected model (Equation 3.3) took additionally into account the species dominance ( $SDOM$ ), i.e., whether or not oak saplings dominated saplings of other species.

$$iH_{ij} = (\alpha_j + b \cdot \sqrt{H_{ij}}) \cdot \frac{1}{1 + \exp\left(1 - \frac{\text{PACL}_{ij}}{c}\right)} + \epsilon_{ij} \quad (3.2)$$

and

$$iH_{ij} = (\alpha_j + b \cdot \sqrt{H_{ij}}) \cdot \frac{1}{1 + \exp\left(1 - \frac{\text{PACL}_{ij}}{c_{SDOM}}\right)} + \epsilon_{ij} \quad (3.3)$$

with

$$\begin{aligned} \alpha_j &\sim dN(0, \theta_\alpha) \\ \epsilon_{ij} &\sim dN(0, \theta_\epsilon) \end{aligned}$$

We further tested whether adding the percentage of transmitted direct radiation improved significantly models containing the percentage of transmitted diffuse radiation. We replaced PACL in the model with a linear combination of the percentage of above direct (DIR) and diffuse light (DIFF):  $e \cdot \text{DIR} + (1-e) \cdot \text{DIFF}$ . The null hypothesis was that direct light would not influence height growth if the diffuse light was already taken into account, i.e.,  $e = 0$ . According to the ratio between diffuse and direct radiation measured by the meteorological institute of Belgium, the mean annual proportion of direct radiation,  $e$ , equals 0.46 above canopy.

Finally, we computed the best linear unbiased estimates of the random factor  $\alpha$  ( $\text{BLUP}_\alpha$ ) and tested the Pearson's correlations between these estimates and indexes of nutrient and water supply as well as microclimatic indexes.

All of the statistical analyses were performed within the R environment (R Core Team, 2013) with a significance level of 0.05. Nonlinear mixed models were adjusted with the nlme package (Pinheiro et al., 2011) using the restricted maximum likelihood approach.

## 3.2 RESULTS

### 3.2.1 Regeneration characteristics

Details of the studied regeneration for every site are given in Table 3.2 and average characteristics are given in Table 3.3. Regeneration density strongly varied across sites, from 0 to 110 saplings  $\text{m}^{-2}$ . Species composition also varied across sites. The proportion of other admixed species was large in some plots (max. 98 %), but exceeded 50 % in only 28 plots.

On average, beech saplings had higher initial height and height increment than oak saplings. Harvested saplings of the two species were 11 years old in average, but the studied regenerations were clearly uneven-aged. Moreover, in plots with a mixture of beech and oak, oak saplings were on average 1.5 years younger (two-way mixed ANOVA,  $F = 5.8$ ,  $P < 0.001$ ).

Negative height increment occurred ( $n = 18$ ) because the three tallest measured saplings were not necessary the same for the two measurements. Saplings measured the first time were not tagged. Before the second measurement, some measured saplings could have died and be no longer among the three tallest saplings.

The Pearson's correlations between PACL and the initial height of oak and beech saplings were respectively 0.387 ( $P < 0.001$ ) and 0.042 ( $P = 0.608$ ). At the beginning of the study, high oak regenerations were thus mostly found in plots with higher light levels.

Overtopped and overtopping oak regenerations occurred in 104 and 70 plots, respectively. Overtopped and overtopping beech regenerations occurred in 120 and 29 plots, respectively. In half of the plots with overtopped oak regeneration, oak saplings represented the major proportion of the total sapling count. By contrast, overtopped regeneration of beech involved only a few individuals.

Table 3.3: Main characteristics of the measured regenerations. Average (minimum and maximum) sapling height, height increment and age for oak, beech and other species encountered in the plots. The last column indicates the number of subplots for which the species dominates the regeneration.

SPECIES	$n$	HEIGHT IN 2009 cm	HEIGHT INCREMENT cm	AGE IN 2009 year	DOMINANT REGE.
Beech	149	153 (23;277)	26 (-9;62)	10 (4;21)	120
Oak	174	125 (13;273)	16 (-10;52)	10 (1;19)	70
Other	93	118 (7;285)	20 (-66;84)	/	51

### 3.2.2 Height growth models

The modeling of height growth for the two species showed that beech saplings grew on average faster than oak saplings, whatever the light conditions (Figure 3.2). For the two species, as PACL increased, growth increased following a sigmoid curve and then reached a horizontal asymptote. This asymptote increased with sapling initial height. For instance, in high-light conditions, the height increment of small beech saplings ( $H_{ij} = 50$  cm) was found to be approximately 20 cm, whereas the height increment of taller beech saplings ( $H_{ij} = 300$  cm) was up to 50 cm. Between saplings of oak and beech of similar height, the beech saplings had a greater height increment than the oak saplings.

Moreover, beech saplings reached their asymptotic growth at lower light levels than oak saplings. Overtopping beeches, overtopping oaks, and overtopped oaks reached 90 % of their asymptotic growth at, respectively, 12 %, 20 % and 29 % of above canopy light. Indeed, the inflection point of the models, denoted by parameter  $c$  in Equation 3.2 and Equation 3.3, varied significantly between models (Table 3.4).

The good dispersal of residuals indicated no evidence of model bias. However, residual scatterplots indicated a substantial residual variation (??) that was greater in the model for beech ( $\theta_\epsilon = 10.5$  cm) than for oak ( $\theta_\epsilon = 6.8$  cm). The between-site variation,  $\theta_\alpha$ , was about 7 cm in both models.

Table 3.4: Parameter estimates (confidence intervals with  $\alpha$  level of 0.05) of the selected models presented in Equation 3.2 and Equation 3.3.  $b$  is the parameters of the asymptotic height growth and  $c$  is the inflection point. In the model for oak, there were two estimates for  $c$  (denoted by  $c_{SDOM}$  in Equation 3.3): one for overtopping regeneration and one for overtopped regeneration.  $\theta_\alpha$  and  $\theta_\epsilon$  are, respectively, the standard deviation associated to the random factor (between-site variation) and the residual error (within-site variation).

SPECIES	$b$	$c$ (overtopping)	$c$ (overtopped)	$\theta_\alpha$	$\theta_\epsilon$
Oak	2.059 (1.642;2.476)	6.058 (3.468;8.648)	10.257 (6.469;14.046)	7.255	6.759
Beech	2.431 (2.035;2.828)	3.964 (2.378;5.550)		7.261	10.491

### 3.2.3 Diffuse and direct radiation

We tested whether adding the percentage of transmitted direct radiation (DIR) into a model already including the percentage of transmitted diffuse radiation (DIFF) improved the prediction of height increment by replacing PACL in Equation 3.2 and Equation 3.3 with  $e \cdot \text{DIR} + (1 - e) \cdot \text{DIFF}$ . The null hypothesis was accepted for beech ( $e = 0.300$ ,  $P = 0.640$ ) which means that DIR did not influence significantly the height growth of beech regeneration. At the opposite, the null hypothesis was rejected for oak ( $e = 1.001$ ,  $P = 0.005$ ). This indicated that the height growth of oak responded mainly to DIR. The same conclusion would have been obtained by adjusting models including only the overtopping saplings.

### 3.2.4 Analyzing site effect

For the oak saplings, the “site effect”, estimated using BLUP $\alpha$ , was positively correlated with soil richness ( $r = 0.562$ ,  $P = 0.015$ ) and mean annual temperature ( $r = 0.638$ ,  $P = 0.004$ ). The site effect was negatively correlated with altitude ( $r = -0.631$ ,  $P = 0.005$ ) and mean annual precipitation ( $r = -0.689$ ,

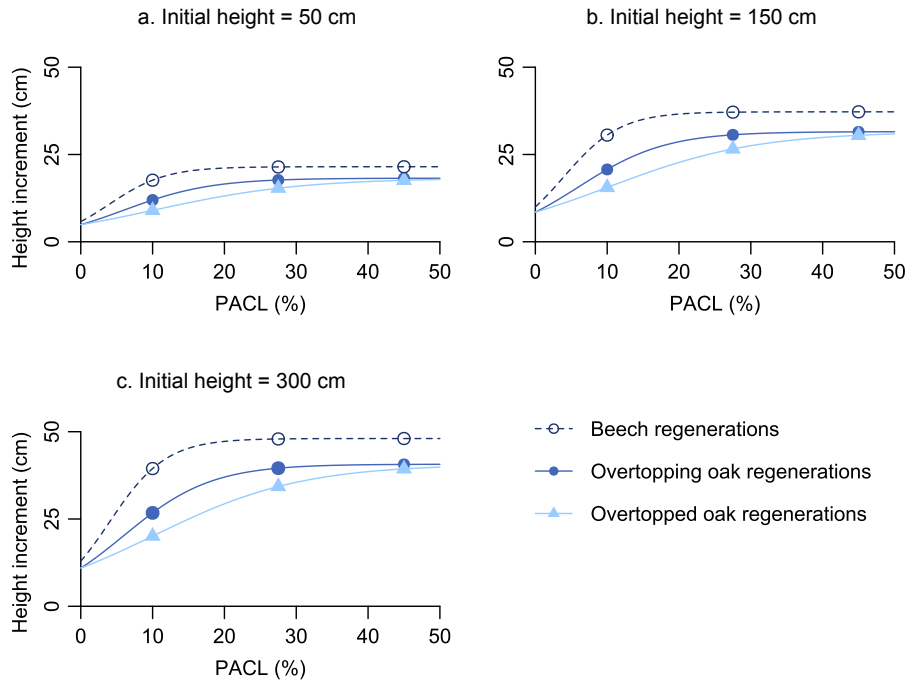


Figure 3.2: Model of the height growth of oak and beech saplings in mixed forests in the Belgium Ardennes. Beech showed a higher growth rate under all light conditions. The presence of taller saplings of beech reduced the growth of the neighboring oak saplings (overtopped oak saplings).

$P = 0.002$ ). In addition, altitude was inversely correlated with mean temperature ( $r = -0.522$ ,  $P = 0.026$ ) but not significantly with mean precipitation.

For beech saplings, the “site effect” was only positively correlated with soil richness ( $r = 0.553$ ,  $P = 0.001$ ).

### 3.3 DISCUSSION

Our large *in situ* sampling of beech and oak regenerations enabled us to adjust mixed nonlinear models of height growth according to initial height, light availability and species dominance (Equation 3.2 and Equation 3.3). We further used the adjusted models to ascertain (i) the height growth of the two studied species under different light conditions, (ii) the effects of species dominance, (iii) the influence of direct radiation, (iv) the between-site variations, (v) and silvicultural implications.

#### 3.3.1 Height growth ranking

The ecological theory of forest succession postulates that under high-light levels, light-demanding species outcompete shade-tolerant species. According to Kobe *et al.* (1995), a high capacity to survive under low-light levels is offset by lower growth rate under high-light levels. Light demanding species

would thus allocate preferentially resources to height growth and hence risk dying from light starvation (Messier et al., 1999).

Our findings indicated well that oak saplings have greater light requirements than beech saplings. We found that the beech and oak saplings needed more than 10 % and 20 % of above canopy light (PACL), respectively, to exhibit more than 90 % of the maximum height growth (Figure 3.2). In accordance with previous studies (Farque et al., 2001; Stancioiu and O'Hara, 2006; Petriřan et al., 2007, 2009), we found that under higher levels of PACL, any increase in PACL induced little variation in height growth (asymptote). Nevertheless, our findings indicated that oak saplings, the less shade-tolerant species, generally exhibited a lower height increment than beech saplings even under high-light conditions (PACL > 20 %, Figure 3.2).

This observation is partly in contradiction with the definition of shade tolerance proposed by Kobe et al. (1995), but similar observations have already been reported with other species (Walters and Reich, 1996; Kunstler et al., 2005). It highlights the strong ability of beech to survive in deep shade (Wagner et al., 2010), and lead us to infer that oak saplings have an insignificant chance of survival under beech saplings. The lower height growth of oak means, that in mixed clumps of oak and beech, oak saplings are naturally suppressed. Nevertheless, the height growth might be traded off with adaptations to low nutrient and water supply (Kobe et al., 1995; Walters and Reich, 1996; Beaudet and Messier, 1998; Collet et al., 2001; Wagner et al., 2010) or herbaceous competition (Walters and Reich, 1996; Coll et al., 2003, 2004).

In this study, we focused on the variations of saplings height growth with light availability and we admit that the response of diameter growth and mortality rate could have led to different conclusions. Nevertheless, height growth has been shown to be a good proxy for sapling mortality (Kobe et al., 1995; Walters and Reich, 1996; Kunstler et al., 2005; Petriřan et al., 2007).

Beech saplings were on average taller and older at the beginning of the experiment, which gave them a competitive advantage over oak saplings. Due to their shade-tolerant nature and the higher frequency of seed production by adult trees, beech saplings often pre-exist in the understory before the canopy opening (Wagner et al., 2010). They maintain large seedling populations in the understory while waiting for more suitable light conditions. Consequently, beech saplings are often established before oak saplings. However, the small age differences between the oak and beech saplings in this study are unlikely to be responsible for the differences in height growth. Indeed, we found that sapling age did not appear as a significant explanatory variable in height growth models. This result is in agreement with the findings of Collet et al. (2001) and partly in agreement with those of Emborg (1998).

Growth ranking might depend upon tree ontogeny and size (Delagrangé et al., 2004; Niinemets, 2006; Balandier et al., 2007), and availability of nutrient and water (Kobe et al., 1995; Walters and Reich, 1996). Our results might therefore be limited to the studied ontogenetic stage characterized by



saplings with a height of less than 300 cm and within the conditions of the Belgian Ardennes.

Moreover, we ensured strict protection of the studied saplings from herbivorous browsing. As deer prefer browsing oak over beech (Gill, 1992), oak regeneration is more severely damaged than beech regeneration and the dominance of beech is intensified by ungulate pressure.

### 3.3.2 *Competition*

Overtopping saplings of beech (and hornbeam) significantly reduced the height growth of overtopped oak saplings. This shifted leftward the inflection point from 10 % to 6 % of above canopy light. Such a reduction was expected because PACL was measured above the regeneration and overtopped species receive only the PACL that was not intercepted by overtopping regenerations. Overtopped beeches were not significantly affected. The levels of transmitted radiation in plots with overtopped beeches were probably too high (average PACL of 15 %) to model the effect of interspecific competition on the growth of beech saplings. In such conditions (PACL > 10 %), a small decrease in transmitted radiation does not really affect beech growth (Table 3.4 and Figure 3.2). Moreover, diameter growth may be more affected by competition than height growth (Collet and Chenost, 2006; Prévosto and Balandier, 2007).

### 3.3.3 *Direct radiation*

We tested whether the height growth of oak and beech saplings was sensitive to direct radiation. Our results suggested that stem elongation of oak saplings was promoted by direct radiation in contrast with the height growth of beech saplings. This result confirmed the higher light requirement of oak saplings. In addition, beech growth was sensitive to light change when PACL was less than 10 %. In these conditions, gaps are generally very small and the periods with transmitted direct radiation are very short (Chazdon and Pearcy, 1991). This stresses the importance of using total PAR radiation to model the growth of less shade-tolerant species. Diaci (2002) and Diaci et al. (2007) demonstrated the relative importance of diffuse and direct radiation on regeneration success of Norway spruce, beech and pedunculate oak in Slovenia. In particular, they reported the successful development of beech under diffuse canopy openings, something that is in accordance with our results. On the other hand, sites with higher levels of direct radiation might also be drier (Diaci et al., 2007). We studied solely the effect of light supply, while, in another study, changes in light conditions were shown to induce changes in microclimatic and soil variables (Aussenac, 2000).

### 3.3.4 *Between-site variation*

In this study, we showed that between-site variations was substantial ( $\theta_\alpha \approx 7.2$  cm) and in the same order of magnitude that the within-site error ( $\theta_\epsilon = 6.7$  cm and 10.5 cm for oak and beech, respectively). We attempted to explain this variation with both biotic and abiotic characteristics of the sites.

Soil richness was the only significantly correlated variable for both species. Both species are known to require similar levels of nutrient availability (Piedallu et al., 2009) and the investigated range of soil richness was small between the sites and it was computed from a floristic survey. These variations might hence denote complex interactions between canopy composition, canopy closure and ground vegetation.

In contrast with beech saplings, the height growth of oak saplings responded positively to mean annual temperature and negatively to mean annual precipitation. Oak has higher mean annual temperature requirements and its optimum temperature is about 11 °C in Western Europe (Piedallu et al., 2009). Rainfall is abundant throughout the study area and should not affect negatively sapling growth in the absence of soil waterlogging. However, abundant rainfall implies greater cloud cover and precipitation that are negatively correlated with temperature. Sites with abundant rainfall could then be characterized by higher cloud cover and lower temperatures, which might negatively affect oak growth within the study area. Taken together, these climatic considerations, underlined the sub-montane trend of the climate of the Ardennes that is less convenient for oak than for beech regeneration, even in high-light environments. Possible additional explanations for within- and between-site variations may lie in genetic variation, incidence of disease, canopy history, unmeasured soil and microclimatic conditions.

## 3.4 CONCLUSION

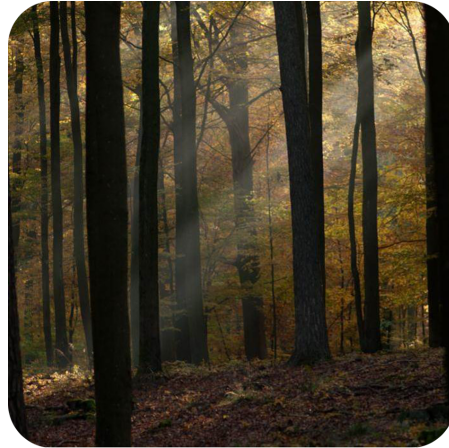
We sampled *in situ* advanced regenerations within the whole range of conditions encountered in beech and oak forests managed with a continuous-cover forestry system in the Belgian Ardennes. Transmittance ranged from 1 % to 60 % under heterogeneous canopies. Transmittance below 3 % is typical under closed canopy (Emborg, 1998), whereas, after canopy release, the level of transmittance might increase up to 15 % (Collet et al., 2001), 30 % (Pacala et al., 1994) or even beyond 60 % according to our data. We observed that beech saplings naturally outgrow oak saplings. Beech saplings reached an optimum growth at 10 % of above-canopy light whereas oak saplings needed twice as much light. In addition, our sapling age analysis highlighted that beech saplings were usually established before oak saplings. After canopy opening, these pre-existing beeches derived greater benefit from the increase of light availability than younger and smaller oaks. In these conditions, oaks are rapidly suppressed and mixed stands of oak and beech evolve naturally toward pure beech stands. The two species have mainly coexisted because beech naturally regenerates under well-

established oak stands where oak has previously been favored by selective thinning, coppicing and plantations (Claessens et al., 2010). The reverse situation is unlikely to occur naturally without frequent disturbances.



## MODEL OF LIGHT INTERCEPTION BY HETEROGENEOUS CANOPY

---



*The sun is new each day.*

Heraclitus

Radiation is fundamental in forest ecology. Besides being the main variable explaining regeneration growth ([Chapter 3](#)), radiation drives plant photosynthesis and exchanges of mass and energy between soil, vegetation, and the atmosphere. As a consequence, the amount of energy and the spectrum of the radiation that is intercepted by trees have been widely studied, as it greatly affects the gross primary production of forests ([Duursma and Mäkelä, 2007](#); [Tian et al., 2010](#)), forest dynamics and competition between species ([Pacala et al., 1996](#)), individual tree growth ([Lieffers et al., 1999](#); [Balandier et al., 2007](#)), and tree morphogenesis ([Balandier et al., 2006a](#); [Galen et al., 2007](#); [Niinemets, 2010](#)).

Measuring the amount of radiation, and photosynthetically active radiation (PAR) in particular, which is intercepted by the diverse components of a forest canopy, is tedious and time-consuming. Compared with PAR measurements in agricultural crops, and due to the complexity of multilayered forest canopy, the spatial and temporal variability of transmitted light beneath the forest canopy is substantial. Vegetation beneath a closed canopy indeed benefits from sunflecks or very brief increases in transmitted irradiance ([Messier et al., 1999](#)). Measurements must then be repeated at numerous points and for rather long periods of time to capture this variability. Moreover, measuring transmitted PAR at various canopy heights is almost impossible without installing a crane ([Mariscal et al., 2004](#)). Faced with these difficulties and given the cost of such measurements, modeling radiative transfer

appears essential for supplementing field measurements and for a greater understanding of how radiation is partitioned among the components of forest ecosystems.

To explore how light regimes under complex canopies can be manipulated with silvicultural practices that could maintain the coexistence of species with contrasting shade tolerances (Chapter 5), the modeling approaches that have been proposed in the literature are firstly synthesized and discussed (Section 4.1). Second, one of these approaches was implemented to explore understory light conditions regarding forest structure and composition in uneven-aged mixed stands (Section 4.2).

#### 4.1 LITERATURE REVIEW

Solar radiation and the attenuation of light through plant canopy were first modeled with physical laws by analogy of the Beer's law in homogeneous medium. Consequently, they were firstly limited to homogeneous crops but were rapidly adapted to forest ecosystems using more complex laws. The general functioning of these latter models have already been presented in several literature reviews (Sinoquet et al., 1993; Brunner, 1998; Lieffers et al., 1999) and have changed little since then. Briefly, they share a common structure that can be divided into three submodels (Figure 4.1). Firstly, most models start by computing above canopy light both in magnitude and angular distribution using standard astronomical laws ("above canopy light model"). Secondly, the interception of light through the canopy ("radiative transfer model") is computed. It depends mainly upon the geometric structure of the canopy and the mathematical formulation used to describe the fractions of light that are intercepted, absorbed, and transmitted by canopy components. Thirdly, a light reflection model can optionally be used ("scattering model") to describe more precisely complex light trajectories within the canopy.

Even though most forest radiative transfer models (FRTMs) share a common general framework, they have special features that rely on different assumptions and they are used to predict different output variables aggregated or not in time and space according to the objectives of the model. The costs of specific field measurements to calibrate the model, the increasing interest in complex forests composed of trees of different species and sizes, and the variety of study purposes have indeed stimulated modelers to adapt FRTMs to their needs. Most of these adaptations concerned the radiative transfer model, one of the submodels depicted in Figure 4.1, which is the main topic of this review. For example, contrasted approaches have been used to model the distribution of foliage within the canopy. Some authors have used very detailed three-dimensional (3D) mock-ups of the canopy, which require intensive field measurements, whereas others describe the canopy as a single horizontal layer. The improvements brought to above canopy light models are very limited as only two standard algorithms (uniform overcast sky or standard overcast sky) have been used among all of the papers that we reviewed. Moreover, the use of one of them does not really affect model perfor-

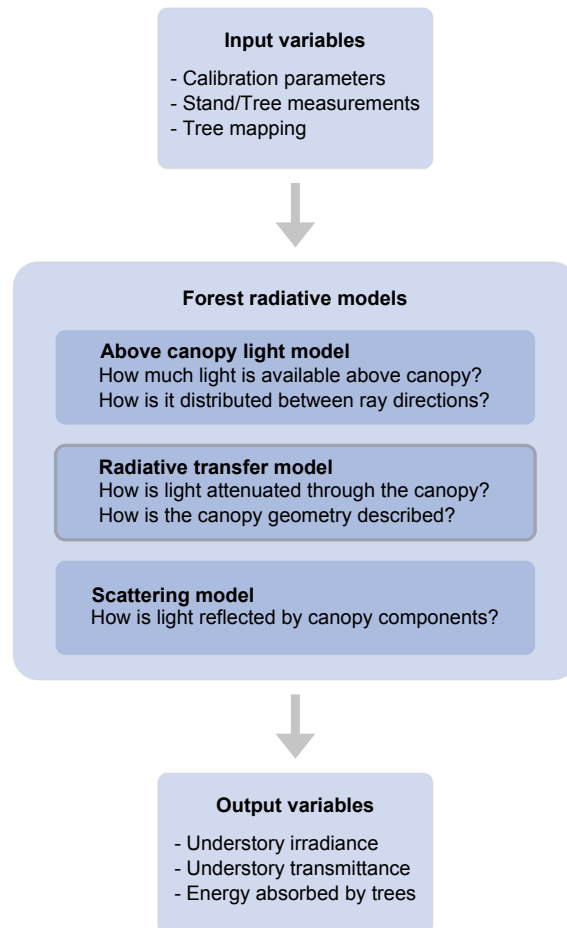


Figure 4.1: Chart flow of forest radiative models indicating the three submodels.

mance (Brunner, 1998), i.e., model ability to predict the measurements with a low level of error and bias. Similarly, the improvements brought to the scattering model affect model performance less than the improvements brought to FRTMs. Scattering depends upon the optical properties of leaves, wood and soil, and the considered radiation wavelength. Radiation scattering is especially low in PAR and in ultraviolet radiation (400–700 nm) (Sinoquet et al., 1993; Parker, 1997). The reflectivity of a green leaf is approximately 0.2 and this value is even lower for an entire crown because of multiple scattering (Brunner, 1998; Landsberg and Sands, 2010). Moreover, scattering models require large numbers of parameters (Kuusk, 1993) and much computation time (Ross, 1981; Rey et al., 2008). Consequently, the use of a scattering model has often been neglected in forestry assuming that leaves and ground behave like black bodies within the PAR waveband (i.e., showing no transmittance and no reflectance) (Sinoquet et al., 1993) even though it might improve the precision of the prediction of transmitted irradiance (Mariscal et al., 2004).

Given the variety of applications and newly developed modeling approaches of FRTMs, it would be of great help for modelers to know which approach enables them to predict the variable of their interest with a given precision, a low bias, and accepted calibration efforts. Moreover, having insight of the expected precision and bias associated with a modeling approach is also precious information in assessing whether it would fulfill the study objectives. Similarly, knowing beforehand to which parameters the models are most sensitive and the order of magnitude of parameter values can speed up and improve the calibration work. This would allow for effort to be invested in estimating precisely the sensitive parameters and using simplification assumptions for the less sensitive parameters.

Unfortunately, as far as forests are concerned, the performance analyses and the sensitivity analysis of different modeling approaches have been reported separately and for very restricted sets of canopy conditions and study objectives. The information is therefore scattered and no general guideline has been formulated to help forest modelers to choose which modeling approach suits best his needs.

We synthesized both the performance analyzes and the sensitivity analyzes of radiation transfer models through forest canopies. After classifying these approaches, we attempted to quantify the expected uncertainty and appraise the calibration efforts associated with most combinations of modeling approaches and model applications. We provided order of magnitude estimates for the main calibration parameters and attempted to report how sensitive models are to these parameters. Finally, we attempted to identify the modeling approaches that best suit to the different applications of FRTMs.

#### 4.1.1 *Classification of FRTMs*

We identified four families of FRTMs that combine three approaches to describe the geometry of forest canopy and two approaches to compute the



proportion of incident radiation intercepted by the canopy (Table 4.1). Below, we briefly describe and discuss each of these approaches; details can be found in previous articles (Sinoquet et al., 1993; Cescatti, 1997a; Brunner, 1998; Lieffers et al., 1999).

#### 4.1.1.1 *Canopy geometry*

**ONE-DIMENSIONAL CANOPY** The simplest approach for modeling the geometry of a forest canopy is to assimilate it to a single horizontal layer of vegetation without individualizing crowns or trees (one-dimensional (1D) model). Due to its simplicity, this approach is particularly appropriate modeling a homogeneous canopy such as the one of pure even-aged stands. This approach is more challenging with heterogeneous stands as additional assumptions and parameters are required (Duursma and Mäkelä, 2007; Kim et al., 2011) to offset the simplicity of the canopy description.

The model developed by Kim et al. (2011) illustrates well this approach. This model requires calibrating for each species three extinction coefficients (corresponding to the distribution of inclination angles of leaves, branches and stems), the one-sided area of leaves, branches and stems, the horizontal crown projection and tree density. Some of these parameters might also depend upon ray directions (i.e., ray zenith angle and ray azimuthal angle). Furthermore, the model assumes that branches and stems are randomly distributed, whereas the distribution of leaves depends upon a clumping factor. Simpler approaches with fewer variables and empirical parameters have been developed. For instance, Duursma and Mäkelä (2007) used a 1D model with four variables (leaf area, crown surface area, number of trees and extinction coefficient) and one empirical parameter.

Another solution to modeling the distribution of leaves consist of subdividing the canopy into several homogeneous regions, e.g., horizontal layers, on the condition that the vertical structure of the stand can be approximated. Such as multilayer models can then predict understory light at different canopy heights.

Moreover, due to the main hypothesis of considering continuous layer(s) of vegetation with the same properties for the whole forest stand we did not expect the 1D model to predict accurately the spatial variation of irradiance beneath the canopy. The 1D model is rather utilized to predict the temporal variation of irradiance (Kim et al., 2011; Govind et al., 2013).

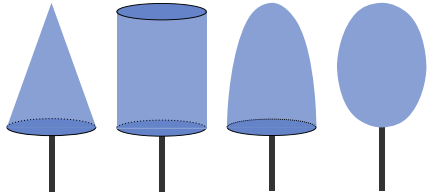
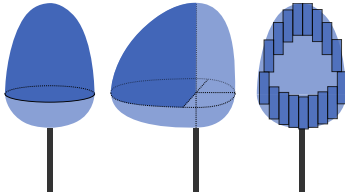
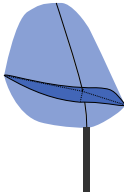
**3D CROWN MODELS** Alternatively, 3D crown models (see 3D-TM and 3D-PE in Table 4.1) assimilate forest stands into a set of spatialized geometric shapes representing tree crowns and, optionally, trunks. Many different geometric shapes have been used (Table 4.2). The simplest are quadratic surfaces such as cylinder, cone, ellipsoid or paraboloid. Such shapes have the advantages of requiring few parameters and allowing analytical computation of the interceptions between light rays and crowns. In contrast, nonquadratic shapes (e.g., combinations of degenerated surfaces) fit well to real crowns but require numerous parameters and more complex numerical computations.

Table 4.1: Classification of FRTM modeling approaches.

FRTM FAMILY	ABBREVIATION	CANOPY	TRANSMITTANCE	MAIN OBJECTIVES
1D model	1D	Stand canopy is composed of one or several horizontal layers	Turbid medium	Ecophysiological processes at stand level
3D crown model with turbid medium	3D-TM	Tree crowns are composed of one or a set of geometric shapes	Turbid medium	Forest growth and yield; Dynamics of stand structure
3D crown model with porous envelope	3D-PE	Tree crowns are composed of one or a set of geometric shapes	Porous envelope	Forest growth and yield; Dynamics of stand structure
3D surface model	3D-S	Trees are composed of surfaces representing the leaves, branches and stems	Porous envelope or radiative transfer theory	Tree architecture; ecophysiological processes at tree level

**Note** : FRTM, forest radiative transfer model; 1D, one-dimensional; 3D, three-dimensional.

Table 4.2: Examples of 3D-geometric crown models used in FRTMs. Most authors used relatively simple quadratic shapes whereas few tested more complicated shapes.

	QUADRATIC SHAPES	COMBINATION OF QUADRATIC SHAPES	COMBINATION OF NONQUADRATIC SHAPES
			
No. of parameters	3	$\geq 4$	8-18
References	<p>Pukkala et al. (1993); Canham et al. (1994); Koop and Sterck (1994); Bartelink (1998b); Stadt and Loeffers (2000); Pinno et al. (2001); Beaudet et al. (2002); Courbaud et al. (2003); Mariscal et al. (2004); Beaudet et al. (2011); Paquette et al. (2008)</p>	<p>Gersonde et al. (2004)</p>	<p>Cescatti (1997a); Brunner (1998); Piboule (2001); Groot (2004); Piboule et al. (2005); Da Silva et al. (2011)</p>

Many refinements to 3D crown models have been described in the literature, and have been notably reviewed by Brunner (1998). For example, crowns can be divided into different sections characterized by different leaf densities. A combination of several shapes can be used to distinguish an illuminated surface (e.g., upper half ellipsoid) from a shaded surface. Similarly, a special foliage envelope can be constructed within a crown, for example with branches that have developed during the last 5 years. Missing parameters are often estimated using allometric relationships to diameter at breast height (Da Silva et al., 2011) or relationships to species shade tolerance (Canham et al., 1999; Beaudet et al., 2011). Algorithms of crown reconstruction according to neighbor competition are also available (Piboule et al., 2005).

In brief, the recent improvements brought to 3D crown models attempted to model crown geometry as realistically as possible taking into account that trees often lean and crown shapes often deviate from simple geometric forms. Hence, they required adjusting a greater set of parameters, and some of them can hardly be measured in the field and must be estimated with additional models.

Moreover, on one hand, the 3D crown model requires determining the position and crown dimensions of every tree whereas the 1D model requires only estimating stand features. On the other hand, measuring crown dimensions is easier and more commonly performed than estimating foliage aggregation within the stand canopy. Additionally, taking explicitly into account stand heterogeneity, 3D crown models can predict the spatial variability of transmitted light.

**3D SURFACE MODELS** 3D surface models (3D-S) represent leaves, branches and stems as realistically as possible with surfaces or shells. This leads to very detailed 3D mock-ups (Figure 4.2) with components that are usually assimilated into opaque envelopes (Section 4.1.1.2). Due to the number of input parameters for these models, they are used to represent single trees (Sinoquet et al., 2001), orchard trees (Da Silva et al., 2008), or agroforestry systems (Dauzat and Eroy, 1997; Leroy et al., 2009) rather than entire forest stands. Homogeneous forest stands could be obtained by replicating one or a few model trees (Figure 4.2), but it seems unlikely to be able to gather all the necessary information to model every single tree of one heterogeneous stand. Hence, we believe that the use of 3D-S models in forestry is nowadays limited to applications involving tree architecture and ecophysiological processes.

#### 4.1.1.2 Radiation attenuation

**TURBID MEDIUM** The first approach to computing the fraction of transmitted light through the canopy ( $\tau$ ) consists of using an analogy to Beer's law. 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). Canopy is assimilated to such a turbid medium and  $\tau$  is computed as a function of

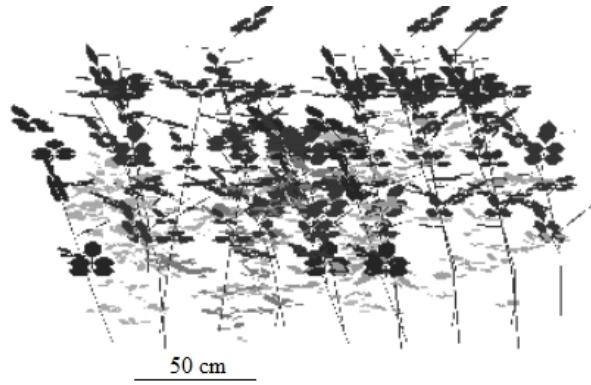


Figure 4.2: 3D plant mock-up. Lateral view of a digitalized scene with six 3- to 4-year-old beech seedlings (in grey), scattered every 50 cm from each other together with a systematic network of raspberry (in black) (Balandier et al., 2009).

the density and the spatial distribution of canopy elements such as leaves and branches (Sinoquet et al., 1993; Lieffers et al., 1999). The turbid medium analogy can be applied to an entire stand canopy, a horizontal layer within a stand canopy, a crown envelope, or even a section of a crown. This approach relies on the assumption that canopies have the properties of such a homogeneous medium. Nevertheless, stand canopies or tree crowns are made up of various size elements often aggregated within crowns and vertices. Therefore, several correction coefficients have been developed to adapt Beer's law to forest canopies. Briefly, the probability of beam interception ( $1 - \tau$ ) by canopy elements is a function of the canopy element density (leaf area density, LAD ( $\text{m}^2 \text{m}^{-3}$ ), the path length of a ray through the canopy ( $l$ ), the extinction coefficient ( $k$ ) and the clumping factor ( $\Omega$ ).  $k$  and  $\Omega$  depend upon canopy element inclination and spatial distribution, respectively (Equation 4.1).  $\Omega$  describes the aggregative pattern of branches and leaves within the canopy. Many different mathematical expressions have been used to adapt the Beer's law models to 1D and 3D models, but all somehow include these three parameters. Equation 4.1 is commonly used to compute  $\tau$ , for a ray of zenith angle  $\eta$  and azimuthal angle  $\gamma$ , with 3D crown models.

$$\tau(\eta, \gamma) = \exp(-k \cdot \Omega \cdot \text{LAD} \cdot l(\eta, \gamma)) \quad (4.1)$$

The advantage of the turbid medium approach lies mainly in its mechanistic formulation and the use of the leaf area because leaf area is a key variable in forest ecology (e.g., used to model photosynthesis and transpiration). However, this approach often requires empirical estimation of  $k$  and  $\Omega$ , and leaf area measurements that remain both difficult to obtain and imprecise (Breda, 2003). Moreover, this is the only approach that applies if the canopy geometry is described with a 1D model.

**POROUS ENVELOPE** The second approach, called porous envelope, assumes that crowns or parts of crown are envelopes with one empirically

estimated parameter, namely the crown openness ( $p$ , Equation 4.2), which is the probability of a ray being intercepted by the foliage. This approach assumes that leaves do not transmit or reflect light (like black bodies). This assumption can be more easily verified for coniferous species with dark foliage than for broadleaved species with lighter foliage (Williams, 1991). Therefore, some authors have adjusted Equation 4.2 for the different radiation wavelength ranges (Goudriaan, 1977). The variable  $p$  is independent of ray direction and path length ( $l$ ) (Canham et al., 1994; Groot, 2004; Da Silva et al., 2008; Boivin et al., 2011) and is also defined as the fraction of sky visible through a crown (Canham et al., 1999).

$$\tau(\eta, \gamma) = p \quad (4.2)$$

In comparison with the previous approach, this one is less mechanistic but requires fewer parameters (usually one per species) and is therefore easier to calibrate. On the other hand, this approach describes the attenuation of radiation through crowns and not through stand canopy. Therefore it cannot be utilized with a 1D model.

Other simplifications of these submodels have also been proposed. For example, Koop and Sterck (1994) used an opaque crown model ( $p = 0$ ). Other authors have simplified the turbid medium submodel by removing  $l$ ,  $\Omega$  and LAD from Equation 4.1. In this way, they obtained a “hit model” with a formulation (Equation 4.3) very close to Equation 4.2 with one empirical parameter,  $k$ , which they called the extinction coefficient (Canham et al., 1994; Koop and Sterck, 1994; Boivin et al., 2011).

$$\tau(\eta, \gamma) = \exp(-k) \quad (4.3)$$

#### 4.1.2 Input variables

Different input data and calibration parameters are required depending upon the chosen modeling approach. These parameters are measured, estimated or adjusted by model inversion. Below, we give an overview of model requirements in terms of input data and summarize their definitions and estimation methods.

##### 4.1.2.1 Stand and tree measurements

Among all FRTM inputs, stand and tree measurements probably require the most workforce and consequently represent one of the major cost in utilizing FRTM. As far as stand and tree measurements are concerned 1D models obviously require less field data than 3D models and, hence, require less field work. 1D models depend mainly upon foliage density and distribution (see Section 4.1.2.2, Section 4.1.2.3 and Section 4.1.2.4) which does not require carrying out intensive tree inventory. In most cases, measuring stand density is enough. However, 3D models often rely on an intensive inventory and

mapping of every tree within a plot. For 3D crown models, at least three parameters are generally needed for each tree: height, crown base height and crown radius (Table 4.2). Additional measurements such as crown radii measured in different directions, height of maximum crown extension, and shape coefficients might be required to construct more complex shapes. For 3D surface models, a geometric description of leaves, branches, and stems can be obtained by vectorization (Fournier et al., 1996), digitalization (Mouliia and Sinoquet, 1993), or simulations of plant morphology (Leroy et al., 2009).

#### 4.1.2.2 *Density of canopy elements*

The stand leaf area index (LAI,  $\text{m}^2 \text{m}^{-2}$ ) is the total one-sided foliage area per unit of soil surface. LAI is the primary descriptor of plant canopy and a key variable in studying plant physiological processes (e.g., photosynthesis, transpiration). In the field, stand LAI is directly assessed with litterfall traps or vertical line intercept sampling coupled with measures of leaf inclination. LAI can also be estimated indirectly with optical methods, mainly using hemispherical photographs or LAI-2000 devices (LI-COR Biosciences, Lincoln, Nebraska, USA) (Jonckheere et al., 2004; Weiss et al., 2004). These last two methods measure the gap fraction (i.e., the fraction of sky visible from the measuring point) and use the turbid medium analogy to infer leaf area. Optical approaches therefore rely on the same assumptions and parameters as Equation 4.1. Moreover, such methods give estimates of the effective LAI, which includes the area of branches and trunks (Jonckheere et al., 2004). Additionally, reference values and allometric relationships are available in the literature for the most common species.

Measurements of leaf area for individual trees are very difficult to replicate for every tree in a stand, even though individual values of leaf area are necessary with 3D-TM. Therefore, tree leaf area is often estimated for each species by the inversion of a turbid medium model (Courbaud et al., 2003) or by measuring leaf area density (LAD,  $\text{m}^2 \text{m}^{-3}$ ) on a sample of trees (Stadt and Lieffers, 2000). Nevertheless, as indicated by Nock et al. (2008), intracrown leaf area decreases with tree age by up to 40 %. It might therefore be preferred to use allometric relationships with, for example, tree diameter (Bartelink, 1998a; Gersonde et al., 2004), tree height (Essery et al., 2008), sapwood area (Gersonde et al., 2004), or tapering equations (Kim et al., 2011).

Moreover, LAI is often used with a 1D model, whereas LAD is usually preferred with 3D crown models. LAD corresponds to the one-sided leaf area divided by the canopy element modeled volume (Gersonde et al., 2004). The reported values of LAD used with 3D-TM models range from  $0.3 \text{ m}^2 \text{m}^{-3}$  to  $6 \text{ m}^2 \text{m}^{-3}$  (Table 4.3). This variation is therefore substantial even for the same species. This encourages improving and harmonizing the methods used to estimate LAD.

Some simplifications used to estimate foliage density might appear rough to some readers but they reflect well the difficulty of measuring it; due to tree size and heterogeneity, its measure in forests is much more challenging than in crops or orchards.

Table 4.3: Reported values of leaf area density (LAD,  $\text{m}^2 \text{m}^{-2}$ ) used in 3D crown models with the turbid medium analogy (3D-TM)

SPECIES	LAD	REFERENCES
not specified	1.86	Kuuluvainen and Pukkala (1991)
SOFTWOOD		
<i>Pinus ponderosa</i>	0.03-0.36	Law et al. (2001)
<i>Tsuga heterophylla</i>	0.38	Mariscal et al. (2004)
<i>Pseudotsuga menziesii</i>	0.38; 0.96; 2.74; 6.00	Webb and Unga (1993); Brunner (1998); Gersonde et al. (2004); Mariscal et al. (2004)
<i>Picea abies</i>	0.40	Courbaud et al. (2003)
<i>Pinus contorta</i>	1.39	Stadt and Lieffers (2000)
<i>Picea glauca</i>	1.80-1.88	Stadt and Lieffers (2000)
<i>Abies balsamea</i>	1.98	Stadt and Lieffers (2000)
not specified	2.00	Sprugel et al. (2009)
<i>Pinus ponderosa</i>	2.01	Gersonde et al. (2004)
<i>Pinus lambertiana</i>	2.56	Gersonde et al. (2004)
<i>Abies concolor</i>	3.36	Gersonde et al. (2004)
<i>Calocedrus sp.</i>	4.51	Gersonde et al. (2004)
HARDWOOD		
<i>Populus balsamifera</i>	0.30	Stadt and Lieffers (2000)
<i>Populus tremuloides</i>	0.44	Stadt and Lieffers (2000)
<i>Fagus sylvatica</i>	0.66	Piboule (2001)
not specified	0.50-1.00	Sprugel et al. (2009)
<i>Betula pendula</i>	0.79	Piboule (2001)
<i>Betula papyrifera</i>	0.80	Stadt and Lieffers (2000)
<i>Quercus kelloggii</i>	1.32	Gersonde et al. (2004)

#### 4.1.2.3 Extinction coefficients

The extinction coefficient,  $k$ , is a parameter of Equation 4.1 and is therefore used whenever the radiation attenuation submodel corresponds to the turbid medium approach. It is usually a species-specific constant but it can also be computed as a function (the “G-function”), which depends mainly upon the orientation and inclination of leaves as well as on the ray zenith angle ( $\eta$ ). The parameter  $k$  has been estimated by measuring leaf inclination and projected leaf areas (Campbell and Norman, 1998; Kim et al., 2011), computed with theoretical functions of leaf distribution (Govind et al., 2013) or deduced from the relationship between transmittance and LAI measured at different canopy heights (Landsberg and Sands, 2010).

With 3D crown models, most authors assume that leaf inclination follows a theoretical distribution that is either spherical with  $k = 0.5$  (Cescatti, 1997a; Brunner, 1998; Piboule, 2001; Courbaud et al., 2003) or ellipsoidal (Stadt and



Lieffers, 2000). With 1D models, authors have sometimes preferred using empirical estimates of  $k$  ranging between 0.2 and 0.6 (Jarvis and Leverenz, 1983; Pierce and Running, 1988; Bartelink, 1998b; Aubin et al., 2000).

#### 4.1.2.4 *Clumping factors*

The assumption of the random spatial distribution of canopy elements is rarely satisfied (Sinoquet et al., 2005; Da Silva et al., 2008), especially with 1D models, because the spatial distribution of trees, but also of canopy elements within trees, is rarely completely random. Moreover, leaves are gathered around branches, and branches are grouped around stems and sometimes grouped in vertices. Whenever the spatial distribution of canopy elements is not known or approximated (e.g., stand map, tree architecture), a clumping factor,  $\Omega$ , is required in Equation 4.1. Indeed, a canopy with regularly spaced elements ( $\Omega > 1$ ) transmits less light than a canopy with randomly scattered elements ( $\Omega = 1$ ). By contrast, a canopy with aggregated elements transmits much more light ( $\Omega < 1$ ) (Niinemets, 2010).

There is a lack of reference values for the clumping factor and this measurement is therefore often estimated by model inversion. Like the extinction coefficient, the clumping factor is rarely measured because measuring it for adult trees is very labor intensive. Consequently, it is often assumed to be constant. With 1D models, Chen et al. (1999) used values of the clumping factor of 0.5 and 0.7 for softwoods and hardwoods, respectively. These values were computed by measuring the canopy gap size distribution (Chen et al., 1997). Kim et al. (2011) estimated the clumping factor by harvesting pine shoots. They observed that the clumping factor varied between 0.2 (upper part of the canopy) and 0.9 (lower part of the canopy), while other studies reported values for long-needled species ranging between 0.4 and 0.9 (Th  r  zien et al., 2007). In addition, some studies have demonstrated a variation in the clumping factor with stand density, crown diameter and ray zenith angle (Wang and Jarvis, 1990; Govind et al., 2013). Because tree aggregation is already taken into account with 3D crown models, the clumping factor in these models is usually assumed to be 1.

#### 4.1.2.5 *Crown openness*

Crown openness ( $p$ ) can be assessed by photographing isolated crowns (Canham et al., 1994, 1999; Beaudet and Messier, 2002; Astrup and Larson, 2006; Paquette et al., 2008; Beaudet et al., 2011; Da Silva et al., 2011) or by model inversion (Groot, 2004). Photographs can be taken using either fish-eye lens (Canham et al., 1994, 1999; Beaudet and Messier, 2002; Astrup and Larson, 2006; Beaudet et al., 2011) or classic lens (Da Silva et al., 2011). In comparison with fish-eye lenses, classic lenses allow smaller isolated parts of the crown to be photographed. Therefore, the use of a classic lens makes it easier to obtain a correct exposure even when sky conditions are not overcast. Subject crowns need to be isolated with no overlapping neighboring crowns. Photographs are processed to compute the proportion of sky pixels (i.e., the

crown openness). [Boivin et al. \(2011\)](#) presented an algorithm that identifies the crown extent and argued that crown delimitation has a strong influence on porosity estimates. [Canham et al. \(1994\)](#) observed no variation in  $p$  with zenith angle and tree dimensions. However, [Astrup and Larson \(2006\)](#) observed that  $p$  varied, to a limited extent, in spruce stands with tree diameter and by regions. Similar to the estimates of LAD, standard methods are required to uniformly estimate  $p$  taking into account the variability among species and individuals.

Crown openness ( $p$ ) and LAD are two related parameters. Indeed, [Da Silva et al. \(2011\)](#) bridged the two approaches proposing a method to compute  $k \cdot \text{LAD}$  from  $p$ . The two approaches of modeling light attenuation through canopy, namely the turbid medium and porous envelope approaches, can therefore be calibrated with field measurements of  $p$ . Even though it applied only to isolated trees, the measurement of  $p$  is more convenient and less laborious than the measurement of LAD. Moreover, the reported variability of  $p$  seems lower than that of LAD with values ranging from 0.03 to 0.29 and, an average around 0.1 ([Table 4.4](#)).

#### 4.1.3 *Model applications and output variables*

Because FRTMs are most often used to model forest ecosystem functioning, they are usually coupled with many other models describing, for example, photosynthesis, transpiration, tree growth, timber production, carbon sequestration, nutrient uptake, or hydrological balance. The applications of FRTMs are therefore numerous but they can be seen, for the sake of simplicity, as either ecophysiological applications or stand-dynamics applications.

**ECOPHYSIOLOGICAL APPLICATIONS** Ecophysiological studies uses FRTMs coupled mainly with process-based models that embody our current knowledge of the functioning of forest ecosystem. Such holistic models include, for instance, equations describing the fluxes of carbon, water, and energy between soil, vegetation, and atmosphere ([Govind et al., 2013](#)). Such studies aim at improving our understanding of forest ecosystem functioning, exploring forest productivity as a function of resource availability, or at exploring how variation of forest structure and composition can affect ecosystem functioning and dynamics. Forest productivity, standing forest biomass, nutrient uptake or hydrological balance as examples can then be predicted for particular environmental conditions and for forecasted modifications of these. Within this context, FRTMs are necessary to predict the irradiance ( $\text{W m}^{-2}$ ) and (or) the spectrum of the intercepted radiation at various scales, from a global scale to a leaf scale.

**STAND-DYNAMICS APPLICATIONS** The second group of studies preferentially uses empirical models. They bring less concerns on ecosystem functioning and focus rather on the dendrometric data of interest for forest managers. They aim mainly at predicting the natural evolution of stand

Table 4.4: Reported values of crown openness used with 3D crown models (3D-PE).

SPECIES	CROWN OPENNESS	REFERENCES
SOFTWOOD		
<i>Abies alba</i>	0.034	Da Silva et al. (2011)
<i>Abies amabilis</i>	0.060	Canham et al. (1999)
<i>Tsuga heterophylla</i>	0.080	Canham et al. (1999)
<i>Pinus sylvestris</i>	0.065 - 0.110	Da Silva et al. (2011)
<i>Abies lasiocarpa</i>	0.090	Canham et al. (1999)
<i>Thuja plicata</i>	0.090	Canham et al. (1999)
<i>Picea glauca</i>	0.109; 0.110; 0.130	Canham et al. (1999); Astrup and Larson (2006); Beaudet et al. (2011)
<i>Abies balsamea</i>	0.111	Beaudet et al. (2011)
<i>Pinus banksiana</i>	0.124	Beaudet et al. (2011)
<i>Pinus contorta</i>	0.135	Canham et al. (1999)
<i>Thuja occidentalis</i>	0.144	Beaudet et al. (2011)
<i>Picea mariana</i>	0.070 - 0.290	Groot (2004)
HARDWOOD		
<i>Fagus sylvatica</i>	0.048	Da Silva et al. (2011)
<i>Fagus grandifolia</i>	0.050	Beaudet et al. (2002)
<i>Malus sylvestris</i>	0.052	Da Silva et al. (2011)
<i>Quercus petraea</i>	0.043 - 0.073	Da Silva et al. (2011)
<i>Betula papyrifera</i>	0.058	Canham et al. (1999)
<i>Populus tremula</i>	0.082	Da Silva et al. (2011)
<i>Sorbus torminalis</i>	0.049 - 0.120	Da Silva et al. (2011)
<i>Betula alleghaniensis</i>	0.097	(Beaudet et al., 2002)
<i>Betula papyrifera</i>	0.101	Beaudet et al. (2011)
<i>Acer saccharum</i>	0.108	Beaudet et al. (2002)
<i>Populus balsamifera</i>	0.140	Canham et al. (1999)
<i>Populus tremuloides</i>	0.163; 0.183	Astrup and Larson (2006); Beaudet et al. (2011)
<i>Betula alleghaniensis</i>	0.206	Canham et al. (1999)
<i>Populus hybrid</i>	0.300	Paquette et al. (2008)

structure and composition and (or) predicting the effect of overstory management on understory light conditions (Courbaud et al., 2001; Beaudet et al., 2002; Sprugel et al., 2009; Beaudet et al., 2011). Also, their objective is the best possible prediction of forest growth and the outcome of intra and inter specific competition. Such models can more precisely predict forest dynamics but, contrary to process-based models, their uses are more strictly limited to the conditions from where they were derived. On the other hand, using empirical models of tree growth allows focusing on light availability without calibrating and programming all of the physiological processes in relation to tree growth. This simplification has often been justified whenever light can be considered as the first limiting factor of vegetation growth (e.g., tree regeneration under closed canopy). Within this context, FRTMs are needed to predict tree irradiance, i.e., the amount of energy absorbed by trees (Courbaud et al., 2003), the proportion of radiation transmitted (transmittance) to the regeneration (Pacala et al., 1996; Lieffers et al., 1999; Beaudet et al., 2002; Sprugel et al., 2009; Beaudet et al., 2011), the amount of light available for understory biodiversity (Balandier et al., 2006a; Barbier et al., 2008), or the vertical gradient of transmittance within the canopy (Gersonde et al., 2004; Mariscal et al., 2004). They are used mostly at plot or stand scales (from 100 m<sup>2</sup> to 1 ha) with a simulated period of at least 1 year.

#### 4.1.4 Model evaluation

Most authors evaluate their model by comparing estimates and measurements of irradiance or transmittance taking into account either total incident light or only the incident diffuse light (e.g., indirect site factor). Light measurements are performed usually with hemispherical photographs and less frequently with light sensors. Hemispherical photography is an indirect method with an associated level of error that can occasionally be substantial. Moreover, this approach uses a radiative model to assess irradiance and transmittance. Using hemispherical photography to evaluate FRTMs therefore leads to a comparative evaluation of one radiative model with another. In addition, FRTMs have been evaluated for their performance in predicting irradiance or transmittance at the ground level, above the understory vegetation, or, occasionally, at different heights within a tree canopy (Mariscal et al., 2004; Kim et al., 2011). In the present study, we compiled published information on the performance of different models, i.e., their ability to predict the measurements with low levels of error and bias. We considered all published light models that were used to predict radiative transfer through forest canopies and for which the performance was evaluated. In Table 4.5, we summarized the reported performance of these models. Unfortunately, authors have used different approaches to assess model performance, making comparison difficult. They often adjusted linear models between estimates and observations and hence assessed model precision using the coefficient of determination ( $R^2$ ) or the root mean square error (RMSE). Model bias was usually examined graphically but some authors have used the coefficients of

the linear regression between measurements and estimates. Moreover, even similar indicators (e.g.,  $R^2$ ) could not be compared without caution. While most authors compared estimates and measurements carried out at different periods (Kim et al., 2011; Govind et al., 2013) or at different positions within plots, others compared average estimates and measurements between sites of areas ranging from 900 m<sup>2</sup> to 1600 m<sup>2</sup> (Stadt and Lieffers, 2000) or the average gap profile (Mariscal et al., 2004). In addition, others compared the statistical distribution of transmittance estimates and measurements (Da Silva et al., 2011). Finally, the numbers of plots and sites were also far from constant among model evaluations.

Most authors found good agreement between measurements and estimates when averaged at the stand scale (Stadt and Lieffers, 2000; Mariscal et al., 2004). In other words, most models predicted transmitted light poorly at a particular location (at sensor scale) beneath the canopy but rather well at the stand scale. After a good calibration, the relationship between measurements and predictions was found to be generally close to a 1:1 relationship and, hence, without unacceptable bias in the point-to-point comparison. Nevertheless, large deviations were often observed between estimates and measurements of transmittance (often up to 20 % of above canopy light) even for low-light levels. Many authors argued that point-to-point variations beneath the forest canopy are rarely predicted with accuracy because minor errors in tree position and crown dimensions can lead to dramatic changes in simulations of transmittance (Fournier et al., 1996; Groot, 2004; Mariscal et al., 2004; Da Silva et al., 2011). On the other hand, site averages were better predicted (Stadt and Lieffers, 2000; Pinno et al., 2001; Mariscal et al., 2004; Da Silva et al., 2011). Similarly, model performance increased with the length of the simulated period (e.g., 1 year versus 1 hour) especially when direct radiation were taken into account (Brunner, 1998; Groot, 2004).

All of the different modeling approaches were reported to perform well but few authors compared the different approaches. Kim et al. (2011) found that their 1D model performed as well as 3D crown models when they took into account the aggregation of trees, leaves and branches with appropriate clumping factors. Similarly, Balandier et al. (2009) obtained very similar results with a 1D model and a 3D surface model in a mixed understory of European beech (*Fagus sylvatica* L.) and European red raspberry (*Rubus idaeus* L.) (Figure 4.2). 3D-TM (e.g., MIXLIGHT) and 3D-PE (e.g., SORTIE-ND) appeared to exhibit a very similar performance, although Canham et al. (1994) found that a hit model (i.e., 3D-PE with  $p = 0$ ) performed better than a 3D-TM. These authors interpreted this result as an effect of foliage scattering at the crown periphery, especially for shade intolerant species. Boivin et al. (2011) used a 3D-PE model and obtained good results in plantations of hybrid poplars, with  $p = 0$ , whereas in the same study, this parameter value provided the worst results in young boreal mixedwoods.

Nevertheless, we noted that the relative performance depended upon the modeled description of canopy geometry (Table 4.5). The highest levels

of model performance were obtained with very detailed 3D-TM models (Cescatti, 1997b; Brunner, 1998). These models used asymmetric crowns described by a combination of nonquadratic shapes and modeled the radiative transfer using a turbid medium approach with  $k = 0.5$  and  $\Omega = 1$ . In addition, Brunner (1998) restricted the foliage to shells within the crown but acknowledged that simplification of his canopy model would have altered the results only slightly. Moreover, he restricted his sample to a single even-aged coniferous stand with a large gradient of transmittance, which made model calibration and validation easier. The model of Cescatti (1997b) differed from the model developed by Brunner (1998) in its inclusion of an algorithm for scattering processes.

Additionally, model performance appears to be related to forest structure (Table 4.5). Model performance decreases from even-aged young stands to multilayered and mixed mature stands. This observation is well supported by pairs of publications in which the same model has been applied to different forest structures. For instance, the model FOREST was shown to provide excellent results in an 80-year-old spruce stand in Finland (Cescatti, 1997b), whereas it provided only moderate results in a multilayered forest of ponderosa pine in Oregon (Law et al., 2001). Similarly, using the model tRAYci, Brunner (1998) successfully predicted the spatial distribution of the transmittance under a 20-year-old stand of Douglas fir, whereas Gersonde et al. (2004) obtained a lower model performance under a mixed conifer forest. MIXLIGHT successfully predicted point-to-point variation in transmittance under aspen-dominated stands aged from 1 to 30 years (Pinno et al., 2001), but it was less successful in predicting the average values of transmittance in various even-aged boreal stands aged from 69 to 159 years (Stadt and Lieffers, 2000). Finally, Boivin et al. (2011) observed the same trend between young boreal forests and hybrid poplar plantations, and Koop and Sterck (1994) found that including measurement points located close to small trees reduced the  $R^2$  from 94 % to 77 %.

#### 4.1.5 Model sensitivity

We attempted to identify which model parameter was reported to have strong effect on FRTM performance. As many studies actually lack a common referenced method, we classified the studied parameters into three qualitative levels according to their impact on FRTM predictions: high, medium, and low. This classification was based mainly on the discussion by the respective authors as part of their studies. For example, given the results of Gersonde et al. (2004), LAD and crown radius were classified respectively in the low and high categories. Indeed, these authors observed that replacing individual LAD with a species average did not reduce the model fit. On the other hand, in the same study, the same simplification applied to the crown radius reduced very significantly model fit ( $R^2$  was reduced from about 75 % to 65 %). Next, we counted the number of publications of each combination of parameter and sensitivity level (Table 4.6). Unfortunately, not all of the

Table 4.5: Summary of the published evaluations of FRTMs. Models are classified by canopy model and type of forest stand forest structure.  $R^2$  with an \* symbol means that the validation was performed with predictions and measurements averaged for each sites rather than by point-to-point comparisons.

PLANTATION	EVEN-AGED PURE STAND	UNEVEN-AGED OR MIXED STANDS
1D CANOPY		
	no model name Govind et al. (2013) $R^2 = 0.93$ ; RMSE = 30 – 70 $\mu\text{mol m}^{-2} \text{s}^{-1}$	
	no model name Kim et al. (2011) RMSE = 0.06 – 135 $\mu\text{mol m}^{-2} \text{s}^{-1}$	
	4C-A-RTM Bertin et al. (2011) good relationship ( $R^2 = 0.92$ ) with seedling growth	
MIXLIGHT Pinno et al. (2001) $R^2 = 0.92$	MIXLIGHT Stadt and Lieffers (2000) $R^2 = 0.74^*$	SORTIE Canham et al. (1999) $R^2 = 0.86$
3D CROWN WITH QUADRATIC SHAPES		
SORTIE-ND Paquette et al. (2008) $R^2 = 0.92$	SORTIE-ND Boivin et al. (2011) $R^2 = 0.52$	SILVI-STAR Koop and Sterck (1994) $R^2 = 0.77 - 0.94$
SORTIE-ND Boivin et al. (2011) $R^2 = 0.46 - 0.92$		SAMSARA Courbaud et al. (2003) RMSE = 5.2 %  OLTREE & SolTran Mariscal et al. (2004) $R^2 = 0.94^*$
	MAESTRO Wang and Jarvis (1990) RMSE = 10 %	tRAYci Gersonde et al. (2004) $R^2 = 0.80$
	TASS/tRAYci Brunner (1998) $R^2 = 0.97$	CORONA Groot (2004) $R^2 = 0.88$
3D CROWN WITH NONQUADRATIC SHAPES		
	tRAYci Piboule (2001) RMSE = 2 %	M $\mu$ SLIM Da Silva et al. (2011) “in the range of model using similar scales of description”
	FOREST Cescatti (1997b) $R^2 = 0.97$	FOREST Law et al. (2001) $R^2 = 0.62$
3D SURFACES OF LEAVES, BRANCHES, AND STEMS		
AmapSim Leroy et al. (2009) no statistical difference in 3/4 sites	no model name Fournier et al. (1996) RMSE $\approx$ 10 – 15 %	
RATP Sinoquet et al. (2001) RMSE = 60 – 120 $\mu\text{mol m}^{-2} \text{s}^{-1}$		

parameters had been tested in similar conditions or with the same model, as far as forest stands are considered. We therefore recognize that our analysis is incomplete, but underlines well the common trends between different studies.

As a general rule, we found that models appeared more sensitive to the parameters describing between-crown gaps than to those describing within-crown gaps or within-crown architecture. In most studies, a larger amount of light was transmitted between rather than through the crowns. Indeed, as shown by the estimates of crown openness in [Table 4.4](#), only 5 % to 30 % of incident light passes through the crown. The parameters describing the between-crown gap geometry were therefore of primary importance, justifying the use of a hit model (3D-PE with  $p = 0$ ) for certain types of stands. Nevertheless, we found that authors often noted that FRTMs were more sensitive to other parameters such as tree clumping or leaf area in dense stands ([Wang and Jarvis, 1990](#); [Boivin et al., 2011](#)).

Stand density and stand edges are not model calibration parameters but they greatly affect transmitted light estimates ([Bartelink, 1998b](#); [Piboule, 2001](#)). Moreover, it is even possible that stand density modifies model sensitivity to the inner-crown parameters. In dense and homogeneous stands, most rays were found to intercept crowns, whereas in low-density stands, the majority of transmitted radiation comes from canopy gaps. Models are thus found to be less sensitive to inner-crown parameters with low-density stands.

#### 4.1.5.1 1D model

The main source of variability of 1D models was found in the areas covered by crowns ([Duursma and Mäkelä, 2007](#)) and leaves ([Duursma and Mäkelä, 2007](#); [Bertin et al., 2011](#); [Kim et al., 2011](#)). These parameters appeared to be highly influential in all the sensitivity analyses that studied their effects. These estimates were further corrected with clumping factors that took into account the aggregation of stems, branches, and (or) leaves. The clumping factor or the spatial structure of trees or crowns therefore played an important role in the corresponding studies. However, model sensitivity to these parameters decreased with stand density, stand LAI and leaf inclination ([Kim et al., 2011](#)).

Parameters of crown architecture played a secondary role. Only a few studies reported that changes in values of branch area, foliage inclination, and vertical distribution of leaves affected notably 1D model predictions. Similarly, crown shape and modeling stem interception had only a minor effect on model prediction.

#### 4.1.5.2 3D crown model

3D crown models appeared highly sensitive to the crown radius in all of the sensitivity analyses that studied the influence of this parameter ([Canham et al., 1994](#); [Cescatti, 1997b](#); [Brunner, 1998](#); [Stadt and Lieffers, 2000](#); [Piboule, 2001](#); [Beaudet et al., 2002](#)). It even appeared that estimating the crown radius using allometric relationships instead of measuring this parameter in the field individually for each tree significantly decreased model precision



Table 4.6: FRTM sensitivity to calibration parameters. For each parameter, we counted the number of publications ( $n$ ) analyzing its effect on model predictions. According to the authors' conclusion, we classified their results into three categories: low, medium or high impact. The score corresponds to  $(\text{high} + 0.5 \cdot \text{medium})/n$ .

PARAMETER	$n$	LOW	MEDIUM	HIGH	SCORE	REFERENCES
3D CROWN MODEL						
crown radius	7			7	1	Beaudet and Messier (2002); Brunner (1998); Gersonde et al. (2004); Piboule (2001); Cescatti (1997b); Da Silva et al. (2011); Stadt and Lieffers (2000)
crown shape	2			2	1	Brunner (1998); Piboule (2001)
stand density	2			2	1	Bartelink (1998b); Essery et al. (2008)
stand edge	1			1	1	Piboule (2001)
understory vegetation	1			1	1	Beaudet and Messier (2002)
tree height	2		1	1	0.8	Beaudet and Messier (2002); Gersonde et al. (2004)
crown length	3		2	1	0.7	Piboule (2001); Stadt and Lieffers (2000); Gersonde et al. (2004)
crown openness	2	1		1	0.5	Beaudet and Messier (2002); Boivin et al. (2011)
LAD	5	2	2	1	0.4	Bartelink (1998b); Brunner (1998); Gersonde et al. (2004); Piboule (2001); Stadt and Lieffers (2000)
foliage clustering within crowns	2	1	1		0.3	Bartelink (1998b); Cescatti (1997b)
trunk interception	2	1	1		0.25	Brunner (1998); Fournier et al. (1996)
crown max-width height	1	1			0	Piboule (2001)
foliage clustering around shoots	1	1			0	Bartelink (1998b)
foliage inclination	1	1			0	Stadt and Lieffers (2000)
foliage as a sub-shell of crown	1	1			0	Gersonde et al. (2004); Cescatti (1997b)
1D CANOPY MODEL						
leaf distribution	1	1			0	Wang and Jarvis (1990)
crown surface	1			1	1	Duursma and Mäkelä (2007)
leaf area	3			3	1	Kim et al. (2011); Bertin et al. (2011); Duursma and Mäkelä (2007)
tree clumping	3		1	2	0.8	Kim et al. (2011); Bertin et al. (2011); Duursma and Mäkelä (2007)
branch area	2		2		0.5	Kim et al. (2011); Bertin et al. (2011)
foliage inclination	1		1		0.5	Kim et al. (2011)
vertical distribution of leaves	1		1		0.5	Kim et al. (2011)
stem area	2	1	1		0.3	Kim et al. (2011); Bertin et al. (2011)
crown shape	1	1			0	Duursma and Mäkelä (2007)

(Piboule, 2001; Da Silva et al., 2011). Indeed, crown dimensions largely depend upon neighboring competition and tree history which are two effects usually not included in allometric relationships and that should be taken into account (Piboule, 2005).

Crown shape, tree height and height to crown base seemed to have less influence (Brunner, 1998; Da Silva et al., 2011). FRTMs appeared highly sensitive to these parameters in less than 50 % of the sensitivity analyses. For instance, Brunner (1998) tested two representations of crowns (with cones or asymmetric ellipsoids) and concluded that the two models gave similar results. Similarly, the height of maximum crown extension is needed to define the most complicated crown shapes and using such complex shape led to only minor improvements (Piboule, 2001).

The density of leaves and branches within crowns (expressed by LAD and crown openness) moderately affected the estimates of transmitted light beneath the forest canopy (Bartelink, 1998b; Brunner, 1998; Lieffers et al., 1999; Stadt and Lieffers, 2000). Interestingly, reasonable changes in LAD affected model predictions markedly in only one of the five corresponding sensitivity analyses (Bartelink, 1998b; Brunner, 1998). It is worth noting that good estimates of LAD (3D-TM) or crown openness (3D-PE) require the correct delimitation of crown volume. Errors in computing the crown volume would lead to, for example, errors in calculating total leaf area. Similarly, LAD, clumping factors and extinction coefficients are strongly correlated (Equation 4.1, Bartelink (1998b)). This finding therefore justifies using fixed values of LAD per species.

Foliage distribution, clustering and inclination were studied to a slightly lesser extent, but these parameters appeared to have a small effect on 3D crown model predictions (Wang and Jarvis, 1990; Cescatti, 1997b; Bartelink, 1998b; Stadt and Lieffers, 2000; Gersonde et al., 2004). Foliage distribution likely depends upon species. For instance, Cescatti (1997b) reported evidence of the aggregation of spruce needles around vertices. Nevertheless, the influence of this aggregation on FRTM predictions appeared weak (Cescatti, 1997b; Bartelink, 1998b), probably because 3D models are used mostly for stands with rather open canopy where gaps between crowns are more important than gaps within crowns. Similarly, modeling trunk interception was reported without significant effects in the two sensitivity analyses studying this parameter (Fournier et al., 1996; Brunner, 1998). With 3D crown model, using the default values of  $k = 0.5$  and  $\Omega = 1$  appeared therefore a reasonable simplification.

#### 4.1.6 Discussion

This review illustrates and provides an overview of the variety of approaches used to represent a forest canopy and to estimate radiation intercepted by

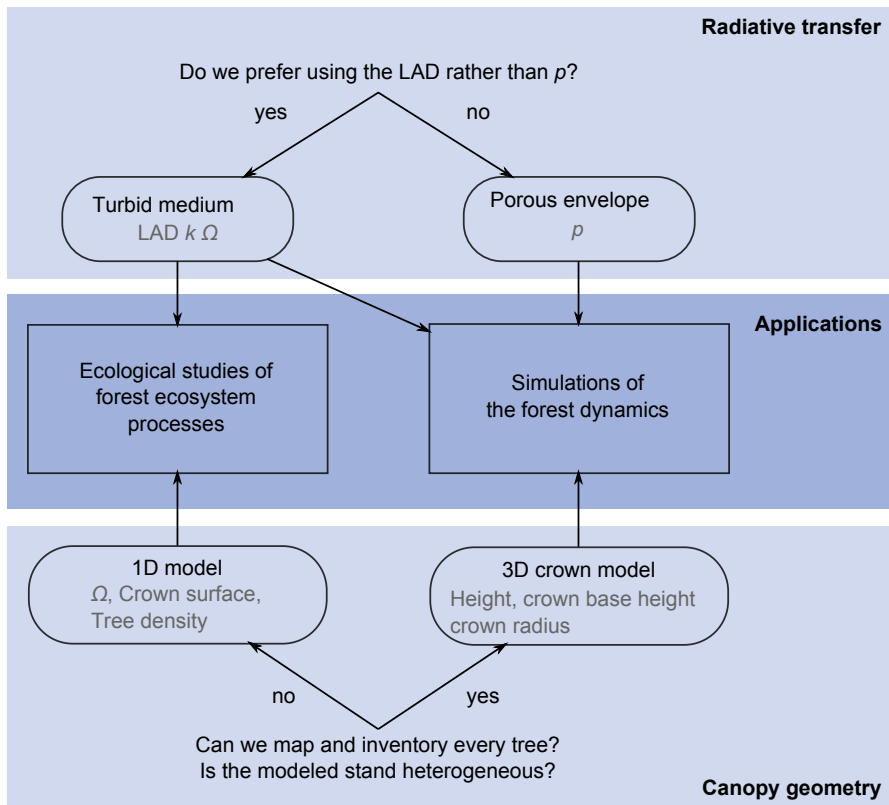


Figure 4.3: Overview of FRTMs according to their end-uses. Most FRTMs included in stand-dynamics models are 3D crown models, whereas most FRTMs used for ecophysiological studies are 1D models. LAD, leaf area density;  $k$ , extinction coefficient;  $\Omega$ , clumping factor;  $p$ , crown openness; 1D, one dimensional; 3D, three-dimensional.

the canopy elements (Figure 4.3). Even though more thoroughgoing conclusions could likely have been formulated with benchmarking of a wide set of FRTMs using a common data set with different stand structures, we were able to highlight the specificity of forest canopy in comparison with many agricultural crops and consequences in terms of modeling. The recent studies that we reviewed enabled us to quantify model uncertainty, to identify sensitive parameters, and to recommend the modeling approaches that best suit the different FRTM applications.

#### 4.1.6.1 Model uncertainty

1D models accurately predict the temporal variations of irradiance (RMSE ranged roughly between  $30 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $120 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) within homogeneous stands (Kim et al., 2011; Govind et al., 2013). The vertical gradient of transmitted light beneath the canopy can be predicted reasonably well with multilayer models (Landsberg and Sands, 2010), but, the spatial variation in irradiance in the understory is not predicted by 1D models.

3D crown models accurately predict averaged measures of transmitted light in a forest plot. The prediction of transmittance at a particular location

beneath the canopy is clearly less accurate with errors often up to 20 % of transmittance (Cescatti, 1997b; Brunner, 1998; Stadt and Lieffers, 2000). 3D crown models are capable of capturing a certain spatial variability of transmitted light but not with a resolution as precise as the one using light sensors. Within forest dynamics models, small errors in the spatial distribution of understory light should be considered as being of minor importance compared with, for example, the prediction of the cumulated area of microsites favorable to regeneration growth, i.e., receiving an irradiance within the range corresponding to the needs of a given species.

Moreover, model uncertainty increases with the complexity of the canopy. Transmittance beneath young plantation is better predicted than beneath uneven-aged and mixed stands. Transmitted light under homogeneous canopy is usually well predicted with every modeling approach. On the contrary, transmitted light under heterogeneous canopy is supposed to be hardly predicted with 1D models. 3D crown model appeared so far the best solution to model the radiative transfer through such complex canopies.

Model uncertainty also decreases with increasing length of the simulated period especially if direct radiation is taken into account. As already pointed out for forest productivity models (Landsberg and Sands, 2010), predicting transmitted radiation for a brief period (e.g., 30 minutes) requires very accurate radiation and canopy measurements. Accurate monthly and yearly averaged predictions are however more easily obtained (Essery et al., 2008; Landsberg and Sands, 2010), probably because of errors compensation.

We found no clear evidence regarding the advantage of using the turbid medium approach (3D-TM) versus the porous envelope approach (3D-PE). Both methods provided satisfactory results. Besides, if the crown openness varies with crown dimensions, both methods are somehow related because  $k \cdot \text{LAD}$  can be deduced from  $p$  (Da Silva et al., 2011). If LAD and  $p$  are species constant, then for every tree, independent of their size, the porous envelope approach affects transmittance to every crown in the same way, whereas it depends upon crown size and beam orientation with the turbid medium approach. In this latter case, model performance of both approaches likely differs with the variability of crown dimensions.

#### 4.1.6.2 Sensitive input parameters

Calibration efforts must focus primarily in the description of between-crown gaps or crown radius, which are the most sensitive parameters of FRTMs. This result is perhaps not intuitive but probably reflects that the forest canopy consist of deep crowns with dense foliage. Therefore, crowns intercept a large amount of light whatever their specific features. As a result, the proportion of transmitted light that is not intercepted by tree crowns, i.e., transmitted through gaps between crowns, is fundamental.

With 1D models, the key calibration parameters are the crown surface and (or) the LAI, which might further be corrected with extinction and clumping factors. On the other hand, 3D models require overall an accurate tree map and individual measurements of the crown radius, especially in order

to characterize heterogeneous canopies. Crown shape appeared of lesser importance than crown radius and we did not find that it was worth using complex crown shapes. Furthermore, standard values of the extinction coefficient and clumping factors ( $k = 0.5$  and  $\Omega = 1$ , respectively) were often used with 3D crown model and frequently gave a good approximation. Therefore, 3D models appear better suited for long simulation periods than 1D model because 3D model usually do not imply predicting changes of extinction and clumping factors.

#### 4.1.6.3 Applications

We identified the advantages and drawbacks of the FRTM modeling approaches which allowed us to identify the approaches, that best suit to different potential applications of FRTM (Table 4.7). Overall, the potential applications depend mainly upon how the canopy is modeled.

1D models predict well the irradiance of canopy with a low number of input data and parameters. They are sensitive to the parameters describing foliage density and distribution ( $k$  and  $\Omega$ , respectively). They are ideally coupled with process-based of photosynthesis rate in order to explore forest productivity, carbon uptake, or nutrient cycling at the stand or greater scale. They are, however, limited to stands with one or two species and a relatively homogeneous (even-aged) structure. Moreover, the simulated forest should have a stable structure or the simulated time period should be limited because the calibration parameter depends strongly upon stand structure and composition. In most cases, 1D models hardly predict light conditions after silvicultural operations such as partial harvests. Silvicultural operations often modify not only stand height, and density but also foliage features and distribution because some categories of trees are preferentially cut or because gaps are created. Through time, tree growth, self-thinning and self-pruning additionally modify the spatial distribution of foliage. In particular, as trees become mature, foliage tends to accumulate in fewer and bigger crowns. Next, as several regeneration cohorts develop, foliage becomes aggregated in crowns of varied dimensions.

3D crown models (3D-TM and 3D-PE) are better used in studies focusing on timber production and stand dynamics because, in many cases, those processes are generally not explicitly related to photosynthesis, transpiration, or nutrient cycling. They accommodate to heterogeneous stand structure. They include explicitly stand spatial structure, which enables studying the impact of forest structure (e.g., testing different silvicultural scenarios) on forest production and yield. This is an interesting feature with the general increasing interest devoted to uneven-aged, shelterwood or close-to-nature silviculture in many countries. Moreover, single tree based models such as 3D crown models offer the best opportunity to analyze forest management strategies (Porte and Bartelink, 2002). Indeed, partial harvest modifies the average dimensions of trees and stand spatial structure. The increase in transmitted light is therefore complex and does not depend only upon changes of stand density. 3D crown models are sensitive to canopy spatial structure

Table 4.7: Synthesis of model advantages and drawbacks with suggested scale of uses, forest structures, and examples of applications.

MODEL	SCALE OF USES	FOREST STRUCTURE	ADVANTAGES	DISADVANTAGES	APPLICATIONS
1D model	from stand to global, from hours to one year	even-aged stand, with one or two species	low number of field data; easy to couple to stand level data and models (canopy gas transfers, canopy cover, Leaf Area Index).	model parameters (foliage distribution) are hardly measured in the field; lack of knowledge to model ade- quately changes of foliage distribution parameters through time and after thinning; do not take ex- plicitly into account spatial structure.	net primary production; car- bon uptake; nutrient cycling; photosynthesis rate
3D-M or 3D-PE	from plot to stand, years	even-aged or unven- aged stand, pure and mixed stand	translate directly changes of stand structure (tree density, species, sizes, spatial distribu- tion) into changes of canopy; allow the calculation of ra- diation interception by each tree; allow the calculation of maps of irradiance under canopy.	require information on tree location (obtained either from field measures or from theoretical distribu- tions); require information on crown characteristics (obtained either from field measures or from allometric relationships)	timber production; un- derstory growth; forest dynamics
3D-S	from leaf to tree, from hours to years	isolated tree, agro- forestry system, homogeneous stand	allow the most precise mod- eling of radiation intercep- tion; can be coupled to plant structure-function models.	require information on plant architecture (either measured or modeled); high computing complexity limit- ing the number of simulated trees.	tree physiology; tree mor- phogenesis; tree architecture

and, hence, require precise mapping and crown measuring. Currently, the cost of these measurements limits the size of the modeled stand but the use of airborne technologies is promising (Essery et al., 2008).

3D surface models require acquiring large amounts of field data to reproduce tree architecture but they enable studying light capture at plant organ to tree levels (Rey et al., 2008). Whenever trees can realistically be duplicated in a forest model, 3D surface models offer good opportunity for studying the effects of tree architecture on tree physiological processes. Future technologies, such as terrestrial LiDAR can also help in acquiring the field data required to build 3D surface models for more complex stands.

#### 4.2 IMPLEMENTING A RADIATIVE TRANSFER MODEL

Exploring how forest managers can manipulate understory light requires a model that is capable of predicting light interception by heterogeneous canopies, especially in uneven-aged forests that are composed of several broadleaved species, and that takes directly into account the structure and density of the simulated stands. According to our literature review, the most efficient strategy for achieving this goal consists in utilizing a 3D crown model. Crowns are best modeled with combinations of quadratic shapes to reproduce accurately the variability of crown dimensions and to compute analytically (i.e., faster than with numerical computations) the interception of radiation by crowns. The turbid medium approach is preferred over the porous envelope approach, where we have hypothesized that this approach might better predict how much radiation is intercepted by crowns of various sizes.

Such a model is implemented in the forest simulation platform Capsis (Dufour-Kowalski et al., 2012) in a library named SamsaraLight. The full description of the functioning of this library is beyond the scope of this thesis. A first version of SamsaraLight was described by Courbaud et al. (2003) and further documentation can be found on the Capsis website (Ligot et al., 2013).

Hereafter, I introduce how a heterogeneous canopy was modeled, i.e., the 3D reconstruction of a stand canopy with models of crown geometry (Section 4.2.1), crown dimensions (Section 4.2.2, Section 4.2.3 and Section 4.2.4), and how foliage features were characterized (Section 4.2.5). Models of crown dimensions and foliage density were adjusted with the data that were gathered in the 27 studied sites (Chapter 2). Next, I report on an evaluation of model predictions (Section 4.2.6).

### 4.2.1 Crown geometry

We modeled crown geometry with one or several sections of asymmetric ellipsoids (Figure 4.4). The choice of one of these options depends mainly upon the tree measurements that are available. For example, in the next chapter, we opted to model crowns with single asymmetric ellipsoids because we did not measure the height to the largest crown cross-section or the 4 crown radii of every tree.

The crown geometry is defined by 4 crown radii, which are measured along the cardinal directions, together with tree height and height to the base of the crown. These measurements enable us to compute the parameters of the equation of an ellipsoid or sections of an ellipsoid (Equation 4.4):

$$\frac{(x - x_0)^2}{a} + \frac{(y - y_0)^2}{b} + \frac{(z - z_0)^2}{c} = 1 \quad (4.4)$$

where  $(x_0, y_0, z_0)$  are the coordinates of the ellipsoid center, and  $a$ ,  $b$ , and  $c$  are the semi-axes that are respectively oriented from West to East, South to North, and from bottom to top.

Furthermore, to estimate missing measurements of crown dimensions and to develop an algorithm describing the evolution of crown dimensions, we adjusted a set of allometric relationships for the six groups of species that were used in our simulation program. In ??, we additionally introduce how the height to the largest crown extension can be estimated to define crown shapes with upper and lower sections of different length (different  $c_{up}$  and  $c_{down}$  in Figure 4.4).

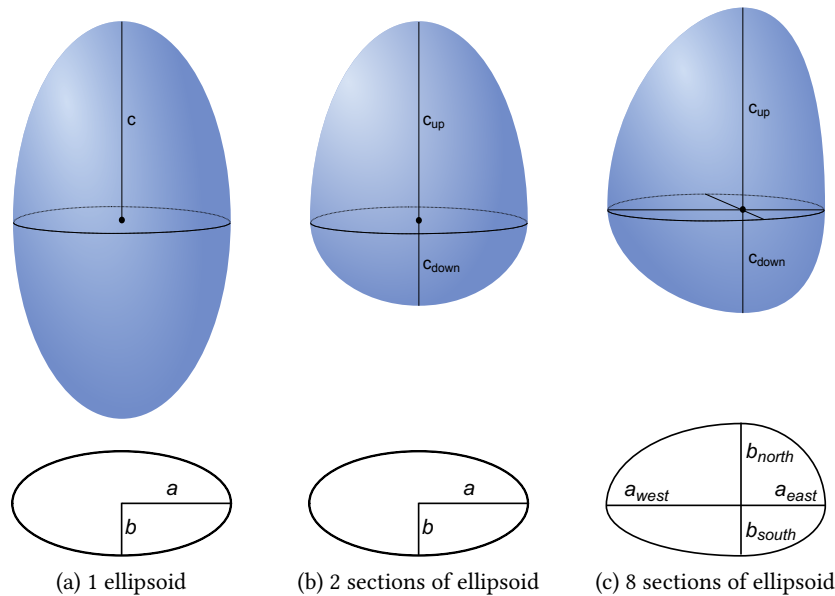


Figure 4.4: Geometric models of tree crown with the parameters of the ellipsoid equation (Equation 4.4).



#### 4.2.2 *Crown radius*

Crown radii (CR) were best modeled with power function of tree diameter (dbh) in a manner similar to that used by [Beaudet et al. \(2011\)](#). The model was adjusted with nonlinear least-squares methods ([R Core Team, 2013](#)). The power function models of crown radius fitted well the 6 groups of species. Root mean square error (RMSE) was less than 81 cm ([Table 4.8](#)). For comparable tree dbhs, individuals of the shade-tolerant species (e.g., hornbeam and beech) had wider crowns than individuals of the less shade-tolerant species (e.g., oak and birch).

#### 4.2.3 *Tree Height*

Tree height was best modeled with Mitscherlich's model of tree diameter (dbh) ([Table 4.9](#)). The model fitted well every group of species and was adjusted with nonlinear least-squares methods ([R Core Team, 2013](#)). With the exception of coniferous trees, root mean square error was less than 2.6 m. However, the models that we have presented should only be used within the range of observed dbh. In particular, we did not measure large coniferous trees and the validity of the model is doubtful for such trees.

#### 4.2.4 *Height to the base of the crown*

The height to the base of the crown ( $H_{cb}$ ) was estimated with the species averaged ratio between crown length and tree length ([Table 4.10](#)). The use of a power model, as was proposed by [Beaudet et al. \(2011\)](#), did not substantially improve the predictions and required the estimation of one additional parameter for each species. However, the parameters of the adjustment of the power model were also reported ([Table 4.11](#)) because they can be used to run simulations with another simulation program of stand dynamics: SORTIE-ND ([Canham, 2011](#)). The parameter estimates underscore our observations that shade-tolerant species have deeper crowns than less shade-tolerant species (greater  $a$  estimate in [Table 4.10](#)).

#### 4.2.5 *Crown openness and leaf area density*

In addition to information about crown geometry, SamsaraLight requires the estimation of either crown openness or crown leaf area density (LAD). We measured both parameters with photographs of isolated crowns in a manner similar to the method that was used to estimate crown openness ([Canham et al., 1999](#); [Beaudet and Messier, 2002](#); [Astrup and Larson, 2006](#)). This method is rapidly executed relative to previously reported methods that use leaf samples or leaf traps ([Bartelink, 1997](#); [Jonard et al., 2006](#)) or vertical line-intersect sampling methods ([Nock et al., 2008](#)), but it applies only to trees with relatively isolated crowns.

Table 4.8: Parameter estimates and their 95 % confidence intervals with  $\alpha = 0.05$  (CI) for the power function model between crown radius (CR) and tree diameter (dbh):  $CR = a \cdot dbh^b$ . Also presented are the number of measured trees ( $n$ ), the ranges of measured dbh, the ranges of measured CR, and the root mean square error (RMSE).

SPECIES	$n$	dbh cm	CR m	$a$		$b$		RMSE m
				Estimate	CI	Estimate	CI	
Oak	314	2.4;92.3	0.5;7.7	0.310	0.240;0.396	0.698	0.634;0.764	0.808
Beech	475	2.4;80.5	0.3;10.4	0.742	0.679;0.808	0.516	0.492;0.541	0.755
Hornbeam	67	2.4;42.0	0.8;5.1	0.854	0.682;1.054	0.503	0.425;0.583	0.632
Birch	40	2.4;49.7	0.6;3.8	0.536	0.457;0.621	0.493	0.444;0.545	0.266
Other hardwoods	43	2.5;19.8	0.7;3.4	0.960	0.616;1.436	0.325	0.144;0.515	0.576
Other softwoods	45	2.4;21.0	0.6;2.5	0.516	0.441;0.601	0.509	0.440;0.579	0.179

Table 4.9: Parameter estimates and their 95 % confidence intervals with  $\alpha = 0.05$  (CI) of Mitscherlich's model between tree height and tree diameter (dbh):  $height = m \cdot (1 - \exp(-(dbh - a)/b))$ . Also presented are the number of measured trees ( $n$ ), the ranges of measured dbh, the ranges of measured tree height, and the root mean square error (RMSE).

SPECIES	$n$	dbh cm	height m	$a$		$b$		$m$		RMSE m
				Estimate	CI	Estimate	CI	Estimate	CI	
Oak	706	2.4;94.9	3.1;35.8	-1.629	-1.93;-1.33	32.733	29.95;35.51	31.524	30.38;32.67	2.565
Beech	1271	2.4;84.4	3.3;39.5	-1.835	-2.15;-1.52	36.298	33.44;39.15	36.424	34.88;37.97	2.626
Hornbeam	175	2.4;42.0	4.1;25.8	-2.441	-3.74;-1.14	32.776	14.31;51.25	32.083	20.43;43.74	2.522
Birch	69	2.4;49.7	3.6;27.3	-0.762	-1.44;-0.08	19.122	13.17;25.07	28.617	24.40;32.84	1.619
Other hardwoods	73	2.5;76.7	3.3;29.3	-1.134	-2.53;0.26	50.156	22.60;77.71	42.830	27.53;58.13	2.354
Other softwoods	60	2.4;21.0	3.1;14.1	-1.822	-4.76;1.12	42.926	-49.86;135.72	29.273	-18.46;77.01	1.207

Table 4.10: Parameter estimates and their 95 % confidence intervals with  $\alpha = 0.05$  (CI) of the model between the crown length ( $CL = H - H_{cb}$ ) and tree height ( $H$ ):  $CL = a \cdot H$ . Also presented are the numbers of measured trees ( $n$ ), the ranges of measured tree diameters (dbh), tree height and height to the crown base ( $H_{cb}$ ), and the root mean square error of the crown length model.

SPECIES	$n$	dbh cm	$H_{cb}$ m	height m	$a$		RMSE m
					Estimate	CI	
Oak	702	2.4;94.9	0.4;23.2	3.1;35.8	0.673	0.66;0.69	4.344
Beech	1083	2.4;84.4	0.1;19.6	3.3;39.0	0.794	0.78;0.80	3.356
Hornbeam	154	2.4;42.0	0.2;11.9	4.1;25.8	0.813	0.79;0.83	1.910
Birch	65	2.4;49.7	0.4;18.3	3.6;27.3	0.669	0.63;0.71	2.691
Other hardwoods	57	2.5;76.7	0.2;20.5	3.4;29.3	0.674	0.63;0.72	3.311
Other softwoods	29	2.4;20.7	0.1;1.9	3.1;12.6	0.774	0.72;0.82	0.864

Table 4.11: Parameter estimates and their 95 % confidence intervals with  $\alpha = 0.05$  (CI) of the power model between the crown length ( $CL = H - H_{cb}$ ) and tree height ( $H$ ):  $CL = a \cdot H^b$ . Also presented are the numbers of measured trees ( $n$ ), the ranges of measured tree diameter (dbh), tree height and height to the crown base ( $H_{cb}$ ), and the root mean square error of the crown length model.

SPECIES	$n$	dbh cm	$H_{cb}$ m	height m	$a$		$b$		RMSE m
					Estimate	CI	Estimate	CI	
Oak	706	2.4;94.9	0.4;23.2	3.1;35.8	1.162	0.82;1.50	0.827	0.74;0.92	4.300
Beech	1271	2.4;84.4	0.1;19.6	3.3;39.0	1.063	0.94;1.18	0.900	0.87;0.94	3.285
Hornbeam	175	2.4;42.0	0.2;11.9	4.1;25.8	1.098	0.85;1.35	0.885	0.80;0.97	1.853
Birch	69	2.4;49.7	0.4;18.3	3.6;27.3	1.298	0.88;1.72	0.719	0.61;0.83	1.952
Other hardwoods	73	2.5;76.7	0.2;20.5	3.4;29.3	0.773	0.32;1.22	0.931	0.74;1.12	3.206
Other softwoods	60	2.4;21.0	0.1;1.9	3.1;12.6	0.547	0.47;0.63	1.233	1.16;1.30	0.441

We took 112 photographs of isolated crowns of 21 oaks, 13 beeches, 8 birches, and 4 hornbeams. The photographs were processed with Pfi-Photem (Adam et al., 2006) to compute the gap fraction, i.e., crown openness. Additionally, for every photographed crown, we recorded 4 crown radii, crown base height and tree height.

We computed the path length,  $l$  (Equation 4.1), as the distance between the intersections between the modeled crown ellipsoids and the photograph direction (Figure 4.5). Computing the intersections between an ellipsoid and a line requires solving a second-degree equation (Equation 4.5).

$$AL^2 + BL + C = 0 \quad (4.5)$$

$$A = \frac{\cos^2(\theta) \cos^2(\alpha)}{a^2} + \frac{\cos^2(\theta) \sin^2(\alpha)}{b^2} + \frac{\sin^2(\theta)}{c^2}$$

$$B = -\frac{2x_1 \cos(\theta) \cos(\alpha)}{a^2} - \frac{2y_1 \cos(\theta) \sin(\alpha)}{b^2} - \frac{2z_1 \sin(\theta)}{c^2}$$

$$C = \frac{x_1^2}{a^2} + \frac{y_1^2}{b^2} + \frac{z_1^2}{c^2} - 1$$

where  $(x_1, y_1, z_1)$  are the coordinates of the ellipsoid center in the same coordinate system as the photograph direction. The distance between the intersections, i.e., the path length of light within the crown Figure 4.5, is given by the difference between  $L$  solutions.

Photograph direction was computed from the recorded photograph elevation angle and the estimated distance to the trunk. The equation of this direction within a polar coordinate system where the origin corresponds to the camera position is given in Equation 4.6.

$$x = L \cos(\theta) \cos(\alpha) \quad (4.6)$$

$$y = L \cos(\theta) \sin(\alpha)$$

$$z = L \sin(\theta)$$

where  $L$  is the distance along the direction from the camera position,  $\theta$  is the direction elevation angle, and  $\alpha$  is its azimuthal angle (Figure 4.5). Because the distance between the photographer and the tree trunk was not recorded in the field, we estimated it by considering that the photographer was 1.7 m tall and always aimed the camera at the mid-height of the targeted crown. The distance  $d$  is estimated as (Equation 4.7):

$$d = \frac{0.5(H - H_{cb}) + H_{cb} - 1.7}{\tan \theta} \quad (4.7)$$

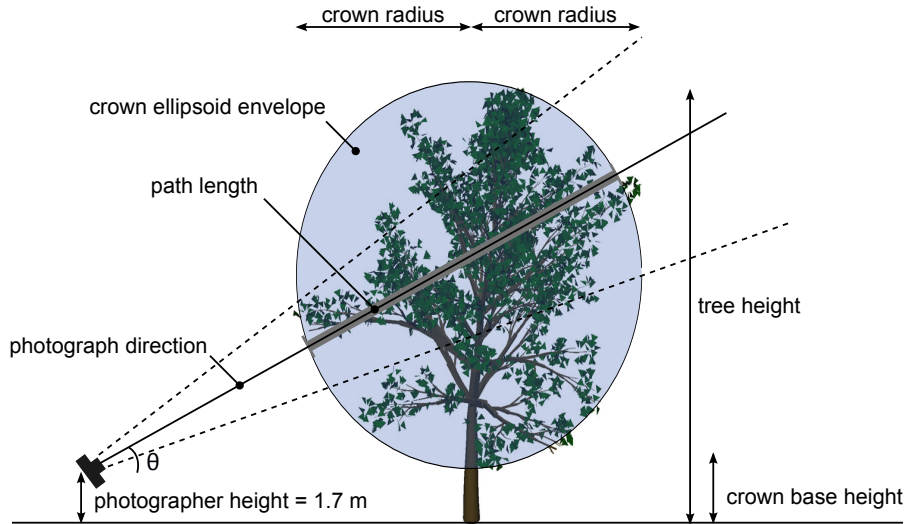


Figure 4.5: Illustration of the different measurements involved in the computation of crown LAD.

where  $H$  is tree height,  $H_{cb}$  is height to the base of the crown, and  $\theta$  is the recorded elevation angle (Figure 4.5).

Finally, LAD values were estimated by inverting Beer's law (Equation 4.1), with the common assumption of spherical distribution of leaves ( $k = 0.5$ ) (Phattaralerphong et al., 2006; Da Silva et al., 2011). We could have used  $k \cdot \text{LAD}$  instead of LAD. Although this would have allowed us to assume that the distribution of leaves was not spherical, it would not have allowed us to compare LAD values with other published work.

We finally modeled the LAD estimates for beech and oak. We obtained the best fits with a polynomial function of dbh that was adjusted according to ordinary least-squares methods (R Core Team, 2013). For the other species we did not collect enough data to model LAD as a function of dbh. Nevertheless, Courbaud et al. (2003) mentioned that SamsaraLight sensitivity to leaf area density was low between  $0.3 \text{ m}^2 \text{ m}^{-3}$  and  $0.9 \text{ m}^2 \text{ m}^{-3}$ . We assumed LAD to be  $0.6 \text{ m}^2 \text{ m}^{-3}$  for all other species as 0.6 corresponded to the LAD average of all measured trees. Trunks were modeled as cylinders of dbh diameter and crown base height and do not transmit light.

Estimates of crown LAD varied noticeably from tree to tree and even from photograph to photograph of the same tree. Foliage biomass is usually assumed to depend upon sapwood area (pipe model) (Shinozaki et al., 1964) and, hence, also upon tree dbh. However, tree dbh explained only 48% and 30% of LAD variability for oak and beech trees, respectively (Table 4.12). LAD decreased with tree dbh and more so for beech than for oak. Additionally, LAD stopped decreasing for beech at around 50 cm dbh and then started to increase gently. Our LAD estimates matched previously reported values of leaf area for beech and oak (Bartelink, 1997; Jonard et al., 2006) and were in

Table 4.12: Parameter estimates and their 95 % confidence intervals (CI) of the polynomial model between crown leaf area density (LAD) and tree diameter (dbh) :  $LAD = a + b \cdot (dbh \cdot \pi) + c \cdot (dbh \cdot \pi)^2$ . Also presented are tree number ( $n_t$ ), photograph number ( $n_p$ ), ranges of measured dbh (in cm), ranges of estimated LAD (in  $m^2 m^{-3}$ ), and the model root mean square error (RMSE). We assumed LAD to be  $0.6 m^2 m^{-3}$  for all other species.

SPECIES	$n_t$	$n_p$	dbh	LAD	$a$		$b$		$c$		RMSE
					Estimate	CI	Estimate	CI	Estimate	CI	
			cm	$m^2 m^{-3}$			$\cdot 10^{-2}$	$\cdot 10^{-2}$	$\cdot 10^{-5}$	$\cdot 10^{-5}$	$m^2 m^{-3}$
Beech	13	71	7.6;71.0	0.23;2.38	1.720	1.450;1.990	-1.88	-2.41;-1.35	6.27	4.21;8.33	0.326
Oak	21	112	5.1;71.9	0.18;2.25	1.207	0.972;1.441	1.04	-1.47;-0.61	3.09	1.34;4.85	0.292
Hornbeam	4	23	7.6;72.2	0.29;0.84	0.521	0.468;0.574					0.125
Birch	8	42	12.7;34.4	0.42;0.90	0.595	0.562;0.628					0.107

the range of reported LAD values for broadleaved species (Stadt and Lieffers, 2000; Piboule, 2001; Gersonde et al., 2004; Sprugel et al., 2009).

#### 4.2.6 Model evaluation

A first version of SamsaraLight was initially validated in one heterogeneous stand of Norway spruce (*Picea abies* (L.) H. Karst.) (Courbaud et al., 2003). Nevertheless, we further evaluated model predictions in mixed broadleaf forests. Additionally, we compared the predictions of SamsaraLight with the predictions of another radiative transfer model (??).

##### 4.2.6.1 Method

In mid-July 2010, we took 307 hemispherical photographs in 19 sites in heterogeneous forests of oak and beech. The photographs were taken just before sunrise and above the regeneration layer of the plots that had been installed every 4 m following a square grid. The number of photographs per site therefore depended upon the area of each site and ranged between 6 and 39. We then computed the percentage of above canopy light ( $PACL_{photo}$ ) that is transmitted through the canopy between 1<sup>st</sup> April and 31<sup>st</sup> October 2012.

To predict understory light with SamsaraLight, we measured and mapped every tree with a circumference greater than 40 cm. We measured the circumference at breast height (1.3 m), total height, and height to the base of the crown for each tree. On 13 sites, we also measured at least 4 crown radii for every tree. The inventoried plots are the same as those that were used in Chapter 3 and had an oval shape of variable area because they surrounded fenced areas in which advanced regeneration has been studied. Trees were measured if they were located at a distance of less than 20 m from the fence. Due to local abundance of the understory, we additionally measured and mapped smaller trees near the points where hemispherical photographs were taken. Two different measurement protocols were applied because of a lack of time and resources. In 10 sites, we measured and mapped every tree with a circumference that was greater than 7.4 cm and 20 cm, which were respectively located less than 7 m or less than 15 m from the points where hemispherical photographs were taken. In the 9 other sites, we measured trees with a circumference that was greater than 20 cm and which were located less than 7 m from the points where hemispherical photographs were taken. Plot area ranged from 2070 m<sup>2</sup> to 10 540 m<sup>2</sup>, with an average of 4340 m<sup>2</sup>.

We compared the hemispherical photograph light estimates ( $PACL_{photo}$ ) with SamsaraLight predictions ( $PACL_{model}$ ) that were computed for the same period and at the same locations. We adjusted linear models with the ordinary least-squares method between  $PACL_{model}$  and  $PACL_{photo}$ . Next, we com-

puted the confidence intervals ( $\alpha = 0.05$ ) of model coefficients to estimate the deviation of the modeled relationship from a 1 : 1 relationship. Using a protocol similar to [Da Silva et al. \(2011\)](#), we also compared the cumulative distribution function (CDF) of  $\text{PACL}_{\text{photo}}$  and  $\text{PACL}_{\text{model}}$  for every site. We computed a Kolmogorov-Smirnov statistic (K-S test) to quantify and test the distance between the two CDFs, against the null hypothesis that the samples are drawn from the same population.

#### 4.2.6.2 Results and discussion

There was a good linear relationship between the modeled  $\text{PACL}_{\text{model}}$  and the measured  $\text{PACL}_{\text{photo}}$  ( $R^2 = 68\%$ ) although our model tended to overestimate  $\text{PACL}_{\text{photo}}$  (intercept significantly greater than 0 and the slope not significantly different from 1). The model predicted better  $\text{PACL}$  values when averaged at the site level ( $R^2 = 87\%$ , with intercept not significantly different from 0 and the slope slightly significantly greater than 1) ([Figure 4.6](#)).

Removing small trees from the dataset significantly altered the relationship between  $\text{PACL}_{\text{model}}$  and  $\text{PACL}_{\text{photo}}$ . For example, removing every tree with a circumference smaller than 20 cm reduced  $R^2$  to 65 %, while removing every tree with a circumference smaller than 40 cm reduced the  $R^2$  to 58 %.

According to K-S tests, the distributions of  $\text{PACL}_{\text{model}}$  and  $\text{PACL}_{\text{photo}}$  differed significantly ( $P < 0.05$ ) from one another for 7 of the 19 plots ([Figure 4.7](#)). Nevertheless, the differences were noteworthy for only 5 plots in which  $\text{PACL}_{\text{model}}$  clearly overestimated  $\text{PACL}_{\text{photo}}$ . These plots were characterized by an abundance of small beech and hornbeam trees that covered the regeneration layer where  $\text{PACL}_{\text{photo}}$  measurements were taken. Yet even in these cases, the variation between the distributions of  $\text{PACL}_{\text{model}}$  and  $\text{PACL}_{\text{photo}}$  was less than 15 %.

Overall, our model captured the variability of  $\text{PACL}$  independently of stand structure. The agreement between  $\text{PACL}_{\text{photo}}$  and  $\text{PACL}_{\text{model}}$  was satisfactory and within the range of previously reported studies ([Law et al., 2001](#); [Boivin et al., 2011](#)). For some plots,  $\text{PACL}_{\text{model}}$  slightly overestimated  $\text{PACL}_{\text{photo}}$ . Such over-estimation mostly occurred in the presence of dense understory trees ([Beaudet et al., 2011](#)). The predictions that were made by the  $\text{PACL}_{\text{model}}$  could be affected by these understory trees, because some had a circumference smaller than our inventory circumference threshold, or had a crown that was not correctly modeled by sections of ellipsoids. Moreover, the precision of  $\text{PACL}_{\text{photo}}$  estimates was poorer in the presence of such dense understories. Nevertheless, the bias was of limited magnitude.

#### 4.2.6.3 Conclusion

After synthesizing and discussing the approaches that have been reported in the literature, we implemented a mechanistic and relatively simple radiative model. Compared to other forest radiative models ([Cescatti, 1997b](#); [Brunner, 1998](#); [Courbaud et al., 2003](#); [Gersonde et al., 2004](#)), we utilized a model with



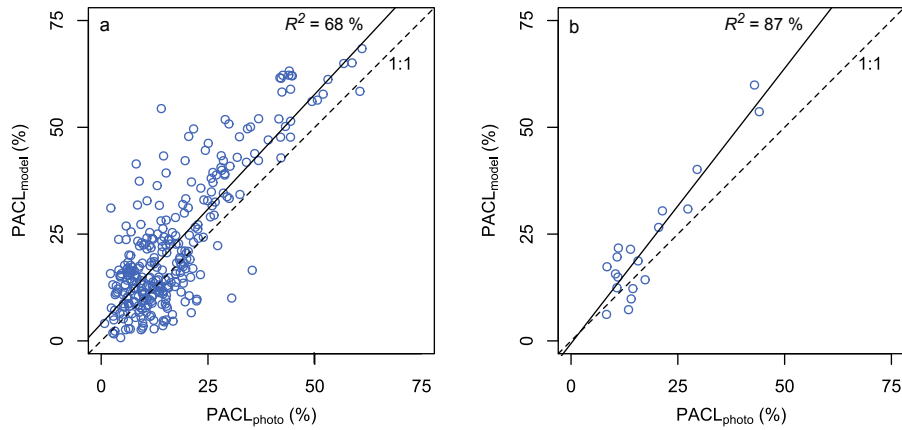


Figure 4.6: Relationships between predicted percentages of above canopy light (PACL<sub>model</sub>) and the percentages of above canopy light estimated from hemispherical photographs (PACL<sub>photo</sub>): point-to-point comparison of all PACL<sub>model</sub> and PACL<sub>photo</sub> (a) and comparison of the PACL<sub>model</sub> and PACL<sub>photo</sub> averaged by site (b). The dotted lines show the 1:1 relationships, whereas the full lines correspond to the linear least-squares regressions.

a low number of parameters that did not require calibration by model inversion.

The model captured well the variability of PACL in stands with varied density, structure and composition ranging from early-successional oak forests to late-successional beech forests. Therefore, we have confidence in the model's robustness for exploring how the understory light regime can be affected by overstory density, overstory structure, overstory composition, and topography. However, caution should be exercised regarding the exactitude of single model predictions, especially where understory is abundant.

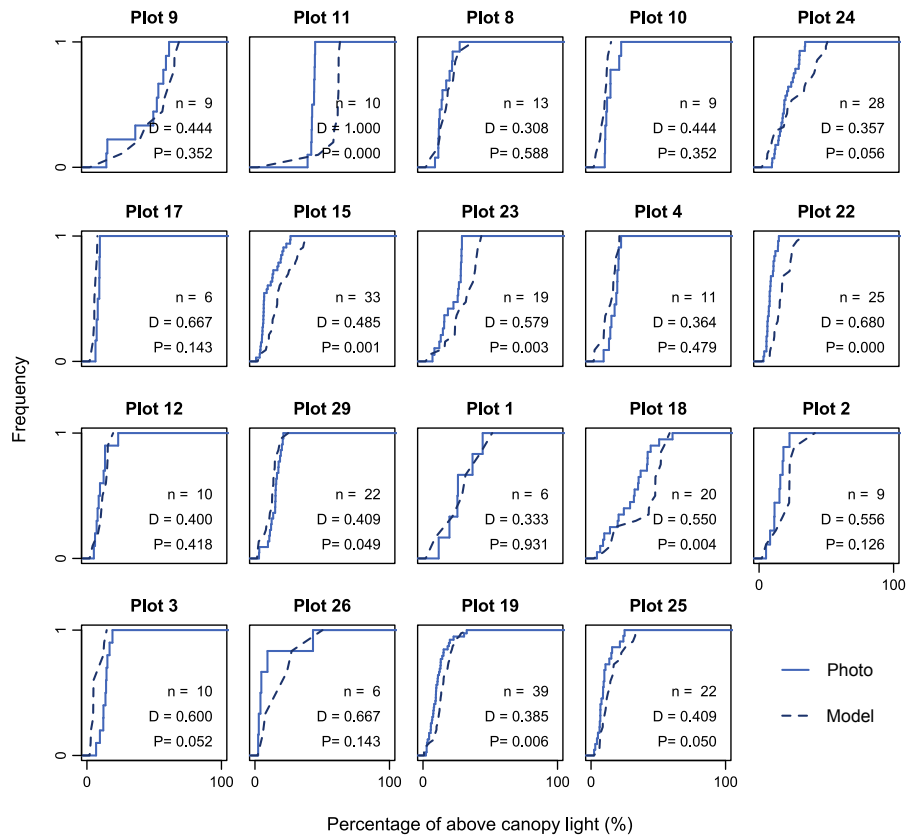


Figure 4.7: Cumulative distributions of modeled (dashed lines) and measured (solid lines) percentages of above canopy light (PACL). The number of measurements and predicted PACL values ( $n$ ), K-S test statistics ( $D$ ) and associated P-values ( $P$ ) are also reported for each plot. Our model captured the variability of PACL, except in sites with an abundant understory. The plots were ordered by decreasing oak proportions showing no effect of stand composition on model performance.



*Nature never hurries: atom by atom, little by little, she achieves her work. The lesson one learns from yachting or planting is the manners of Nature; patience with the delays of wind and sun, delays of the seasons, bad weather, excess or lack of water.*

Ralph Waldo Emerson

As understory light is the main driver of regeneration growth (Chapter 3), controlling understory light is a key factor in regenerating mixed stands (Lieffers et al., 1999). The control of understory light with partial cutting requires properly modifying stand structure and composition, in addition to solely managing stand density. To date, this question of how changes in stand structure and composition affect understory light has rarely been addressed, especially for heterogeneous broadleaf forests. Only a few field experiments have successfully defined levels of canopy openness that are suitable for the regeneration of mixed species (von Lüpke, 1998; Prévost and Pothier, 2003), and simulation studies have been limited to particular ecosystems. Cutting groups of spatially aggregated trees or creating gaps has been reported to drastically increase light availability for the regeneration in boreal mixedwoods (Coates et al., 2003; Beaudet et al., 2011), even-aged western hemlock or Douglas-fir forests (Sprugel et al., 2009), or in uneven-aged spruce forests (Courbaud et al., 2001; Lafond et al., 2013). Additionally, cutting understory poles and trees with branches immediately above the regeneration, or cutting from below in some way, has often been recommended

for shelterwood systems. These poles and trees, unless they are removed, compete strongly with regeneration for nutrients, water and light resources (Nyland, 1996). Moreover, removing shade-tolerant species presumably increases understory light more effectively than removing trees randomly because shade-tolerant species usually have wider, deeper and denser crowns than less shade-tolerant species (Coates et al., 2003; Beaudet et al., 2011).

In this chapter, the radiative transfer model that was established in Chapter 4 is used to explore how silvicultural regeneration treatments that modify stand structure and composition can affect understory light and what is the best treatment to promote the regeneration of mixed species given the light requirements of two species with contrasting shade tolerances (Chapter 3). In particular, the aims are:

- To compare different cutting scenarios by hypothesizing that at similar levels of harvest intensity, gap creation, cutting from below, removing shade-tolerant species (species-specific cutting), cutting randomly and cutting from above respectively induced high to low responses in transmitted light ( $H_1$ );
- To test whether our first hypothesis is general or depends upon initial stand structure ( $H_2$ );
- To identify the combinations of cutting scenarios that maximize the understory area receiving 10–20 % (levels favorable to regeneration of shade-tolerant species) or 20–40 % (levels favorable to regeneration of mid-tolerant species) and above 40 % (little light limitation for most regeneration) of above canopy light.

## 5.1 METHODS

### 5.1.1 Study sites

In the Belgian Ardennes, we selected 27 sites with varying stand structures and compositions, and with established regeneration of oak and (or) beech (Chapter 2). These studied stands characterized the diversity of forest structures that can be found during forest succession from early-successional oak forests to late-successional pure beech forests (Figure 5.1).

Every tree with a circumference greater than 40 cm was mapped and measured. We measured the circumference at breast height, total height, and height to the base of the crown for each tree. On 13 sites, we also measured at least 4 crown radii for every tree. Besides oak and beech, our data set contained 7 % hornbeam (*Carpinus betulus* L.), 4 % small coniferous trees (*Pseudotsuga menziessi* (Mirb.) Franco, *Picea abies* (L.) Karst, and *Pinus sylvestris* L.), 2 % birches (*Betula pendula* Roth, *Betula pubescens* Ehrh.), and 2 % other broadleaved species (*Acer pseudoplatanus* L., *Acer platanoides* L., *Sorbus aucuparia* L., and *Corylus avellana* L.).

The inventoried plots had an oval shape of variable area because they surrounded fenced areas in which advanced regeneration has been studied

(Chapter 3). Trees were measured if they were located at a distance of less than 20 m from the fence. Plot area ranged from 2070 m<sup>2</sup> to 10 540 m<sup>2</sup> with an average of 4340 m<sup>2</sup>.

### 5.1.2 Light model settings

We set SamsaraLight to sample 130 diffuse and 81 direct ray directions for each month of the growing period (from April to October). Ray directions are sampled at regular increasing zenithal angles with a starting value of 10° and an angle step of 15°. For every direction, parallel rays are cast at ground level in either cell centers or any other specified locations (virtual sensor). SamsaraLight then identifies the interceptions of light rays by tree crowns and computes radiation attenuation using Beer's law (Equation 4.1).

SamsaraLight predicts transmitted light within a rectangular plot. Since our inventory plots were not rectangular, we developed an algorithm that added virtual trees in order to obtain a rectangular plot (Figure 5.2). For each site, virtual trees were randomly drawn with replacement from the measured trees. Their location outside the inventoried area was then randomly generated. This process was repeated until the basal area of the rectangular plot equaled the basal area of the inventoried plot. The number of virtual trees created in each plot ranged between 0 and 68, and the area over which they were simulated represented on average 28 % of the rectangular plot area. The dimensions and foliage density of the modeled crowns were measured and estimated as described in Section 4.2.5.

SamsaraLight additionally required monthly meteorological records of total and diffuse irradiances in MJ m<sup>-2</sup>. We computed such monthly averaged data from data recorded between 2007 and 2011 by the meteorological institute of Belgium in Humain (50°33'N 5°43'E). Furthermore, we set SamsaraLight to predict percentages of above canopy light (PACL) at 2 m above the forest floor at each intersection of a 7 × 7 rectangular grid (Figure 5.2). We thus obtained 49 estimates of PACL for each simulation.

### 5.1.3 Cutting scenarios

For the 27 inventoried stands, we simulated 5 cutting types that reproduced 5 silvicultural regeneration strategies commonly practiced in forests of the Belgian Ardennes; namely: cutting from above, cutting from below, gap creation, species-specific cutting and uniform cutting (Table 5.1). Cutting from above harvests the most valuable trees. Typically, the trees with a diameter greater than the exploitable diameter are cut, i.e., these are diameter limit cuts. In contrast, cutting from below harvests small trees with low economic value. Such a strategy is typically applied to promote the growth of dominant trees, increase light for natural regeneration and mimics self-thinning. Cutting that creates gaps are especially used to increase light for a clump of saplings and promote regeneration. Species-specific cutting has been practiced recently because oak has become scarce. Therefore, foresters conserve

oak seed trees even if, for example, their diameter exceeds the exploitable diameter or if they are wounded. Finally, we simulated uniform cuttings in which trees were randomly harvested. This scenario can be considered to be the control treatment.

The 5 algorithms of the 5 cutting types started computing  $score_t$  (Table 5.1) for every tree and then cut the trees by order of decreasing  $score_t$  until the harvest intensity level was reached.  $score_t$  computed for cuttings from below and from above were on average greater for narrow and large trees, respectively.  $score_t$  included a random component that ensured that tree selection differed between simulations. The weight given to this random contribution for the cuttings from above and from below was set to 0.2 so that the distribution of the diameter of cut trees followed a realistic normal distribution. Gap creation scenarios harvested trees around a random location that must lie within the central part of the plots (Figure 5.2). Furthermore with cutting intensities greater or equal to 0.4, the gap radius was often greater than 20 m which corresponded to the buffer distance between the plot boundary and the central part of the plots (Figure 5.2). In such cases, the gap shape became a truncated circle. These algorithms are now available in Capsis (Dufour-Kowalski et al., 2012) for most individual tree growth models.

The 5 cutting types were applied to the 27 stands with 4 different levels of harvest intensity (10 %, 20 %, 40 % and 60 % of initial plot basal area). Since the algorithms of every cutting type had stochastic components, we repeated the simulation 10 times. For each simulation, 49 estimates of PACL were computed according to the grid introduced in Section 5.1.2. We therefore tested 20 cutting scenarios with 5427 simulations and 265 923 computations of  $PACL_{\text{model}}$ .

#### 5.1.4 Statistical analyses

In order to compare the different scenarios, we computed the differences between the average of the 49 estimates of transmitted light before and after harvesting ( $\Delta PACL$ ). Then, we adjusted a linear mixed model (Equation 5.1 with lme4 R package (Bates et al., 2013) to quantify the relationship between  $\Delta PACL$  and cutting intensity ( $I_i$ ).

$$\begin{aligned} \Delta PACL &= (b_l + \beta_{jl}) I_i + \epsilon_{ijkl} \\ \beta_{jl} &\sim N(0, \theta_\beta) \\ \epsilon_{ijkl} &\sim N(0, \theta_\epsilon) \end{aligned} \tag{5.1}$$

With  $i, j, k, l$  the indices corresponding to the cutting intensity, plot, the simulation run and the cutting type, respectively.  $b_l$  was the fixed-effect parameter which was estimated for each  $l$  cutting type.  $\beta_{jl}$  was a random-effect parameter varying between plot and cutting type. Similarly to the residual term,  $\beta_{jl}$  followed a centered normal distribution. This model assumed that  $\Delta PACL$  was proportional to  $I_i$  and that the slope of this relationship ( $b_l + \beta_{jl}$ )

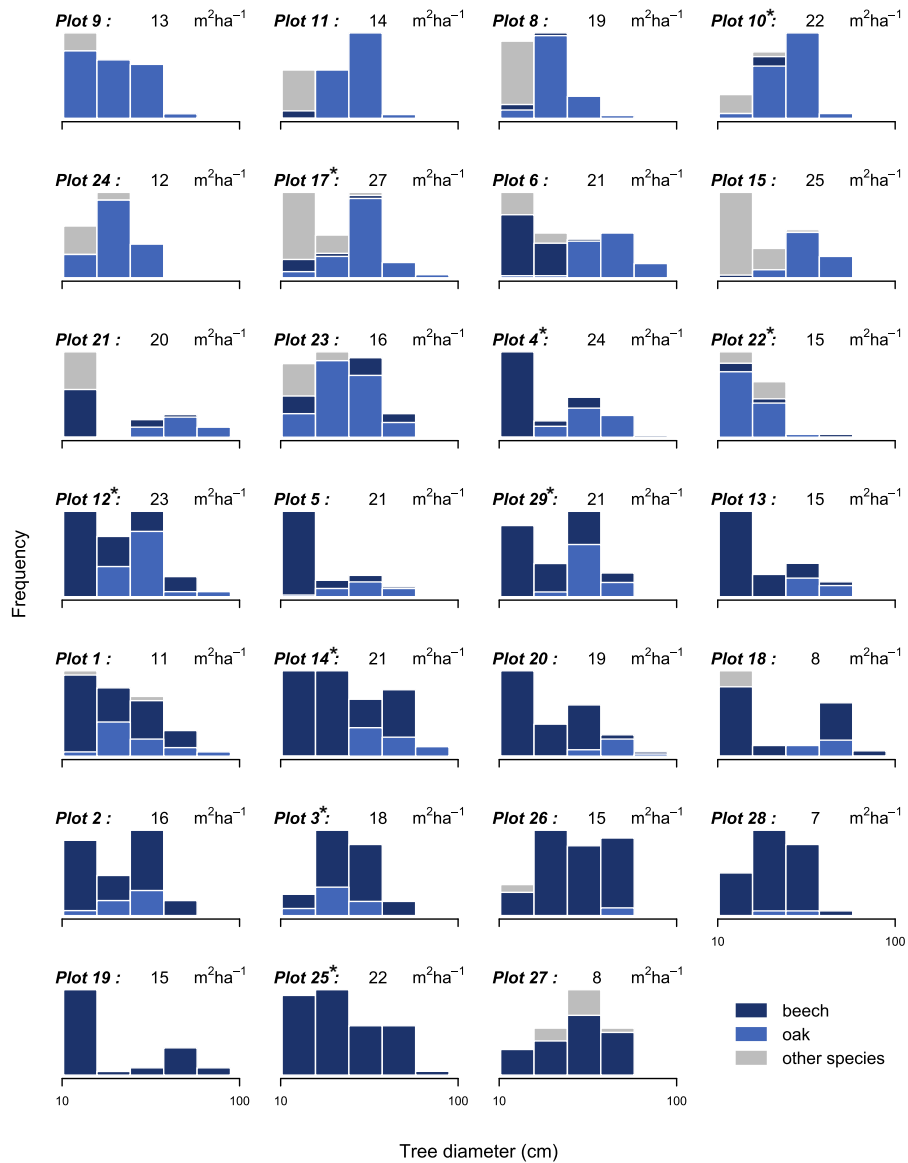


Figure 5.1: Stand structure and composition of the 27 studied plots expressed as tree frequency by diameter class. The charts are sorted by decreasing proportion of oak. Plot basal area is reported next to the plot id number showing no trend between plot basal area and plot composition. The asterisks next to plot id numbers denote the 9 plots where initial mean percentage of above canopy light (PACL) was below 20 %.

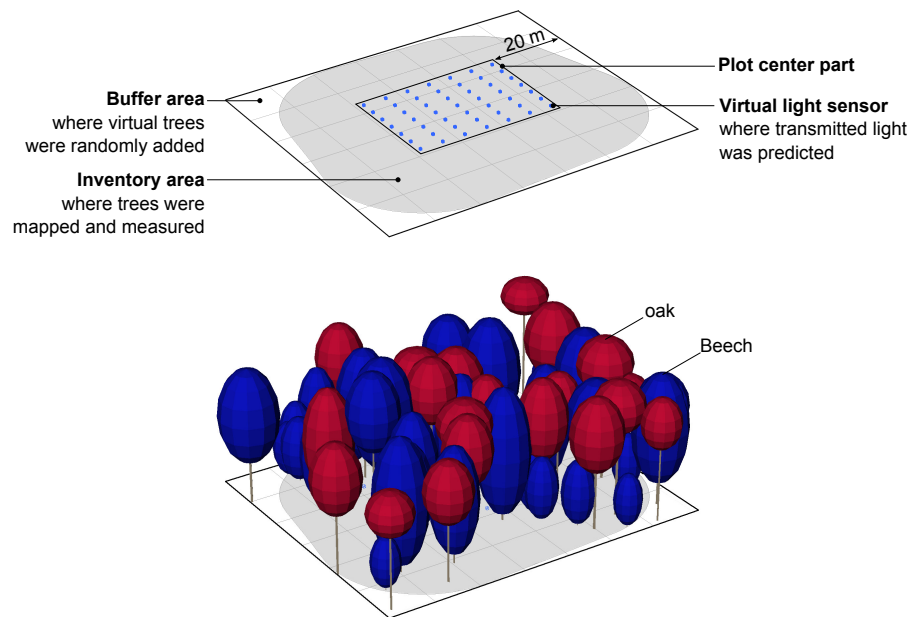


Figure 5.2: Three dimensional visualizations of the different zones within a plot with and without trees. In order to evaluate the cutting scenarios, our model was set to predict the percentage of above canopy light at 2 m above forest ground and at every intersection of a  $7\text{ m} \times 7\text{ m}$  grid within the center part of the plots.



Table 5.1: Description of the 5 cutting types. With  $(x_t ; y_t)$  the tree coordinates,  $(x_g ; y_g)$  the random gap center coordinates that must be within the central part of the plot (i.e., within  $(x_{min}, x_{max}, y_{min}, y_{max})$ ,  $dbh_t$  the diameter of tree  $t$ ,  $dbh_{min}$  and  $dbh_{max}$  the minimum and maximum of dbh,  $u$  a random number generated between 0 and 1.

CUTTING TYPE	DESCRIPTION	$score_t$
Uniform cutting	Random harvest of trees	$score_t \sim u$
Species-specific cutting	Preferential harvest of beech and hornbeam ( $\beta = 2$ ), then the other species ( $\beta = 1$ ) and finally oak ( $\beta = 0$ )	$score_t = \beta + u$
Cutting from below	Preferential harvest of small trees	$score_t = 0.2u + 0.8 \left(1 - \frac{dbh_t - dbh_{min}}{dbh_{max} + dbh_{min} + 1}\right)$
Cutting from above	Preferential harvest of large trees	$score_t = 0.2u + 0.8 \left(1 - \frac{dbh_{max} - dbh_t}{dbh_{max} + dbh_{min} + 1}\right)$
Gap creation	Harvest of all trees around a gap center. The location of the gap center was determined at random but must be within the central part of a plot (Figure 5.2).	$score_t = \sqrt{(x_t - x_g)^2 + (y_t - y_g)^2}$ $x_g \sim U_{[x_{min}, x_{max}]}$ $y_g \sim U_{[y_{min}, y_{max}]}$

varied with cutting type and initial site conditions. The hypothesis  $H_1$  was tested computing the approximate confidence intervals of  $b_l$ . These confidence intervals were obtained from the likelihood profile of  $b_l$  (Bates et al., 2013).

In order to further analyze how initial stand structure affected the response ( $H_2$ ), we fitted five additional models that included the effects of 5 different stand structure parameters (denoted by  $P_j$  in Equation 5.2). These parameters were stand basal area, quadratic mean diameter, basal area proportion of oak, standard deviation of dbh, Clark-Evans aggregation index and basal area of trees with dbh smaller than 25 cm. With the exception of the latter parameter, they have commonly been used to describe stand density and structure in similar studies (Sprugel et al., 2009; Beaudet et al., 2011; Lafond et al., 2013). These indices describe the stand density and structure before harvest. The Clark-Evans aggregation index (Equation 5.3) gives values greater than 1 for regular tree distributions and lower than 1 for aggregated tree distributions. The basal area of small trees was added because poles and small trees were sometimes abundant in the understory and were expected to capture a high proportion of transmitted radiation. We tested the addition of the corresponding fixed-effect parameter  $c_l$  with the log likelihood ratio test (Bates et al., 2013).

$$\Delta\text{PACL} = (b_l + c_l \cdot P_j + \beta_{jl}) \cdot I_i + \epsilon_{ijkl} \quad (5.2)$$

$$CE = \frac{\bar{r}}{0.5 \sqrt{A/N}} \quad (5.3)$$

where  $\bar{r}$  is the mean distance between trees and their nearest neighbor,  $A$  the plot area and  $N$  the number of trees within the plot.

Next, we created four classes of PACL. These classes had PACL values ranging between 0–10 %, 10–20 %, 20–40 %, and 40–100 %. They corresponded respectively to light levels that are unfavorable to natural regeneration of tree species, favorable to beech sapling growth, favorable to beech and oak sapling growth and above light saturation point (Chapter 3).

Furthermore, we computed the average frequency of the predictions by PACL classes and cutting intensity. In order to provide a guide to forest managers, we repeated these computations replacing the harvest intensity by the resulting post-harvest basal area. We restricted these analyses to the 9 plots where the mean PACL before cutting was less than 20 %, i.e., where cutting was necessary to promote the natural regeneration of less shade-tolerant species.

## 5.2 RESULTS

### 5.2.1 *Tree inventory*

According to the field data, stand composition and stand density varied considerably among study sites (Figure 5.1 and Table 5.2). The proportion of oak in the overstory ranged between 0 % and 98 %. High proportions of oak occurred mostly in stands with high basal area ( $r = 0.389$ ,  $P = 0.045$ ) and low quadratic mean diameter ( $r = -0.523$ ,  $P = 0.004$ ). Additionally, in some sites, the distribution of tree diameters followed an inverted j-shaped curve while in other sites it approximated a bell-shaped curve (Figure 5.1). Tree aggregation was greater in stands with complex vertical structure. Clark-Evans aggregation index was indeed negatively correlated with the standard deviation of tree diameter ( $r = -0.500$ ,  $P = 0.008$ ).

### 5.2.2 *Cutting scenarios*

The different cutting scenarios harvested the same quantities of basal area but caused very different modifications to stand structure. Firstly, post-harvest density varied notably between cutting scenarios. Cutting from below harvested the greatest number of trees while cutting from above harvested the fewest number of trees. The other cutting scenarios harvested an intermediate number of trees.

Secondly, harvests affected stand composition. Species-specific cutting increased the proportion of oak trees. Moreover, because the understory was mainly composed of shade-tolerant species (beech and hornbeam), cutting from below also tended to increase the proportion of oak trees. Cutting from above tended to harvest more oak trees than the other scenarios.

Thirdly, stand spatial structure was little affected by harvests except by gap creation. Gap creation increased the aggregation of trees as indicated by a reduction in the Clark-Evan aggregation index. Even at low harvest intensity, large gaps were created and remaining trees were aggregated along gap periphery. For example, removal of 10 % and 20 % stand basal area using gap harvesting led to an average opening of 475 m<sup>2</sup> and 1182 m<sup>2</sup>, respectively.

### 5.2.3 *Simulation*

The increase in understory light levels ( $\Delta\text{PACL}$ ) varied significantly between the cutting scenarios as illustrated by Figure 5.3 and the results of the adjusted model (Table 5.3). In agreement with our first hypothesis ( $H_1$ ), the cutting types ordered by decreasing  $\Delta\text{PACL}$  response were: gap creation, cutting from below, species-specific cutting, uniform cutting and cutting from above. This hypothesis was verified by ordering the slopes of the relationship ( $b_l$ ) between changes in PACL and cutting intensity for all the scenarios. The slope of this relationship was statistically different among cutting treatments except between cutting from below and species-specific cutting.

Table 5.2: Stand structure and composition in the studied sites. The presented parameters are density (N), basal area (BA), quadratic mean diameter (Dg), the Clark-Evans aggregation index (CE) and the minimum ( $dbh_{\min}$ ) and maximum ( $dbh_{\max}$ ) of tree diameter. Plots are ordered by increasing oak proportion.

Site	STAND				OAK				BEECH			
	N	BA	Dg	CE	BA	Dg	$dbh_{\min}$	$dbh_{\max}$	BA	Dg	$dbh_{\min}$	$dbh_{\max}$
19	98.3	14.94	43.98	0.96					14.94	43.98	12.73	84.35
25	127.2	21.84	46.75	1.05					21.84	46.75	13.05	84.35
27	35.3	7.82	53.13	1.05					6.45	52.97	12.73	72.57
28	51.4	7.47	43.04	1.19	0.28	47.42	41.70	52.52	7.19	42.89	12.73	64.94
26	61.7	14.60	54.89	1.27	1.94	75.76	75.76	75.76	12.63	53.62	14.32	78.30
3	113.6	18.10	45.03	1.07	3.17	39.42	28.01	60.16	14.93	46.57	14.32	65.57
18	46.7	7.52	45.29	0.97	1.40	62.32	54.43	64.30	6.06	45.33	12.73	79.90
1	87.2	11.15	40.34	1.18	2.86	44.33	27.06	65.25	7.90	39.35	12.73	71.62
2	113.9	16.33	42.73	0.97	4.35	49.30	16.23	59.21	11.95	41.35	12.73	72.26
14	124.5	21.21	46.57	1.28	6.70	65.64	54.43	82.76	14.51	42.00	12.73	69.71
20	143.9	19.49	41.52	1.04	6.97	71.87	55.70	92.31	12.52	35.46	12.73	80.53
29	127.0	20.56	45.41	1.20	11.14	55.42	40.43	68.12	9.42	38.53	12.73	65.25
13	133.8	15.37	38.25	1.09	8.69	60.21	46.15	72.89	6.68	28.70	12.73	69.71
5	217.8	20.51	34.62	1.03	11.95	53.87	17.83	71.30	8.56	25.67	12.73	68.12
12	156.6	22.65	42.92	1.16	13.61	53.24	39.47	80.85	9.04	34.74	12.73	75.76
4	207.3	24.16	38.52	0.97	16.70	57.73	38.20	72.26	7.46	25.72	12.73	84.03
22	216.5	15.31	30.00	1.12	11.07	29.02	13.69	49.66	3.62	43.36	17.51	77.99
21	120.3	19.54	45.48	0.97	14.71	73.06	57.61	94.86	3.91	31.51	12.73	76.39
23	121.5	16.31	41.35	1.00	12.41	43.87	14.64	75.76	2.76	45.31	14.32	77.03
15	190.5	24.69	40.62	1.06	19.80	57.21	32.15	71.62	0.06	13.05	12.73	13.37
17	188.5	26.89	42.62	1.31	22.27	54.85	24.51	73.85	1.76	29.13	12.73	49.34
6	107.5	20.79	49.62	1.12	17.38	66.59	28.97	89.76	2.51	27.71	12.73	49.02
10	135.2	21.65	45.15	1.29	19.29	48.99	16.55	59.52	1.06	30.41	29.60	31.19
8	215.3	19.06	33.58	1.08	17.31	40.77	16.55	63.03	0.23	21.35	13.05	30.56
24	111.9	11.80	36.64	1.30	10.85	40.35	20.05	55.07				
11	114.6	14.44	40.05	1.00	13.51	48.22	12.73	66.85	0.23	19.69	17.51	21.65
9	122.5	12.74	36.40	1.25	12.46	37.54	13.24	69.71				

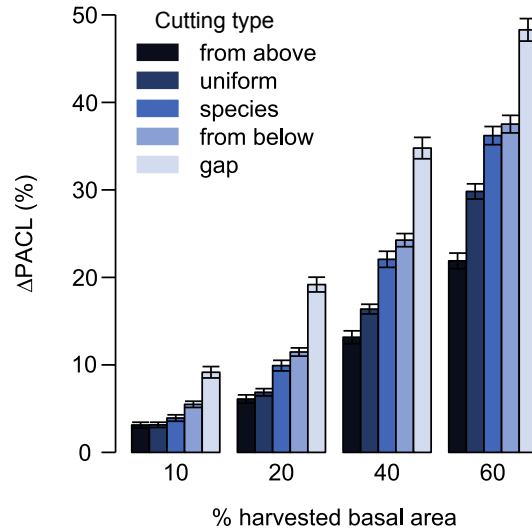


Figure 5.3: Mean increase of transmitted light levels ( $\Delta\text{PACL}$ ) by cutting scenario and by intensity. The adjusted mixed model indicated that the differences between cutting types are significant (Table 5.3) and accentuated as cutting intensity increased. Gap creation induced the greatest  $\Delta\text{PACL}$  responses.

We found no evidence that the relationship between  $\Delta\text{PACL}$ , cutting type and cutting intensity depended upon the initial stand structure. All likelihood ratio tests indicated that adding any stand parameter  $P_j$  in the model (Equation 5.2) did not significantly improve it. Within the conditions of our sampled study sites, our first hypothesis appeared rather general and independent of initial stand conditions. Furthermore, the between-site variability of  $\Delta\text{PACL}$  response ( $\theta_\beta$  ranged from 0.172 to 3.870) was limited in comparison to the within-site variability ( $\theta_\epsilon = 4.150$ ).  $\Delta\text{PACL}$  response depended more likely upon the conditions of the immediate surroundings of the measurement point rather than on general stand structure.

For the 9 plots where initial mean PACL was below 20 % (Figure 5.1), we analyzed the percentage of understory area receiving PACL ranging between

Table 5.3: Fixed-effect estimates,  $b_l$ , of the adjusted model (Equation 4.1) with approximate confidence intervals with  $\alpha = 0.05$  (CI) and standard errors. Our model assumed that any removal of 1 % of stand basal area induced an increase in PACL of  $b_l$ . additionally,  $\theta_\beta$  is the standard deviation of the random effect and indicated the variability of this relationship between plots.

CUTTING TYPE	$b_l$		$\theta_\beta$
	Estimate	CI	
gap creation	0.835	0.76;0.90	1.580
cutting from below	0.615	0.57;0.67	2.635
species-specific cutting	0.579	0.53;0.63	3.148
uniform cutting	0.459	0.43;0.48	3.870
cutting from above	0.349	0.30;0.40	0.172

0–10 %, 10–20 %, 20–40 % or 40–100 %. Contrary to  $\Delta$ PACL, changes in percentage of microsites above a given light level depended noticeably upon an interaction between cutting type and harvest intensity (Figure 5.4) or post-harvest basal area (Figure 5.5).

As most plots received an average of more than 10 PACL before harvest, the proportion of understory area receiving less than 10 PACL decreased with harvest intensity (Figure 5.4a). The proportion of microsites receiving 10–20 PACL also decreased rapidly with harvest intensity. Nevertheless, harvesting only 10 % of stand basal area did not significantly reduce the proportion of these microsites except with gap creation (Figure 5.4b). A cutting intensity of 10 %, with all cutting types but gap creation, maintained basal area around 15–20 m<sup>2</sup> ha<sup>-1</sup> (Figure 5.5).

The different cutting scenarios provided very different proportions of microsites receiving 20–40 PACL which is the range of light conditions that promotes the less shade-tolerant oak (Figure 5.4c and Figure 5.5c). Gap creation maximized this proportion at 10 % harvest intensity (target basal area 20–25 m<sup>2</sup> ha<sup>-1</sup>) but, at higher harvest intensities, very little area was in the 20–40 PACL range. Cutting from below and species-specific harvesting maximized the proportion of microsite receiving 20–40 PACL at about 20 % of harvest intensity (target basal area of 15–20 m<sup>2</sup> ha<sup>-1</sup>) but they provided more than 40 % of the area in the 20–40 PACL range in all but the most intense harvesting scenario. Uniform cutting maximized the area receiving 20–40 PACL at about 40 % of harvest intensity (target basal area of 10–15 m<sup>2</sup> ha<sup>-1</sup>) whereas cutting from above provided about 40 % of the area in the 20–40 PACL range independently of harvest intensity.

Cutting from above maintained a remarkably high proportion of microsites with less than 20 PACL at all cutting intensities and only created a low proportion of microsites with more than 40 PACL (Figure 5.4d). In contrast, the proportion of microsites with more than 40 PACL was the greatest for all cutting intensities with gap creation. The difference in microsite with greater than 40 PACL between gap-harvesting and the other cutting types was particularly notable at harvest intensity of 20 %.

### 5.3 DISCUSSION

#### 5.3.1 Mean light response to the different cutting scenarios

The different cutting types led to different increases in mean PACL that were ordered according to our first hypothesis ( $H_1$ ) independently of initial stand structure and composition (in contradiction with  $H_2$ ). On average, harvesting 10 % of stand basal area increased mean PACL by about 8.4 % with gap creation, 6.2 % with cutting from below, 5.8 % with species-specific cutting, 4.6 % with uniform cutting and 3.5 % with cutting from above (Table 5.3 and Figure 5.3).

Similar to the findings of numerous studies (Canham et al., 1994; Cescatti, 1997a; Brunner, 1998; Stadt and Lieffers, 2000; Beaudet and Messier, 2002;

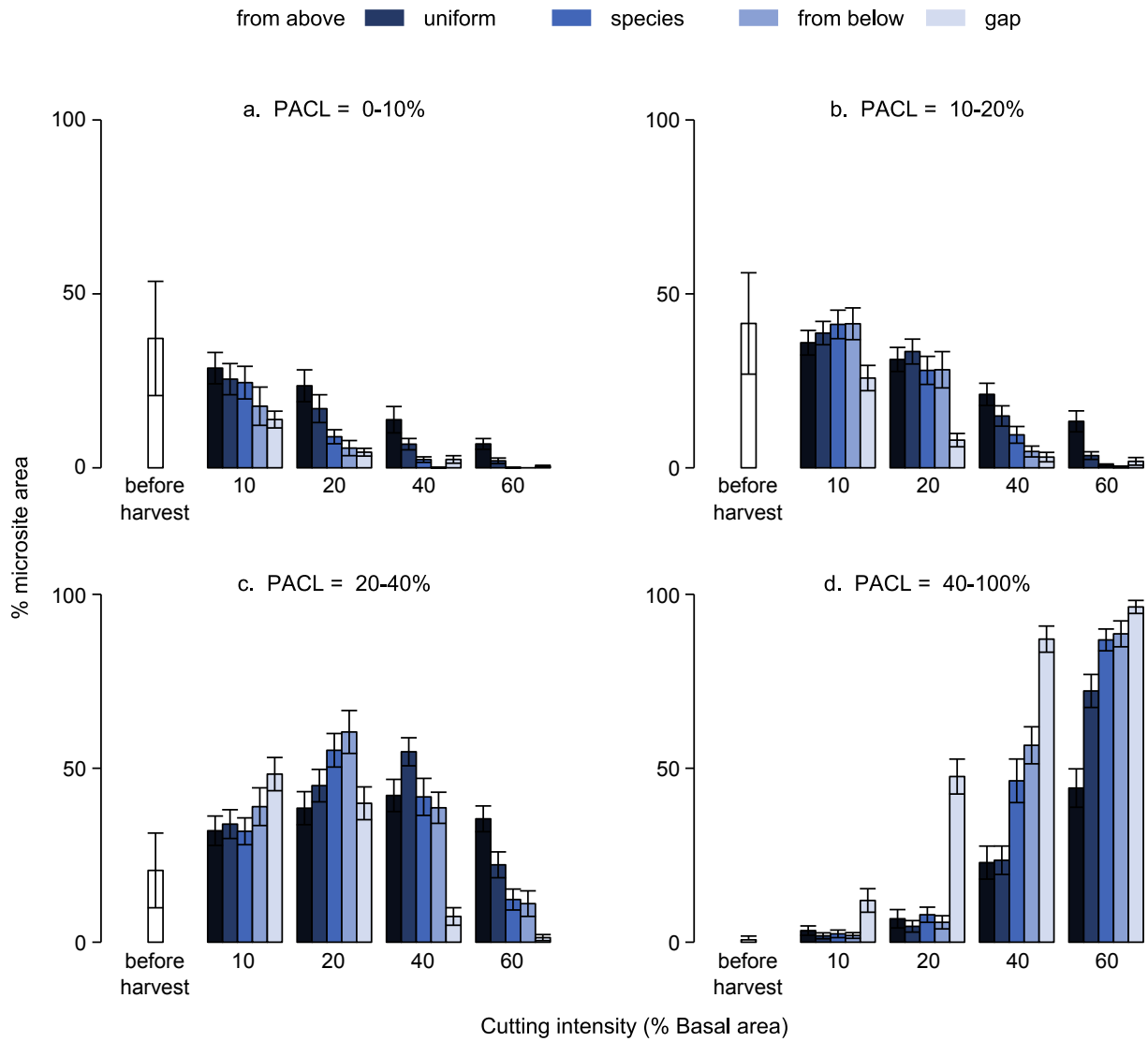


Figure 5.4: Frequency of microsites with percentage of above canopy light (PACL) ranging between 0–10 %, 10–20 %, 20–40 % and 40–100 %. These frequencies were computed by harvest intensity in the 9 plots where initial mean PACL was below 20 %. The proportion of microsites with PACL of 0–10 (a) or 10–20 (b) was high prior to cutting (white bar on the left). This proportion decreased the most rapidly with gap creation in contrast with cutting from above. High proportions of microsites receiving 20–40 PACL (c) were obtained with 10 % gap creation, 20 % cutting from below, 20 % species-specific cutting, or 40 % uniform cutting.

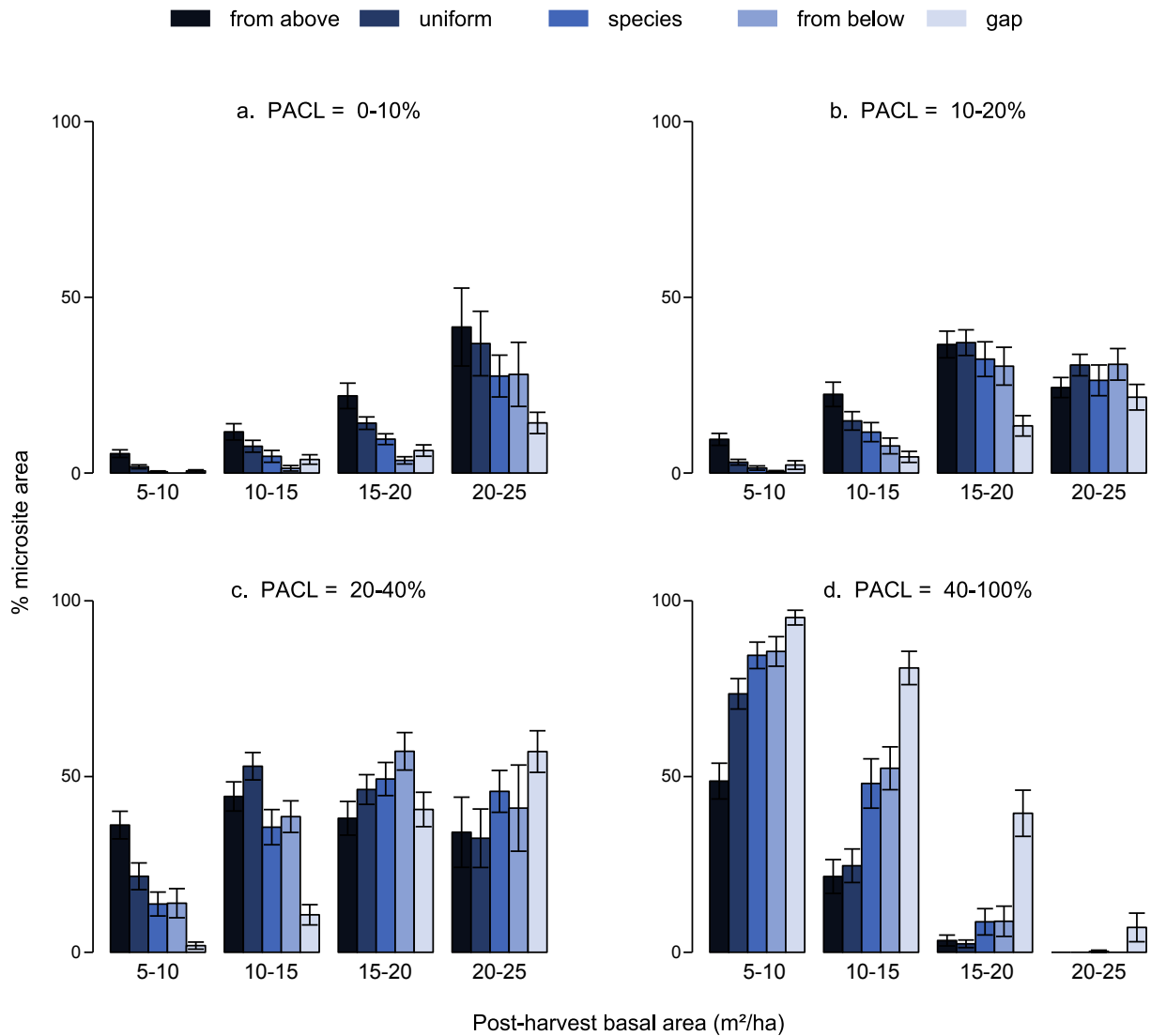


Figure 5.5: Frequency of microsites by class of percentage of above canopy light (PACL) and post-harvest basal area. The frequencies were computed from the 9 plots where initial mean PACL was below 20% and, next, averaged by classes of post-harvest basal area. Cutting scenarios that maximized the understorey area receiving 10–20 PACL (b) reduced stand basal area to about 15–20  $m^2 ha^{-1}$ . Cutting From above only slightly affected the proportion of microsites with 20–40 PACL (c). High proportions of microsites with 20–40 PACL were obtained with cutting that created gaps that reduced basal area to 20–25  $m^2 ha^{-1}$ , with cutting from below that reduced basal area to 15–20  $m^2 ha^{-1}$ , or with uniform cutting and cutting from above that reduced basal area to 10–15  $m^2 ha^{-1}$ .



Beaudet et al., 2011; Da Silva et al., 2011), the main factor limiting understory light was the absence of gaps between crowns. Consequently, at similar cutting intensities, harvests that create gaps strongly increased understory light. Additionally, we only considered immediate post-harvest conditions while the evolution of understory light several years after cutting may lead to increased or reduced differences between treatments. In particular, the increase in understory light due to the creation of large gaps would be expected to last longer than the effects of the other cutting types since larger openings would take longer to close (Sprugel et al., 2009).

Another factor that strongly limits light availability for regeneration is the presence of a sublayer of shade-tolerant species. We already noticed this influence of a dense understory when evaluating the performance of our light model (Chapter 4). In addition, our simulation confirmed that understory trees might intercept a large proportion of light and that cutting from below can increase significantly understory light levels and can therefore be essential to promote the regeneration of less shade-tolerant species.

Preferentially harvesting shade-tolerant species, i.e., species-specific cutting, increased more transmitted light than harvesting trees randomly. Trees of shade-tolerant species intercept more light than trees of less shade-tolerant species since they have wider, deeper and denser crowns (Table 4.8, Table 4.10 and Table 4.12). Additionally, shade-tolerant species are usually more abundant in the understory than less shade-tolerant species. Species-specific cutting therefore tend to harvest a high proportion of poles and small trees similarly to the cutting from below.

### 5.3.2 *Optimum cutting scenario*

The optimum cutting scenario within the context of this study maximized the understory area that is favorable to the natural regeneration of less shade-tolerant species, i.e., the area receiving 20–40 PACL. Contrary to mean PACL, the area receiving 20–40 PACL depended upon the interactions between cutting type and cutting intensity. High proportions of microsites with 20–40 PACL were obtained by either harvesting few trees or by harvesting more than 50 % of stand basal area.

Creating gaps appears particularly promising to promote small clumps of oak regeneration with limited reduction of stand stocking. Harvesting the few trees located within and around these clumps largely increase the proportion of microsites with 20–40 PACL. In our simulations, the gaps that maximize this proportion of microsites are about 470 m<sup>2</sup> in size which corroborates the recommendations by von Lüpke (1998) and Bruciamacchie and de Turckheim (2005) as well as the observations of Rugani et al. (2013) in old growth beech forests. These authors reported that oak regeneration was possible in gaps of at least 500 m<sup>2</sup> created by harvesting 4–5 mature trees (Bruciamacchie and de Turckheim, 2005). Larger gaps increase the proportion of microsites with more than 40 PACL and should likely be avoided during the first stages of regeneration development because such conditions are favorable to the rapid development of competitive herbaceous species (Gaudio et al., 2008, 2011).

Cutting from below and cutting preferentially shade-tolerant species were the best techniques to promote the recruitment of less shade-tolerant regeneration especially if saplings were uniformly spread in the understory as it happens after generalized masting. For the studied stands, the optimum harvest intensity was about 20 % which corresponded approximately to a target basal area of about 15–20 m<sup>2</sup> ha<sup>-1</sup>.

Randomly cutting trees requires a greater harvest intensity to maximize the proportion of microsites with 20–40 PACL than gap creation, cutting from below and species-specific cutting. We obtained an optimum number of microsites with 20–40 PACL with a harvest intensity of 40 % which corresponded to a target basal area of about 10–15 m<sup>2</sup> ha<sup>-1</sup> and agrees with the results obtained by [Balandier et al. \(2006b\)](#) in even-aged oak stands.

Cutting from above maintained large understory areas receiving less than 40 % full light. It maintained a more asymmetric right-skewed distribution of PACL ([Beaudet et al., 2011](#)) than the other cuttings and, hence, a high proportion of microsites in shady conditions even after harvesting up to 60 % of stand basal area. By preferentially eliminating large overstory oaks and maintaining low-light levels in the understory, this treatment can be expected to quickly lead to a successional transition to dominance by shade-tolerant species.

In conclusion, promoting less shade-tolerant species can be achieved with various regeneration treatments. Forest managers should consider whether the seedlings of less shade-tolerant species are aggregated or uniformly spread, whether a small reduction in stand stocking is more appropriate, and what is the desired composition of the different tree layers after harvest. The results from this study provide foresters with the necessary tools to evaluate how silvicultural treatments can be manipulated to create or maintain favorable conditions for the regeneration of species of different shade tolerances.



*Science goes from question to question; big questions, and little, tentative answers. The questions as they age grow ever broader, the answers are seen to be more limited.*

George Wald

#### 6.1 MAINTAINING THE MIXTURE OF SPECIES WITH CONTRASTED SHADE TOLERANCES

The main purpose of this thesis was to determine how forest managers could maintain a mixture of species with contrasting shade tolerances in uneven-aged and mixed forests that are managed using continuous-cover forestry systems.

The results suggest that maintaining a mixture of species with contrasting shade tolerances requires fine control of understory light to promote regeneration of the different species. Such a control of understory light can be achieved by controlling the density and structure of the overstory with partial cutting. Moreover, regeneration cleaning may be essential to suppress regeneration of the shade-tolerant species and to promote regeneration of the less shade-tolerant species.

Understory light was found to be a key parameter in the dynamics of heterogeneous stands, as it affects regeneration growth and composition. There

are interspecific differences in survival and growth response to the availability of light. Under the deep shade of a closed canopy (PACL < 5 %), only small seedlings of shade-tolerant species are able to survive (Madsen and Larsen, 1997; Emborg, 1998; Le Duc and Havill, 1998; Lieffers et al., 1999; von Lüpke and Hauskeller-Bullerjahn, 1999; Emborg et al., 2000; Collet et al., 2001; von Lüpke and Hauskeller-Bullerjahn, 2004; Collet and Chenost, 2006; Petriřan et al., 2007). Consistent with other studies, as understory light increases (PACL = 10–20 %), the seedlings of less shade-tolerant species are able to survive and grow, but the seedlings of shade-tolerant species grow faster and suppress the seedlings of less shade-tolerant species. After canopy release (PACL = 20–40 %), the regeneration of both shade-tolerant and less shade-tolerant species develops well (Dineur, 1951; Emborg, 1998; von Lüpke, 1998; Stancioiu and O'Hara, 2006a). Less shade-tolerant species require indeed greater amount of radiation than shade-tolerant species. Additionally, less shade-tolerant likely require sufficient amount of direct radiation that can be obtained after such canopy release (Diaci, 2002; Diaci et al., 2007). Following further canopy opening (PACL > 40 %), the growth of the regeneration saturates and becomes less sensitive to variations in light availability (Stancioiu and O'Hara, 2006a; Van Couwenberghe et al., 2013). Such large canopy openings alter the microclimate of the understory and regeneration can additionally suffer from the development of competitive herbaceous species (Gaudio et al., 2008).

The control of understory light is consequently an important issue, although it is also a difficult task. I explored different strategies that forest managers could apply to increase the availability of light to the understory. This work provided indications of how partial cutting can be manipulated to change stand composition and structure and how such changes affect understory light. The control of understory light requires controlling harvest intensity jointly with the location, size and species of the harvested trees. Different silvicultural treatments can be utilized to control understory light. For example, forest managers can preferentially harvest small or large trees, trees of shade-tolerant species, or aggregated groups of trees. All of these silvicultural strategies could provide satisfactory results as long as harvest intensity is adapted to the chosen strategy (Figure 6.1).

The results of this thesis also underscore the problem that even under good light conditions (PACL > 20 %), regeneration of less shade-tolerant species might not overcome the regeneration of shade-tolerant species. This finding goes against the theory of shade tolerance as proposed by Kobe et al. (1995) and the results of greenhouse experiments (Dreyer et al., 2005). Indeed, according to Kobe et al. (1995), there is a tradeoff between high-light growth and low-light survival. In low-light environments, shade-tolerant species survive better than less shade-tolerant species, whereas in high-light environments, shade-tolerant species grow slower than less shade-tolerant species. Nevertheless, the results of this thesis are in accordance with the observations of forest managers within the study area and with the recently published results of Van Couwenberghe et al. (2013) and

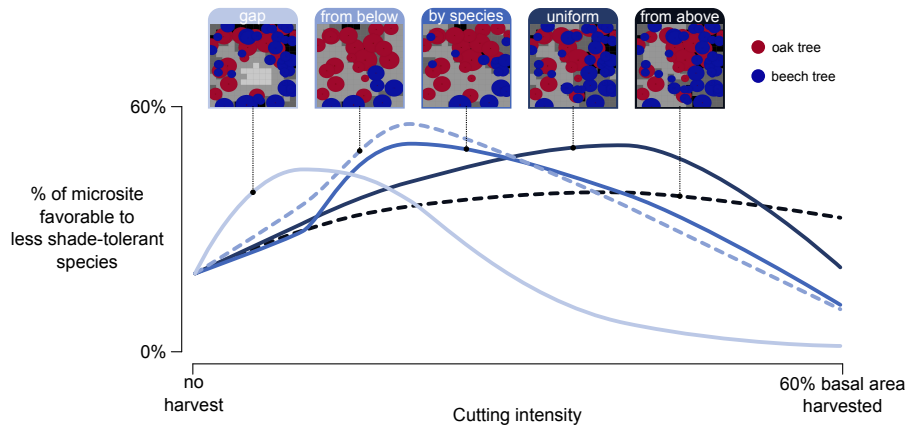


Figure 6.1: Post-harvest understory light conditions depend upon cutting intensity and cutting type. To maximize the understory surface that is favorable to regeneration of less shade-tolerant species, forest managers need to choose an adequate combination of cutting type and cutting intensity.

Petrișan et al. (2014), who studied the same two species in France and in Romania, respectively. Additionally, the suppression of the regeneration of less shade-tolerant species by regeneration of shade-tolerant species in high-light environments has been reported in other mixed forests: in France with mixtures of *Quercus pubescens*-*Fagus sylvatica* (Kunstler et al., 2005), in central Europe with mixtures of *Acer pseudoplatanus*-*Fraxinus excelsior*-*Fagus sylvatica* (Petrișan et al., 2009), or in Quebec with mixtures of *Acer saccharum*-*Fagus grandifolia* (Delagrange et al., 2010).

Consequently, maintaining less shade-tolerant species in stands with shade-tolerant species might require silvicultural interventions jointly in the overstory and regeneration layers. Establishing saplings of less shade-tolerant species may require competition from the saplings of shade-tolerant species to be decreased manually. The dominant saplings of less shade-tolerant regeneration would have a greater chance of survival if they are taller than any neighboring saplings of shade-tolerant species.

## 6.2 SILVICULTURAL RECOMMENDATIONS FOR MAINTAINING MIXTURES OF OAK AND BEECH

Beech saplings naturally outgrow oak saplings under a partially closed canopy. In addition, beech saplings usually establish before oak saplings and require half as much light to reach an optimum growth than do oak saplings. In these conditions, oaks are rapidly suppressed and mixed stands of oak and beech evolve naturally toward pure beech stands. The two species mainly coexist because beech naturally regenerates under well-established oak stands where oak has previously been favored by selective thinning, coppicing and plantations (Claessens et al., 2010). The reverse situation is unlikely to occur naturally without frequent disturbances (Messier et al.,

1999) and (or) disturbances that damage the beech regeneration (Reyes et al., 2010).

As a result, foresters applying continuous-cover silviculture need to proceed in three phases:

First, in waiting for the emergence of oak seedlings, they must maintain low-light levels in the understory (PACL < 5 %) to reduce the development of beech seedlings that continuously emerge under the canopy. Indeed, germination does not depend upon light conditions (Turbang, 1954; Welander and Ottosson, 1998; Chaar and Colin, 1999; Nicolini et al., 2000).

Second, reducing overstory density is essential to promote oak regeneration. This can be achieved with partial cutting that increases the availability of radiation to oak regeneration to about 20–40 PACL. The target basal area after partial cutting ranges between  $10 \text{ m}^2 \text{ ha}^{-1}$  and  $25 \text{ m}^2 \text{ ha}^{-1}$ , depending upon residual stand structure. The creation of gaps of about  $500 \text{ m}^2$  provides locally large amounts of radiation while minimizing the reduction of stand stocking. Preferential cutting of small trees and individuals of shade-tolerant species provides sufficient amounts of light with a target basal area of about  $15\text{--}20 \text{ m}^2 \text{ ha}^{-1}$ . Cutting without consideration of tree species, size and location requires a lower target basal area, i.e., about  $10\text{--}15 \text{ m}^2 \text{ ha}^{-1}$ . Preferentially cutting large trees maintains large areas in the understory with low-light availability, which favors shade-tolerant species. However, as saplings become taller, foresters need to gradually open the gaps and reduce residual stand density to satisfy the increasing light requirements of older saplings (Messier et al., 1999).

Third, given the ecological conditions of the Belgian Ardennes, oak could not be promoted over beech by only managing the overstory. Foresters need to frequently remove or break manually the dominant and co-dominant beech competitors that will systematically overtop oak saplings (von Lüpke, 1998), especially if beech seedlings were established before oak seedlings. At the end of this treatment, the dominant oak saplings must indeed dominate all remaining beech saplings.

### 6.3 STUDY LIMITATIONS AND PERSPECTIVES

This study provides us with a better understanding of the regeneration dynamics of uneven-aged stands with a mixture of species with contrasting shade tolerances. I was not able to study all of the processes that drive the dynamics of such a complex ecosystem. In the following discussion, I acknowledge the limitations of my work and, consequently, indicate remaining knowledge gaps and interesting research perspectives.

I assumed that the coexistence between tree species depends mainly upon interspecific differences in the development of established regeneration, as only the dominant saplings survive and reach the upper canopy layers. Even though the evolution of stand composition does not depend only upon competition between saplings of different species, the suppression of all saplings of a given species from the regeneration layer certainly affects future stand

composition because new regeneration establishment usually does not occur where there is abundant advance regeneration (Reyes et al., 2010). The composition of tree recruitment could additionally depend upon interspecific competition between poles and trees, interspecific differences in tree survival, seed production, seed dispersal, and seed germination.

I assumed that sapling survival depends upon the capacity of saplings to grow taller than their neighbors and, consequently, to capture a larger amount of solar radiation. Consequently, the analysis of regeneration height growth (primary growth) was prioritized over the analysis of regeneration diameter growth (secondary growth) and regeneration survival. Van Couwenberghe et al. (2013) studied the growth of regeneration of sessile oak and European beech in France and found that diameter growth is closely related to height growth. In their study, diameter growth of oak saplings was less than the diameter growth of beech saplings under all investigated light levels. Baudry (2013) had studied the survival of sessile oak and European beech in Belgium and demonstrated that sapling survival depends largely upon sapling capacity to dominate neighboring individuals. Moreover, a relationship can usually be found between sapling mortality and diameter growth (Kobe et al., 1995; Pacala et al., 1996). The probability of sapling mortality decreases as sapling radial growth increases. Sustained growth indicates good photosynthetic activity and reduces the period in which saplings are exposed to competition with neighboring vegetation or other agents that could cause damage such as wild game (e.g., deer) or disease (e.g., oak powdery mildew).

I assumed that the development of advance regeneration mostly depends upon light quantity, as expressed by the percentage of above canopy light. The findings of this thesis corroborate the paramount importance of the amount of light that is required for regeneration development and composition. Nevertheless, other factors certainly drive competition between species with contrasting shade tolerances because some of the results of this thesis are in contradiction with the results of other studies. Particularly, in a greenhouse experiments (Dreyer et al., 2005), saplings of sessile oak outgrew beech saplings in high-light conditions. While, in the field experiments that was performed for this thesis project, beech saplings dominated oak saplings under all of the study conditions, even though regeneration was measured over a wide gradient of light availability. In stands that are managed with continuous-cover forestry systems, the availability of light does not necessarily allow conditions to be identified in which the saplings of less shade-tolerant species outgrow saplings of shade-tolerant species. I hypothesize that other factors drive competition between species with contrasting shade tolerances, and subsequently explain why the saplings of less shade-tolerant species do not outgrow saplings of shade-tolerant species in bright understories. Different results could therefore be obtained in other areas or with other tree species. In particular, a rank reversal between the growth of species with contrasting shade tolerances along a light gradient has been observed and modeled in other mixed forests (Pacala et al., 1994).

Site conditions might also affect species performance ranks (Kobe, 2006; Valladares and Niinemets, 2008). Consequently, the promotion of less shade-tolerant species over shade-tolerant species does not automatically require regeneration tending. Among the factors that have already been identified as modifying the performance rank of species of differing shade tolerance, the availability of water likely plays a key role. The other factors that should be considered are tree ontogeny, nutrient availability, and sunfleck duration and frequency (Valladares and Niinemets, 2008).

Regeneration of less shade-tolerant species likely requires direct radiation whereas diffuse radiation can be enough for regeneration of shade-tolerant species (Diaci, 2002). Further investigations are required to better identify the requirements of regenerations to direct radiation and how forest manager can control the amount of transmitted direct radiation. I hypothesize that (i) an increase in the availability of direct radiation promotes the regeneration of less shade-tolerant species, (ii) post-harvest availability of direct radiation depends upon cutting type, and (iii) gap creation is the cutting type that induce the greatest increase in the availability of direct radiation.

The availability of understory light was investigated under particular conditions. The availability of understory light depends upon complex interactions between latitude, canopy height, topography, and foliage orientation and aggregation (Canham et al., 1990; Kuuluvainen, 1992; Prévost and Raymond, 2012). In the northern hemisphere, maximum solar elevation decreases with latitude and maximum light penetration through canopy gaps is offset northwards from the gap center (Figure 6.2). At high latitudes, the area receiving the largest gains in understory light is located closer to the northern gap edge or even under closed canopy. Consequently, the area receiving the largest gain in understory light does not coincide with the area of increased nutrient and water availability (Lieffers et al., 1999). Moreover, south-facing surfaces (sloping ground and leaves) receive greater amounts of energy from direct radiation than north-facing surfaces because direct radiation strikes the surface at an angle closer to the perpendicular. In hilly areas, some of the radiation entering at low elevation angles is also intercepted by the horizon. For example, west-facing slopes do not receive direct radiation at the beginning of sunrise. The study forests were around 50°N latitude, had a canopy height of about 30 m, and were present on gentle slopes. In different forest types, at different latitudes, and (or) on hilly terrain, different results could be obtained regarding the effects of partial cutting on understory light. For example, I hypothesize that (i) smaller gaps (and higher stand densities) are required on south-facing slopes or at lower latitudes in order to promote the regeneration of less shade-tolerant species, and (ii) cutting from below induces a lower increase in understory light at low latitude than at high latitude.

Furthermore, the availability of light for regenerating stems evolves through time due to canopy closure and growth of regeneration. In irregular forest stands that are managed with continuous-cover forestry systems, saplings, poles and trees react to canopy release. The crowns of poles



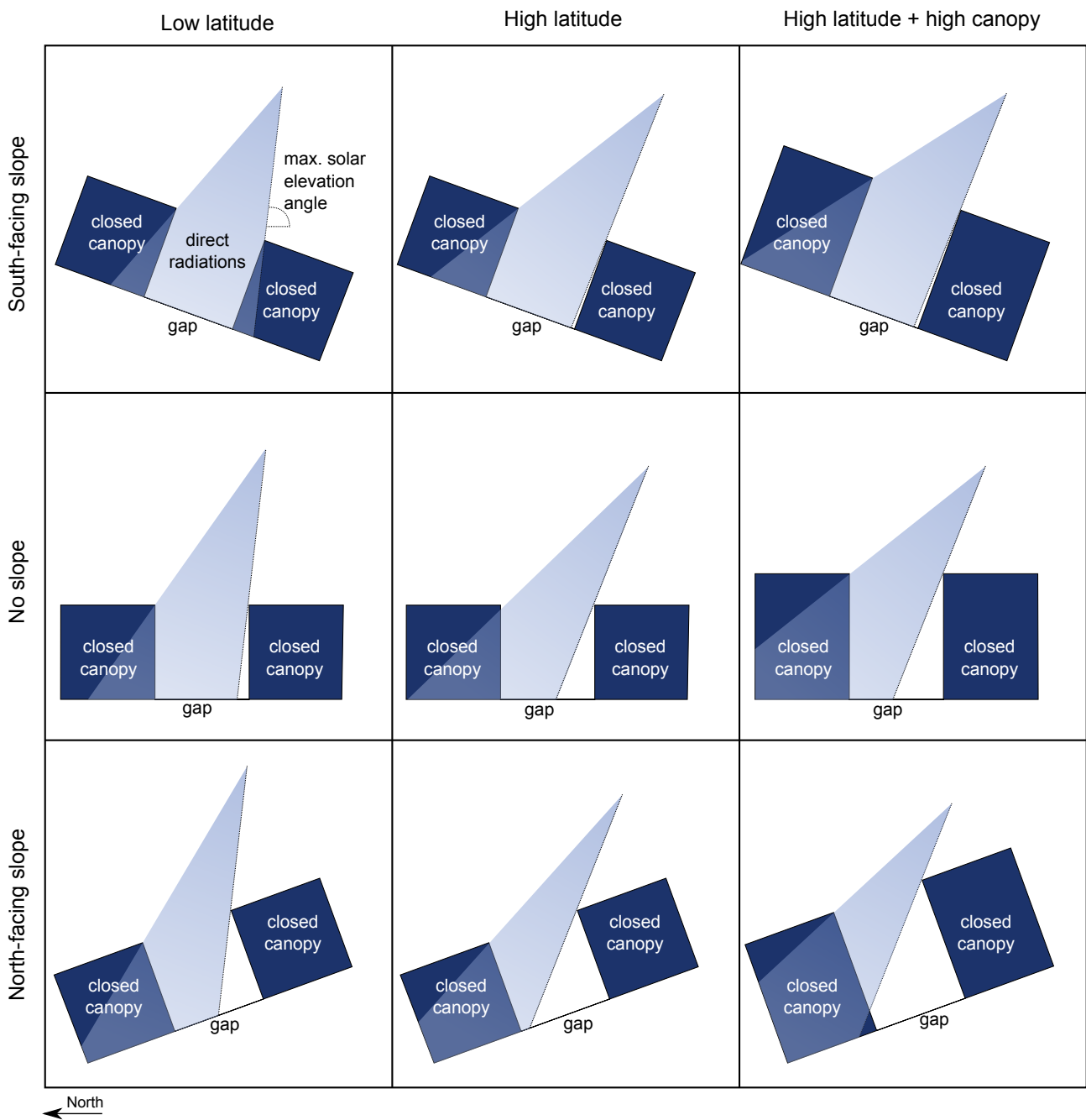


Figure 6.2: The transmission of direct radiation through canopy gaps depends upon the interaction between site latitude, forest type (e.g., canopy height), slope and aspect. For each combination of these factors, the figure schematically depicts the spatial distribution of direct radiation along a North-South transect that is centered on a canopy gap. The angular distribution of diffuse radiation can be considered as relatively uniform. Consequently, microsites in gap center receive the greatest amount of diffuse radiation.

and trees expand laterally and vertically. As saplings become taller, the availability of light does not necessarily increase because of the proximity of the crowns of poles and trees (Ban et al., 1998). Regeneration growing under the canopy or at the edge of canopy gaps can therefore face more rapid and more severe competition from the remaining trees and poles than does regeneration growing in the center of a canopy gap. When analyzing the effects of partial cutting, I considered understory light conditions immediately after the harvest, whereas different findings could have been obtained if I had considered understory light conditions several years after the harvest. Further work is required to tackle the modeling of canopy closure and investigate the evolution of understory light conditions with canopy closure. As gap centers, northern gap edges, and southern gap edges are microsites with different light regimes (Diaci, 2002)(Figure 6.3), some interesting hypotheses that could be tested are that (i) the availability of light to regenerating stems at gap edges decreases as regenerating stems become taller because of the competition with dominated trees and canopy closure, and (ii) there is a rank reversal over time in the availability of light between the gap center and northern gap edge.

The studied regeneration was protected from game browsing by fences, as browsing by wildlife is known to affect regeneration composition (Hidding et al., 2013; McGarvey et al., 2013). Indeed, palatable species are preferentially browsed by deer and less palatable species are therefore promoted. This is a severe limitation to the results of this thesis, especially if game populations are abundant. Depending upon the shade tolerance of the palatable species, game browsing can either promote shade-tolerant species (e.g., European beech versus sessile oak in the study area) or less shade-tolerant species (e.g., spruce versus fir in the Vosges mountains (Heuze et al., 2005) or on Anticosti Island (Casabon and Pothier, 2007; Hidding et al., 2013)). Within the studied area, I hypothesize that (i) abundant deer populations accelerate the transition of secondary forests to late-successional forests, (ii) density of deer populations is a more important factor than understory light availability to the diversity of understory regeneration, and (iii) maintaining the coexistence of beech and oak requires control of the density of wild game populations.

Competition between species is likely affected by changes in environmental conditions. Climate change displaces the ecological niches of species and ecosystem boundaries. Depending upon site conditions, species autecology and interspecific interactions, species will either benefit or suffer from climate change, which in the long run can modify stand composition (Bontemps et al., 2012; Mette et al., 2013). However, the effects of climate change on the dynamics of uneven-aged and mixed stands require further investigation. Interactions between the admixed species can attenuate the sensitivity of species to climate change (Pretzsch et al., 2013b). Therefore, it is unclear

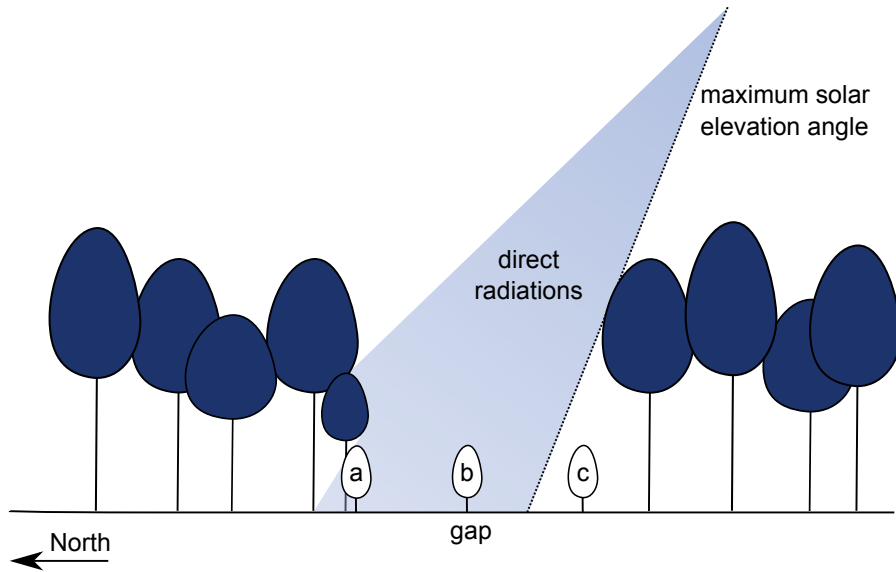


Figure 6.3: Northern gap edge (a), gap center (b) and southern gap edge (c) are microsites with different light regimes. The availability of light to saplings hypothetically decreases as saplings grow because of competition with dominated trees at gap edges; a rank reversal over time of the availability of light between the gap center and northern gap edge can be expected.

whether the findings about interspecific competition in the understory are likely hold under a future climate. Further studies should identify whether interspecific competition in the understory of uneven-aged forests, when managed with a continuous-cover forestry system, is sensitive to climate change.

The reaction of regeneration to a sudden increase in solar radiation due to canopy disturbances or silvicultural treatments was not investigated. Modification of stem allometry is expected in the years following canopy release (Collet et al., 2001), but further work is required to quantify the reaction of saplings to canopy release and assess the efficiency of regeneration cleaning. In particular, the growth of released saplings should be further studied in order to provide more precise silvicultural recommendations, such as the appropriate timing for regeneration tending.

In order to further generalize the findings of this thesis, the simulation approach that was outlined in this study should be replicated for other forest ecosystems with different species compositions, stand structures, topography, and at different latitudes. With this in mind, developing models of stand structure and crown dimensions would be particularly helpful. Such models would enable us to simulate the dynamics of stands with controlled density, composition and structure with limited field work. Rigorous experimental planning could hence be elaborated to identify clearly the importance of the various factors of understory light regime.

#### 6.4 CONCLUSION

The increasing awareness of decision makers and forests managers with respect to the necessity of preserving biodiversity and ecosystem services with sustainable management practices have provided the impetus for promoting a silviculture of mixed and uneven-aged stands that mimics natural processes. However, a lack of knowledge of the natural dynamics of such stands has hindered our ability to manage for some desired mixture of tree species.

In order to fill this gap, I modeled some key processes of the dynamics of mixed and uneven-aged stands. I modeled the development of mixed regeneration under partially closed canopies and the interception of light by heterogeneous canopies. I implemented these models in a simulation program to explore how these factors affect stand dynamics and how various silvicultural treatments can be manipulated to provide or maintain favorable understory light conditions for natural regeneration. The results provide guidelines for forest managers who want to maintain the coexistence of species with contrasting shade tolerances.

Finally, maintaining mixtures of species with different shade tolerances offers many advantages, but at the same time runs contrary to natural forest succession. Mixtures preserve forest biodiversity, forest productivity and ecosystem services, and enhance forest resilience. In the context of pursuing sustainable forest management practices combined with global change, maintaining species mixtures is a good strategy. However, continuous-cover silviculture of mixed stands with species of different shade tolerances requires many efforts to fight against the natural transition of secondary forests towards late-successional forests. Despite the numerous silvicultural advantages of mixed stands, maintaining such species mixtures is questionable, since they do not mimic natural forest dynamics, might prove to be labor intensive and, therefore, partly contradict the essence of close-to-nature forestry, the goal of which is to rely upon natural processes over human interventions. At the end of this thesis, I therefore wonder whether the management of mixed stands should accommodate natural forest succession rather than maintaining, by any and all means, unstable ecological communities.

## BIBLIOGRAPHY

---

- Adam, B., Benoit, J., Sinoquet, H., Balandier, P., and Marquier, A., 2006. Piaf-Photem - software to threshold hemispherical photographs. Version 1.0.
- André, F., Jonard, M., and Ponette, Q., 2008. Spatial and temporal patterns of throughfall chemistry within a temperate mixed oak-beech stand. *Sci. Total Environ.*, 397(1-3):215–228. doi: [10.1016/j.scitotenv.2008.02.043](https://doi.org/10.1016/j.scitotenv.2008.02.043).
- Astrup, R. and Larson, B. C., 2006. Regional variability of species-specific crown openness for aspen and spruce in western boreal Canada. *For. Ecol. Manage.*, 228(1-3):241–250. doi: [10.1016/j.foreco.2006.02.048](https://doi.org/10.1016/j.foreco.2006.02.048).
- Aubin, I., Beaudet, M., and Messier, C., 2000. Light extinction coefficients specific to the understory vegetation of the southern boreal forest, Quebec. *Can. J. For. Res.*, 30(1):168–177. doi: [10.1139/x99-185](https://doi.org/10.1139/x99-185).
- Aussenac, G., 2000. Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. *Ann. For. Sci.*, 57(3):287–301. doi: [10.1051/forest:2000119](https://doi.org/10.1051/forest:2000119).
- Backes, K. and Leuschner, C., 2000. Leaf water relations of competitive *Fagus sylvatica* and *Quercus petraea* trees during 4 years differing in soil drought. *Can. J. For. Res.*, 30(3):335–346. doi: [10.1139/x99-205](https://doi.org/10.1139/x99-205).
- Balandier, P., Collet, C., Miller, J. H., Reynolds, P. E., and Zedaker, S. M., 2006a. Designing forest vegetation management strategies based on the mechanisms and dynamics of crop tree competition by neighbouring vegetation. *Forestry*, 79(1):3–27. doi: [10.1093/forestry/cpi056](https://doi.org/10.1093/forestry/cpi056).
- Balandier, P., Sonohat, G., Sinoquet, H., Varlet-Grancher, C., and Dumas, Y., 2006b. Characterisation, prediction and relationships between different wavebands of solar radiation transmitted in the understorey of even-aged oak (*Quercus petraea*, *Q. robur*) stands. *Trees*, 20(3):363–370. doi: [10.1007/s00468-006-0049-3](https://doi.org/10.1007/s00468-006-0049-3).
- Balandier, P., Sinoquet, H., Frak, E., Giuliani, R., Vandame, M., Descamps, S., Coll, L., Adam, B., Prevosto, B., and Curt, T., 2007. Six-year time course of light-use efficiency, carbon gain and growth of beech saplings (*Fagus sylvatica*) planted under a Scots pine (*Pinus sylvestris*) shelterwood. *Tree Physiol.*, 27(8):1073–1082. doi: [10.1093/treephys/27.8.1073](https://doi.org/10.1093/treephys/27.8.1073).
- Balandier, P., Marquier, A., Gaudio, N., Wehrlen, L., Casella, E., Coll, L., Kiewitt, A., and Harmer, R., 2009. Methods for describing light capture by understorey weeds in temperate forests: consequences for tree regeneration. In Bentsen, N., editor, *Final COST E47 Conference, Forest vegetation management towards environmental sustainability*, pages 73–75.

- Ban, Y., Xu, H., Bergeron, Y., and Kneeshaw, D. D., 1998. Gap regeneration of shade-intolerant *Larix gmelini* in old-growth boreal forests of northeastern China. *J. Veg. Sci.*, 9(4):529–536. doi: [10.2307/3237268](https://doi.org/10.2307/3237268).
- Barbier, S., Gosselin, F., and Balandier, P., 2008. Influence of tree species on understory vegetation diversity and mechanisms involved - a critical review for temperate and boreal forests. *For. Ecol. Manage.*, 254(1):1–15. doi: [10.1016/j.foreco.2007.09.038](https://doi.org/10.1016/j.foreco.2007.09.038).
- Bartelink, H. H., 1997. Allometric relationships for biomass and leaf area of beech (*Fagus sylvatica* L.). *Ann. For. Sci.*, 54(1):39–50. doi: [10.1051/forest:19970104](https://doi.org/10.1051/forest:19970104).
- Bartelink, H. H., 1998a. A model of dry matter partitioning in trees. *Tree Physiol.*, 18(2):91–101. doi: [10.1093/treephys/18.2.91](https://doi.org/10.1093/treephys/18.2.91).
- Bartelink, H. H., 1998b. Radiation interception by forest trees: a simulation study on effects of stand density and foliage clustering on absorption and transmission. *Ecol. Model.*, 105(2-3):213–225. doi: [10.1016/S0304-3800\(97\)00165-8](https://doi.org/10.1016/S0304-3800(97)00165-8).
- Bartoli, M., Tran-Ha, M., Largier, G., Dume, G., and Larrieu, L., 2000. Ecoflore, un logiciel simple de diagnostic écologique. *Rev. For. Fr.*, 56(6):530–547. doi: [10.4267/2042/5386](https://doi.org/10.4267/2042/5386).
- Bates, D., Maechler, M., Bolker, B., and Walker, S., 2013. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-4.
- Baudry, O., 2013. *Réponse de la régénération naturelle de chêne et de hêtre au stade fourré à la refermeture du couvert*. PhD thesis, UCL, Louvain-la-Neuve, Belgique.
- Beaudet, M. and Messier, C., 1998. Growth and morphological responses of yellow birch, sugar maple, and beech seedlings growing under a natural light gradient. *Can. J. For. Res.*, 28(7):1007–1015. doi: [10.1139/cjfr-28-7-1007](https://doi.org/10.1139/cjfr-28-7-1007).
- Beaudet, M. and Messier, C., 2002. Variation in canopy openness and light transmission following selection cutting in northern hardwood stands: an assessment based on hemispherical photographs. *Agric. For. Meteorol.*, 110(3):217–228. doi: [10.1016/S0168-1923\(01\)00289-1](https://doi.org/10.1016/S0168-1923(01)00289-1).
- Beaudet, M., Messier, C., and Canham, C. D., 2002. Predictions of understorey light conditions in northern hardwood forests following parameterization, sensitivity analysis, and tests of the SORTIE light model. *For. Ecol. Manage.*, 165(1-3):235–248. doi: [10.1016/S0378-1127\(01\)00621-1](https://doi.org/10.1016/S0378-1127(01)00621-1).
- Beaudet, M., Harvey, B. D., Messier, C., Coates, K. D., Poulin, J., Kneeshaw, D. D., Brais, S., and Bergeron, Y., 2011. Managing understory light conditions in boreal mixedwoods through variation in the intensity and spatial pattern of harvest: a modelling approach. *For. Ecol. Manage.*, 261(1):84–94. doi: [10.1016/j.foreco.2010.09.033](https://doi.org/10.1016/j.foreco.2010.09.033).

- Bertin, S., Palmroth, S., Kim, H. S., Perks, M. P., Mencuccini, M., and Oren, R., 2011. Modelling understorey light for seedling regeneration in continuous cover forestry canopies. *Forestry*, 84(4):397–409. doi: [10.1093/forestry/cpr026](https://doi.org/10.1093/forestry/cpr026).
- Bock, J., Vinkler, I., Duplat, P., Renaud, J., Badeau, V., and Dupouey, J., 2005. Stabilité au vent des hêtraies: les enseignements de la tempête de 1999. *Rev. For. Fr.*, 57(2):143–158. doi: [10.4267/2042/5032](https://doi.org/10.4267/2042/5032).
- Boivin, F., Paquette, A., Racine, P., and 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. For. Res.*, 41(9):1827–1835. doi: [10.1139/x11-107](https://doi.org/10.1139/x11-107).
- Bonhomme, R., 1993. The solar radiation: characterization and distribution in the canopy. In Varlet-Grancher, C., Bonhomme, R., and Sinoquet, H., editors, *Crop structure and light microclimate: Characterization and applications*, pages 17–28. INRA, Paris. doi: [10.1002/qj.49712052020](https://doi.org/10.1002/qj.49712052020).
- Bontemps, J.-D., Herve, J.-C., Duplat, P., and Dhôte, J.-F., 2012. Shifts in the height-related competitiveness of tree species following recent climate warming and implications for tree community composition: The case of common beech and sessile oak as predominant broadleaved species in Europe. *Oikos*, 121(8):1287–1299. doi: [10.1111/j.1600-0706.2011.20080.x](https://doi.org/10.1111/j.1600-0706.2011.20080.x).
- Branquart, E. and De Keersmaecker, L., 2010. Effet du mélange d'essences sur la biodiversité forestière. *Forêt Wallonne*, 106:17–26.
- Bréda, N., Cochard, H., Dreyer, E., and Granier, A., 1993. Field comparison of transpiration, stomatal conductance and vulnerability to cavitation of *Quercus petraea* and *Quercus robur* under water stress. *Ann. For. Sci.*, 50(6):571–582. doi: [10.1051/forest:19930606](https://doi.org/10.1051/forest:19930606).
- Breda, N., 2003. Ground-based measurements of leaf area index: a review of methods, instruments and current controversies. *J. Exp. Bot.*, 54(392): 2403–2417. doi: [10.1093/jxb/erg263](https://doi.org/10.1093/jxb/erg263).
- Bruciamacchie, M. and de Turckheim, B., 2005. *La futaie irrégulière: théorie et pratique de la sylviculture irrégulière, continue et proche de la nature*. Édisud, Aix-en-Provence.
- Brunner, A., 1998. A light model for spatially explicit forest stand models. *For. Ecol. Manage.*, 107(1-3):19–46. doi: [10.1016/S0378-1127\(97\)00325-3](https://doi.org/10.1016/S0378-1127(97)00325-3).
- Campbell, G. S. and Norman, J. M., 1998. *An introduction to environmental biophysics*. Springer, New-York. doi: [10.1007/978-1-4612-1626-1](https://doi.org/10.1007/978-1-4612-1626-1).
- Canham, C. D., 2011. SORTIE-ND user manual. <http://www.sortie-nd.org/help/manuals/Help/index.html>.

- Canham, C. D., Denslow, J. S., Platt, W. J., Runkle, J. R., Spies, T. A., and White, P. S., 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.*, 20(5):620–631. doi: [10.1139/x90-084](https://doi.org/10.1139/x90-084).
- Canham, C. D., Finzi, A. C., Pacala, S. W., and Burbank, D. H., 1994. Causes and consequences of resource heterogeneity in forests - interspecific variation in light transmission by canopy trees. *Can. J. For. Res.*, 24(2):337–349. doi: [10.1139/x94-046](https://doi.org/10.1139/x94-046).
- Canham, C. D., Coates, K. D., Bartemucci, P., and Quaglia, S., 1999. Measurement and modeling of spatially explicit variation in light transmission through interior cedar-hemlock forests of British Columbia. *Can. J. For. Res.*, 29(11):1775–1783. doi: [10.1139/x99-151](https://doi.org/10.1139/x99-151).
- Casabon, C. and Pothier, D., 2007. Browsing of tree regeneration by white-tailed deer in large clearcuts on Anticosti Island, Quebec. *For. Ecol. Manage.*, 253(1-3):112–119. doi: [10.1016/j.foreco.2007.07.009](https://doi.org/10.1016/j.foreco.2007.07.009).
- Cavin, L., Mountford, E. P., Peterken, G. F., and Jump, A. S., 2013. Extreme drought alters competitive dominance within and between tree species in a mixed forest stand. *Funct. Ecol.*, 27(6):1424–1435. doi: [10.1111/1365-2435.12126](https://doi.org/10.1111/1365-2435.12126).
- Cescatti, A., 1997a. Modelling the radiative transfer in discontinuous canopies of asymmetric crowns. I. Model structure and algorithms. *Ecol. Model.*, 101(2-3):263–274. doi: [10.1016/S0304-3800\(97\)00050-1](https://doi.org/10.1016/S0304-3800(97)00050-1).
- Cescatti, A., 1997b. Modelling the radiative transfer in discontinuous canopies of asymmetric crowns .II. Model testing and application in a Norway spruce stand. *Ecol. Model.*, 101(2-3):275–284. doi: [10.1016/S0304-3800\(97\)00055-0](https://doi.org/10.1016/S0304-3800(97)00055-0).
- Chaar, H. and Colin, F., 1999. Développement en hauteur des régénérations de chêne sessile. *Rev. For. Fr.*, 51(2):341–354. doi: [10.4267/2042/5441](https://doi.org/10.4267/2042/5441).
- Chazdon, R. and Pearcy, R., 1991. The importance of sunflecks for forest understory plants. *BioScience*, 41(11):760–766. doi: [10.2307/1311725](https://doi.org/10.2307/1311725).
- Chen, J. M., Blanken, P. D., Black, T. A., Guilbeault, M., and Chen, S., 1997. Radiation regime and canopy architecture in a boreal aspen forest. *Agric. For. Meteorol.*, 86(1-2):107–125. doi: [10.1016/S0168-1923\(96\)02402-1](https://doi.org/10.1016/S0168-1923(96)02402-1).
- Chen, J. M., Liu, J., Cihlar, J., and Goulden, M. L., 1999. Daily canopy photosynthesis model through temporal and spatial scaling for remote sensing applications. *Ecol. Model.*, 124(2-3):99–119. doi: [10.1016/S0304-3800\(99\)00156-8](https://doi.org/10.1016/S0304-3800(99)00156-8).
- Claessens, H., Périn, J., Latte, N., Lecomte, H., and Brostaux, Y., 2010. Une chênaie n'est pas l'autre: analyse des contextes sylvicoles du chêne en forêt wallonne. *Forêt Wallonne*, 108:3–18.



- Coates, K. D., Canham, C. D., Beaudet, M., Sachs, D. L., and Messier, C., 2003. Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests. *For. Ecol. Manage.*, 186(1-3):297–310. doi: [10.1016/S0378-1127\(03\)00301-3](https://doi.org/10.1016/S0378-1127(03)00301-3).
- Coll, L., Balandier, P., Picon-Cochard, C., Prevosto, B., and Curt, T., 2003. Competition for water between beech seedlings and surrounding vegetation in different light and vegetation composition conditions. *Ann. For. Sci.*, 60(7):593–600. doi: [10.1051/forest:2003051](https://doi.org/10.1051/forest:2003051).
- Coll, L., Balandier, P., and Picon-Cochard, C., 2004. Morphological and physiological responses of beech (*Fagus sylvatica*) seedlings to grass-induced belowground competition. *Tree Physiol.*, 24(1):45–54. doi: [10.1093/treephys/24.1.45](https://doi.org/10.1093/treephys/24.1.45).
- Collet, C. and Chenost, C., 2006. Using competition and light estimates to predict diameter and height growth of naturally regenerated beech seedlings growing under changing canopy conditions. *Forestry*, 79(5):489–502. doi: [10.1093/forestry/cpl03](https://doi.org/10.1093/forestry/cpl03).
- Collet, C. and Frochot, H., 1996. Effects of interspecific competition on periodic shoot elongation in oak seedlings. *Can. J. For. Res.*, 26(11):1934–1942. doi: [10.1139/x26-218](https://doi.org/10.1139/x26-218).
- Collet, C., Colin, F., and Bernier, F., 1997. Height growth, shoot elongation and branch development of young *Quercus petraea* grown under different levels of resource availability. *Ann. For. Sci.*, 54(1):65–81. doi: [10.1051/forest:19970106](https://doi.org/10.1051/forest:19970106).
- Collet, C., Lanter, O., and Pardos, M., 2001. Effects of canopy opening on height and diameter growth in naturally regenerated beech seedlings. *Ann. For. Sci.*, 58(2):127–134. doi: [10.1007/s00468-001-0159-x](https://doi.org/10.1007/s00468-001-0159-x).
- Courbaud, B., Goreaud, F., Dreyfus, P., and Bonnet, F. R., 2001. Evaluating thinning strategies using a tree distance dependent growth model: some examples based on the CAPSIS software “uneven-aged spruce forests” module. *For. Ecol. Manage.*, 145(1-2):15–28. doi: [10.1016/S0378-1127\(00\)00571-5](https://doi.org/10.1016/S0378-1127(00)00571-5).
- Courbaud, B., de Coligny, F., and Cordonnier, T., 2003. Simulating radiation distribution in a heterogeneous Norway spruce forest on a slope. *Agric. For. Meteorol.*, 116(1-2):1–18. doi: [10.1016/S0168-1923\(02\)00254-X](https://doi.org/10.1016/S0168-1923(02)00254-X).
- Da Silva, D., Boudon, F., Godin, C., and Sinoquet, H., 2008. Multiscale framework for modeling and analyzing light interception by trees. *Multiscale Model. Simul.*, 7(2):910–933. doi: [10.1137/08071394X](https://doi.org/10.1137/08071394X).
- Da Silva, D., Balandier, P., Boudon, F., Marquier, A., and Godin, C., 2011. Modeling of light transmission under heterogeneous forest canopy: an appraisal of the effect of the precision level of crown description. *Ann. For. Sci.*, 69(2):191–193. doi: [10.1007/s13595-011-0139-2](https://doi.org/10.1007/s13595-011-0139-2).

- Dauzat, J. and Eroy, M. N., 1997. Simulating light regime and intercrop yields in coconut based farming systems. *Eur. J. Agron.*, 7(1-3):63–74. doi: [10.1016/S1161-0301\(97\)00029-4](https://doi.org/10.1016/S1161-0301(97)00029-4).
- de Turckheim, B., 2006. La sylviculture irrégulière continue et proche de la nature (SICPN), un moyen d'améliorer la rentabilité de la forêt. *Forêt Wallonne*, 85:20–26.
- Delagrangé, S., Messier, C., Lechowicz, M. J., and Dizengremel, P., 2004. Physiological, morphological and allocational plasticity in understory deciduous trees: importance of plant size and light availability. *Tree Physiol.*, 24(7):775–784. doi: [10.1093/treephys/24.7.775](https://doi.org/10.1093/treephys/24.7.775).
- Delagrangé, S., Nolet, P., and Bannon, K., 2010. Effet de l'ouverture du couvert, du dégagement et du chaulage sur la composition et la croissance de la régénération d'érablières envahies par le hêtre: Remesure 3 ans après sa mise en place. Technical report, Institut québécois d'Aménagement de la Forêt feuillue.
- Diaci, J., Gyoerek, N., Gliha, J., and Nagel, T., 2007. Response of *Quercus robur* L. seedlings to north-south asymmetry of light within gaps in floodplain forests of Slovenia. *Ann. For. Sci.*, 65(1):105–105. doi: [10.1051/forest:2007077](https://doi.org/10.1051/forest:2007077).
- Diaci, J., 2002. Regeneration dynamics in a Norway spruce plantation on a silver fir-beech forest site in the Slovenian Alps. *For. Ecol. Manage.*, 161(1-3):27–38. doi: [10.1016/S0378-1127\(01\)00492-3](https://doi.org/10.1016/S0378-1127(01)00492-3).
- Dineur, P., 1951. Quelques données sur l'écologie de la régénération du chêne rouvre. *Bull. Soc. For. Belg.*, 58(2):38–50.
- Dolling, A., 1996. Interference of bracken (*Pteridium aquilinum* L. Kuhn) with Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L. Karst.) seedling establishment. *For. Ecol. Manage.*, 88(3):227–235. doi: [10.1016/S0378-1127\(96\)03846-7](https://doi.org/10.1016/S0378-1127(96)03846-7).
- Doucet, J. L., Kouadio, Y. L., Monticelli, D., and Lejeune, P., 2009. Enrichment of logging gaps with moabi (*Baillonella toxisperma* Pierre) in a Central African rain forest. *For. Ecol. Manage.*, 258(11):2407–2415. doi: [10.1016/j.foreco.2009.08.018](https://doi.org/10.1016/j.foreco.2009.08.018).
- Dreyer, E., Collet, C., Montpied, P., and Sinoquet, H., 2005. Caractérisation de la tolérance à l'ombrage des jeunes semis de hêtre et comparaison avec les essences associées. *Rev. For. Fr.*, 57(2):175–188. doi: [10.4267/2042/5034](https://doi.org/10.4267/2042/5034).
- Dufour-Kowalski, S., Courbaud, B., Dreyfus, P., Meredieu, C., and de Coligny, F., 2012. Capsis: an open software framework and community for forest growth modelling. *Ann. For. Sci.*, 69(2):221–233. doi: [10.1007/s13595-011-0140-9](https://doi.org/10.1007/s13595-011-0140-9).

- Duursma, R. A. and Mäkelä, A., 2007. Summary models for light interception and light-use efficiency of non-homogeneous canopies. *Tree Physiol.*, 27 (6):859–870. doi: [10.1093/treephys/27.6.859](https://doi.org/10.1093/treephys/27.6.859).
- Ellenberg, H., 1974. *Indicator values of vascular plants in central Europe*, volume 9 of *Scripta geobotanica*. Germany.
- Emborg, J., 1998. Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. *For. Ecol. Manage.*, 106(2-3):83–95. doi: [10.1016/S0378-1127\(97\)00299-5](https://doi.org/10.1016/S0378-1127(97)00299-5).
- Emborg, J., Christensen, M., and Heilmann-Clausen, J., 2000. The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. *For. Ecol. Manage.*, 126(2):173–189. doi: [10.1016/S0378-1127\(99\)00094-8](https://doi.org/10.1016/S0378-1127(99)00094-8).
- Essery, R., Bunting, P., Rowlands, A., Rutter, N., Hardy, J., Melloh, R., Link, T., Marks, D., and Pomeroy, J., 2008. Radiative transfer modeling of a coniferous canopy characterized by airborne remote sensing. *J. Hydrometeor.*, 9(2):228–241. doi: [10.1175/2007jhm870.1](https://doi.org/10.1175/2007jhm870.1).
- Farque, L., Sinoquet, H., and Colin, F., 2001. Canopy structure and light interception in *Quercus petraea* seedlings in relation to light regime and plant density. *Tree Physiol.*, 21(17):1257–1267. doi: [10.1093/treephys/21.17.1257](https://doi.org/10.1093/treephys/21.17.1257).
- Finegan, B., 1984. Forest succession. *Nature*, 312(8):109–114. doi: [10.1038/312109a0](https://doi.org/10.1038/312109a0).
- Fournier, R. A., Landry, R., August, N. M., Fedosejevs, G., and Gauthier, R. P., 1996. Modelling light obstruction in three conifer forests using hemispherical photography and fine tree architecture. *Agric. For. Meteorol.*, 82(1-4): 47–72. doi: [10.1016/0168-1923\(96\)02345-3](https://doi.org/10.1016/0168-1923(96)02345-3).
- Frazer, G., Canham, C., and Lertzman, K., 1999. *Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation*. Simon Fraser University, British Columbia, and the Institute of Ecosystem Studies, New York.
- Galen, C., Rabenold, J. J., and Liscum, E., 2007. Functional ecology of a blue light photoreceptor: effects of phototropin-1 on root growth enhance drought tolerance in *Arabidopsis thaliana*. *New Phytol.*, 173(1):91–99. doi: [10.1111/j.1469-8137.2006.01893.x](https://doi.org/10.1111/j.1469-8137.2006.01893.x).
- García-Plazaola, J. and Becerril, J., 2000. Effects of drought on photoprotective mechanisms in European beech (*Fagus sylvatica* L.) seedlings from different provenances. *Trees*, 14(8):485–490. doi: [10.1007/s004680000068](https://doi.org/10.1007/s004680000068).

- Gaudio, N., Balandier, P., and Marquier, A., 2008. Light-dependent development of two competitive species (*Rubus idaeus*, *Cytisus scoparius*) colonizing gaps in temperate forest. *Ann. For. Sci.*, 65(1):104. doi: [10.1051/forest:2007076](https://doi.org/10.1051/forest:2007076).
- Gaudio, N., Balandier, P., Philippe, G., Dumas, Y., Jean, F., and Ginisty, C., 2011. Light-mediated influence of three understorey species (*Calluna vulgaris*, *Pteridium aquilinum*, *Molinia caerulea*) on the growth of *Pinus sylvestris* seedlings. *Eur. J. For. Res.*, 130(1):77–89. doi: [10.1007/s10342-010-0403-2](https://doi.org/10.1007/s10342-010-0403-2).
- Gersonde, R., Battles, J. J., and O'Hara, K. L., 2004. Characterizing the light environment in Sierra Nevada mixed-conifer forests using a spatially explicit light model. *Can. J. For. Res.*, 34(6):1332–1342. doi: [10.1139/x04-013](https://doi.org/10.1139/x04-013).
- Gill, R. M. A., 1992. A review of damage by mammals in north temperate forests .1. Deer. *Forestry*, 65(2):145–169. doi: [10.1093/forestry/65.2.145](https://doi.org/10.1093/forestry/65.2.145).
- Goudriaan, J., 1977. *Crop micrometeorology: a simulation study*. PhD thesis, Wageningen University, Nederland.
- Govind, A., Guyon, D., Roujean, J.-L., Yauschew-Raguenees, N., Kumari, J., Pisek, J., and Wigneron, J.-P., 2013. Effects of canopy architectural parameterizations on the modeling of radiative transfer mechanism. *Ecol. Model.*, 251:114–126. doi: [10.1016/j.ecolmodel.2012.11.014](https://doi.org/10.1016/j.ecolmodel.2012.11.014).
- Groot, A., 2004. A model to estimate light interception by tree crowns, applied to black spruce. *Can. J. For. Res.*, 34(4):788–799. doi: [10.1139/x03-242](https://doi.org/10.1139/x03-242).
- Grubb, P., 1977. The maintainance of species-richness in plant communities; The importance of the regeneration niche. *Biol. Rev.*, 52(1):107–145. doi: [10.1111/j.1469-185X.1977.tb01347.x](https://doi.org/10.1111/j.1469-185X.1977.tb01347.x).
- Gruselle, M.-C., 2002. *Etude des potentialités de production de chêne de qualité en Ardenne belge*. Mémoire de fin d'étude.
- Hall, J. S., 2008. Seed and seedling survival of African mahogany (*Entandrophragma* spp.) in the Central African Republic: Implications for forest management. *For. Ecol. Manage.*, 255(2):292–299. doi: [10.1016/j.foreco.2007.09.050](https://doi.org/10.1016/j.foreco.2007.09.050).
- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimitrakopoulos, P. G., Finn, J. A., Freitas, H., Giller, P. S., Good, J., Harris, R., Högberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Körner, C., Leadley, P. W., Loreau, M., Minns, A., Mulder, C. P. H., O'Donovan, G., Otway, S. J., Pereira, J. S., Prinz, A., Read, D. J., Scherer-Lorenzen, M., Schulze, E.-D., Siamantziouras, A.-S. D., Spehn, E. M., Terry, A. C., Troumbis, A. Y., Woodward, F. I., Yachi, S., and Lawton, J. H., 1999. Plant diversity and productivity experiments in European grasslands. *Science*, 286(5442):1123–1127. doi: [10.1126/science.286.5442.1123](https://doi.org/10.1126/science.286.5442.1123).

- Henin, J., Huart, O., and Rondeux, J., 2003. Biogeographical observations on four scolytids (Coleoptera, Scolytidae) and one lymexylonid (Coleoptera, Lymexylonidae) in Wallonia (Southern Belgium). *Belg. J. Zool.*, 133(2): 175–180.
- Heuze, P., Schnitzler, A., and Klein, F., 2005. Is browsing the major factor of silver fir decline in the Vosges Mountains of France? *For. Ecol. Manage.*, 217(2–3):219–228. doi: [10.1016/j.foreco.2005.06.003](https://doi.org/10.1016/j.foreco.2005.06.003).
- Hidding, B., Tremblay, J. P., and Côté, S. D., 2013. A large herbivore triggers alternative successional trajectories in the boreal forest. *Ecology*, 94(12): 2852–2860. doi: [10.1890/12-2015.1](https://doi.org/10.1890/12-2015.1).
- Huston, M., 1979. A general hypothesis of species diversity. *Am. Nat.*, 113 (1):81–101.
- IPCC, 2007. Contribution of working groups I, II and III to the fourth assessment. In Pachauri, R. and Reisinger, A., editors, *Climate Change 2007: Synthesis Report*, page 104p. IPCC, Geneva.
- IPCC Working group I, 2013. Climate change 2013, the physical science basis, summary for policymaker. page 27. Switzerland.
- Jabiol, B., Brêthes, A., Ponge, J., Toutain, F., and Brun, J., 1995. *L'humus sous toutes ses formes*. ENGREF, Nancy.
- Jactel, H., Brockerhoff, E., and Duelli, P., 2005. A test of the biodiversity-stability theory: meta-analysis of tree species diversity effects on insect pest infestations, and re-examination of responsible factors. *For. Diversity and Funct.*, 176:235–262. doi: [10.1007/3-540-26599-6\\_12](https://doi.org/10.1007/3-540-26599-6_12).
- Jaderlund, A., Zackrisson, O., and Nilsson, M. C., 1996. Effects of bilberry (*Vaccinium myrtillus* L.) litter on seed germination and early seedling growth of four boreal tree species. *J. Chem. Ecol.*, 22(5):973–986. doi: [10.1007/BF02029948](https://doi.org/10.1007/BF02029948).
- Jarret, P., 2004. *La chênaie atlantique*. Lavoisier, Paris.
- Jarvis, P. G. and Leverenz, J. W., 1983. Productivity of temperate, deciduous and evergreen forests. In Lange, O. L., Nobel, P. S., and Osmond, C. B., editors, *Encyclopedia of Plant Physiology*, volume 12, chapter 8, pages 234–280. Springer, Berlin. doi: [10.1007/978-3-642-68156-1\\_9](https://doi.org/10.1007/978-3-642-68156-1_9).
- Jonard, M., Andre, F., and Ponette, Q., 2006. Modeling leaf dispersal in mixed hardwood forests using a ballistic approach. *Ecology*, 87(9):2306–2318. doi: [10.1890/0012-9658\(2006\)87\[2306:MLDIMH\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2306:MLDIMH]2.0.CO;2).
- Jonard, M., Andre, F., and Ponette, Q., 2008. Tree species mediated effects on leaf litter dynamics in pure and mixed stands of oak and beech. *Can. J. For. Res.*, 38(3):528–538. doi: [10.1139/X07-183](https://doi.org/10.1139/X07-183).

- Jonckheere, I., Fleck, S., Nackaerts, K., Muys, B., Coppin, P., Weiss, M., and Baret, F., 2004. Review of methods for *in situ* leaf area index determination - Part I. Theories, sensors and hemispherical photography. *Agric. For. Meteorol.*, 121(1-2):19–35. doi: [10.1016/j.agrformet.2003.08.027](https://doi.org/10.1016/j.agrformet.2003.08.027).
- Keenan, R. J. and Kimmins, J. P., 1993. The ecological effects of clear-cutting. *Environmental Reviews*, 1(2):121–144. doi: [doi:10.1139/a93-010](https://doi.org/10.1139/a93-010).
- Kim, H. S., Palmroth, S., Thérézien, M., Stenberg, P., and Oren, R., 2011. Analysis of the sensitivity of absorbed light and incident light profile to various canopy architecture and stand conditions. *Tree Physiol.*, 31(1):30–47. doi: [10.1093/treephys/tpq098](https://doi.org/10.1093/treephys/tpq098).
- Kobe, R., 2006. Sapling growth as a function of light and landscape-level variation in soil water and foliar nitrogen in northern Michigan. *Oecologia*, 147(1):119–133. doi: [10.1007/s00442-005-0252-8](https://doi.org/10.1007/s00442-005-0252-8).
- Kobe, R., Pacala, S., Silander, J., and Canham, C., 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.*, 5(2):517–532. doi: [10.2307/1942040](https://doi.org/10.2307/1942040).
- Koop, H. and Sterck, F. J., 1994. Light penetration through structurally complex forest canopies - an example of a lowland tropical rain-forest. *For. Ecol. Manage.*, 69(1-3):111–122. doi: [10.1016/0378-1127\(94\)90223-2](https://doi.org/10.1016/0378-1127(94)90223-2).
- Kunstler, G., Curt, T., Bouchaud, M., and Lepart, J., 2005. Growth, mortality, and morphological response of European beech and downy oak along a light gradient in sub-Mediterranean forest. *Can. J. For. Res.*, 35(7):1657–1668. doi: [10.1139/x05-097](https://doi.org/10.1139/x05-097).
- Kuuluvainen, T., 1992. Tree architectures adapted to efficient light utilization: is there a basis for latitudinal gradients? *Oikos*, 65(2):275–284. doi: [10.2307/3545019](https://doi.org/10.2307/3545019).
- Kuuluvainen, T. and Pukkala, T., 1991. Interaction between canopy architecture and photosynthetically active direct radiation at different latitudes: simulation experiments and their ecological implications. *L'arbre. Biologie et développement.*, h.s.:277–291.
- Kuusk, A., 1993. Simulation of crop reflectance (including hot spot effect). In Varlet-Grancher, C., Bonhomme, R., and Sinoquet, H., editors, *Crop structure and light microclimate*, pages 263–270. INRA, Lusignan, France.
- Lafond, V., Lagarrigues, G., Cordonnier, T., and Courbaud, B., 2013. Uneven-aged management options to promote forest resilience for climate change adaptation: effects of group selection and harvesting intensity. *Ann. For. Sci.*, 71(2):173–186. doi: [10.1007/s13595-013-0291-y](https://doi.org/10.1007/s13595-013-0291-y).
- Landsberg, J. J. and Sands, P., 2010. *Physiological ecology of forest production: principles, processes and models*, volume 4. Academic Press.

- Laurent, C., Perrin, D., Bemelmans, D., Carnol, M., Claessens, H., De Cannière, C., François, L., Gerard, E., Grégoire, J., and Herman, M., 2009. Le changement climatique et ses impacts sur les forêts wallonnes. Recommandations aux décideurs et aux propriétaires et gestionnaires. Technical report, Ministre de l'Agriculture, de la Ruralité, de l'Environnement et du Tourisme.
- Law, B. E., Cescatti, A., and Baldocchi, D. D., 2001. Leaf area distribution and radiative transfer in open-canopy forests: implications for mass and energy exchange. *Tree Physiol.*, 21(12-13):777-787. doi: [10.1093/treephys/21.12-13.777](https://doi.org/10.1093/treephys/21.12-13.777).
- Le Duc, M. G. and Havill, D. C., 1998. Competition between *Quercus petraea* and *Carpinus betulus* in an ancient wood in England: seedling survivorship. *J. Veg. Sci.*, 9(6):873-880. doi: [10.2307/3237052](https://doi.org/10.2307/3237052).
- Lecomte, H., Florquin, P., Morimont, J.-P., and Thirion, M., 2003. La forêt wallonne, état de la ressource à la fin du 20<sup>e</sup> siècle. Technical report, Ministère de la Région Wallonne, Division de la nature et des forêts.
- Lemaire, J., 2001. Chênaies wallonnes. État des lieux après un siècle de conversion et perspectives sylvicoles. *Forêt wallonne*, 53:20-30.
- Leroy, C., Sabatier, S., Wahyuni, N., Barczy, J.-F., Dauzat, J., Laurans, M., and Auclair, D., 2009. Virtual trees and light capture: a method for optimizing agroforestry stand design. *Agroforest. Syst.*, 77(1):37-47. doi: [10.1007/s10457-009-9232-z](https://doi.org/10.1007/s10457-009-9232-z).
- Licoppe, A., 2005. Réflexion sur le rôle du cerf dans des programmes de conservation de la nature. *Forêt wallonne*, 74(1):32-37.
- Lieffers, V. J., Messier, C., Stadt, K. J., Gendron, F., and Comeau, P. G., 1999. Predicting and managing light in the understory of boreal forests. *Can. J. For. Res.*, 29(6):796-811. doi: [10.1139/x98-165](https://doi.org/10.1139/x98-165).
- Ligot, G., Courbaud, B., de Coligny, F., and Jonard, M., 2013. SamsaraLight. [http://capsis.cirad.fr/capsis/help\\_en/samsaralight](http://capsis.cirad.fr/capsis/help_en/samsaralight).
- Lochhead, K. D. and Comeau, P. G., 2012. Relationships between forest structure, understorey light and regeneration in complex Douglas-fir dominated stands in south-eastern British Columbia. *For. Ecol. Manage.*, 284(0):12-22. doi: [10.1016/j.foreco.2012.07.029](https://doi.org/10.1016/j.foreco.2012.07.029).
- Löf, M. and Welander, N. T., 2004. Influence of herbaceous competitors on early growth in direct seeded *Fagus sylvatica* L. and *Quercus robur* L. *Ann. For. Sci.*, 61(8):781-788. doi: [10.1051/forest:2004075](https://doi.org/10.1051/forest:2004075).
- Madsen, P. and Larsen, J. B., 1997. Natural regeneration of beech (*Fagus sylvatica* L.) with respect to canopy density, soil moisture and soil carbon content. *For. Ecol. Manage.*, 97(2):95-105. doi: [10.1016/S0378-1127\(97\)00091-1](https://doi.org/10.1016/S0378-1127(97)00091-1).

- Mariscal, M. J., Martens, S. N., Ustin, S. L., Chen, J., Weiss, S. B., and Roberts, D. A., 2004. Light-transmission profiles in an old-growth forest canopy: simulations of photosynthetically active radiation by using spatially explicit radiative transfer models. *Ecosystems*, 7(5):454–467. doi: [10.1007/s10021-004-0137-4](https://doi.org/10.1007/s10021-004-0137-4).
- McGarvey, J. C., Bourg, N. A., Thompson, J. R., McShea, W. J., and Shen, X., 2013. Effects of twenty years of deer exclusion on woody vegetation at three life-history stages in a mid-Atlantic temperate deciduous forest. *Northeastern Naturalist*, 20(3):451–468. doi: [10.1656/045.020.0301](https://doi.org/10.1656/045.020.0301).
- Messier, C., Doucet, R., Ruel, J. C., Claveau, Y., Kelly, C., and Lechowicz, M. J., 1999. Functional ecology of advance regeneration in relation to light in boreal forests. *Can. J. For. Res.*, 29(6):812–823. doi: [10.1139/x99-070](https://doi.org/10.1139/x99-070).
- Mette, T., Dolos, K., Meinardus, C., Bräuning, A., Reineking, B., Blaschke, M., Pretzsch, H., Beierkuhnlein, C., Gohlke, A., and Wellstein, C., 2013. Climatic turning point for beech and oak under climate change in Central Europe. *Ecosphere*, 4(12):art145. doi: [10.1890/ES13-00115.1](https://doi.org/10.1890/ES13-00115.1).
- Mölder, I. and Leuschner, C., 2014. European beech grows better and is less drought sensitive in mixed than in pure stands: tree neighbourhood effects on radial increment. *Trees*, 28(3):1–16. doi: [10.1007/s00468-014-0991-4](https://doi.org/10.1007/s00468-014-0991-4).
- Mouliat, B. and Sinoquet, H., 1993. Three-dimensional digitizing systems for plant canopy geometrical structure: a review. In Varlet-Grancher, C., Bonhomme, R., and Sinoquet, H., editors, *Crop structure and light microclimate*, pages 183–193. INRA, Lusignan, France.
- Newbold, A., Goldsmith, F., and Harding, J., 1981. The regeneration of oak and beech: a literature review. Discussion Papers in Conservation 33, University College, London.
- Nicolini, E., Barthelemy, D., and Heuret, P., 2000. Effects of canopy density on architectural development of young sessile oak, *Quercus petraea* (Matt.) Liebl. (Fagaceae) during forest regeneration. *Can. J. Bot.*, 78(12):1531–1544. doi: [10.1139/cjb-78-12-1531](https://doi.org/10.1139/cjb-78-12-1531).
- Niinemets, U., 2006. The controversy over traits conferring shade-tolerance in trees: ontogenetic changes revisited. *J. Ecol.*, 94(2):464–470. doi: [10.1111/j.1365-2745.2006.01093.x](https://doi.org/10.1111/j.1365-2745.2006.01093.x).
- Niinemets, U., 2010. A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. *Ecol. Res.*, 25(4):693–714. doi: [10.1007/s11284-010-0712-4](https://doi.org/10.1007/s11284-010-0712-4).
- Nock, C. A., Caspersen, J. P., and Thomas, S. C., 2008. Large ontogenetic declines in intra-crown leaf area index in two temperate deciduous tree species. *Ecology*, 89(3):744–753. doi: [10.1890/07-0531.1](https://doi.org/10.1890/07-0531.1).



- Nyland, R. D., 1996. *Silviculture: concepts and applications*. McGraw-Hill, New-York.
- Pacala, S. W., Canham, C. D., Silander, J. A., and Kobe, R. K., 1994. Sapling Growth as a Function of Resources in a North Temperate Forest. *Can. J. For. Res.*, 24(11):2172–2183. doi: [10.1139/x94-280](https://doi.org/10.1139/x94-280).
- Pacala, S. W., Canham, C. D., Saponara, J., Silander, J. A., Kobe, R. K., and Ribbens, E., 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol. Monogr.*, 66(1):1–43. doi: [10.2307/2963479](https://doi.org/10.2307/2963479).
- Paquette, A., Messier, C., Perinet, P., and Cogliastro, A., 2008. Simulating light availability under different hybrid poplar clones in a mixed intensive plantation system. *For. Sci.*, 54(5):481–489.
- Parker, G. G., 1997. Canopy structure and light environment of an old-growth Douglas-fir/western hemlock forest. *Northwest Sci.*, 71(4):261–270.
- Pedersen, B. S., 1998. The role of stress in the mortality of midwestern oaks as indicated by growth prior to death. *Ecology*, 79(1):79–93. doi: [10.1890/0012-9658\(1998\)079\[0079:TROSIT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[0079:TROSIT]2.0.CO;2).
- Petrișan, A. M., von Lüpke, B., and Petrișan, I. C., 2007. Effects of shade on growth and mortality of maple (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*) saplings. *Forestry*, 80(4):397–412. doi: [10.1093/forestry/cpm030](https://doi.org/10.1093/forestry/cpm030).
- Petrișan, A. M., von Lüpke, B., and Petrișan, I. C., 2009. Influence of light availability on growth, leaf morphology and plant architecture of beech (*Fagus sylvatica* L.), maple (*Acer pseudoplatanus* L.) and ash (*Fraxinus excelsior* L.) saplings. *Eur. J. For. Res.*, 128(1):61–74. doi: [10.1007/s10342-008-0239-1](https://doi.org/10.1007/s10342-008-0239-1).
- Petrișan, I. C., Marzano, R., Petrișan, A. M., and Lingua, E., 2014. Overstory succession in a mixed *Quercus petraea*-*Fagus sylvatica* old growth forest revealed through the spatial pattern of competition and mortality. *For. Ecol. Manage.*, 326:9–17. doi: [10.1016/j.foreco.2014.04.017](https://doi.org/10.1016/j.foreco.2014.04.017).
- Phattaralerphong, J., Sathornkitch, J., and Sinoquet, H., 2006. A photographic gap fraction method for estimating leaf area of isolated trees: Assessment with 3D digitized plants. *Tree Physiol.*, 26(9):1123–1136. doi: [10.1093/treephys/26.9.1123](https://doi.org/10.1093/treephys/26.9.1123).
- Piboule, A., Août 2001. Validation et analyse de sensibilité d'un modèle de transfert radiatif en vue de son application à la cartographie de l'éclairement en peuplement forestier. D.E.A., ENGREF-INRA.
- Piboule, A., 2005. *Influence de la structure du peuplement forestier sur la distribution de l'éclairement sous couvert. Cas d'une forêt hétérogène feuillue sur plateau calcaire*. PhD thesis, UMR INRA-ENGREF, Nancy, France.

- Piboule, A., Collet, C., Frochot, H., and Dhôte, J.-F., 2005. Reconstructing crown shape from stem diameter and tree position to supply light models. I. Algorithms and comparison of light simulations. *Ann. For. Sci.*, 62(7): 645–657. doi: [10.1051/forest:2005071](https://doi.org/10.1051/forest:2005071).
- Piedallu, C., Perez, V., Gégout, J.-C., Lebourgeois, F., and Bertrand, R., 2009. Impact potentiel du changement climatique sur la distribution de l'Épicéa, du Sapin, du Hêtre et du Chêne sessile en France. *Rev. For. Fr.*, 61(6):567–593. doi: [10.4267/2042/32924](https://doi.org/10.4267/2042/32924).
- Pierce, L. L. and Running, S. W., 1988. Rapid estimation of coniferous forest leaf area index using a portable integrating radiometer. *Ecology*, 69(6): 1762–1767. doi: [10.2307/1941154](https://doi.org/10.2307/1941154).
- Pinheiro, J., Bates, D., DebRoy, S., and Sarkar, D., 2011. nlme: Linear and nonlinear mixed effects models. R package version 3.1-109.
- Pinno, B. D., Lieffers, V. J., and Stadt, K. J., 2001. Measuring and modelling the crown and light transmission characteristics of juvenile aspen. *Can. J. For. Res.*, 31(11):1930–1939. doi: [10.1139/cjfr-31-11-1930](https://doi.org/10.1139/cjfr-31-11-1930).
- Plak, S., 1987. *Recherche de relations entre la qualité du bois de chêne et les paramètres de ses stations d'origine*. Mémoire de fin d'étude.
- Pommerening, A. and Murphy, S., 2004. A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. *Forestry*, 77(1):27–44. doi: [10.1093/forestry/77.1.27](https://doi.org/10.1093/forestry/77.1.27).
- Porte, A. and Bartelink, H. H., 2002. Modelling mixed forest growth: a review of models for forest management. *Ecol. Model.*, 150(1-2):141–188. doi: [10.1016/S0304-3800\(01\)00476-8](https://doi.org/10.1016/S0304-3800(01)00476-8).
- Poskin, A., 1934. *Le chêne pédonculé et le chêne rouvre. Leur culture en Belgique*. Bibliothèque Agronomique Belge, Gembloux.
- Pretzsch, H., Bielak, K., Block, J., Bruchwald, A., Dieler, J., Ehrhart, H. P., Kohnle, U., Nagel, J., Spellmann, H., Zasada, M., and Zingg, A., 2013a. Productivity of mixed versus pure stands of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) and European beech (*Fagus sylvatica* L.) along an ecological gradient. *Eur. J. For. Res.*, 132(2):263–280. doi: [10.1007/s10342-012-0673-y](https://doi.org/10.1007/s10342-012-0673-y).
- Pretzsch, H., Schütze, G., and Uhl, E., 2013b. Resistance of European tree species to drought stress in mixed versus pure forests: Evidence of stress release by inter-specific facilitation. *Plant Biol.*, 15(3):483–495. doi: [10.1111/j.1438-8677.2012.00670.x](https://doi.org/10.1111/j.1438-8677.2012.00670.x).
- Prévost, M. and Raymond, P., 2012. Effect of gap size, aspect and slope on available light and soil temperature after patch-selection cutting in yellow birch-conifer stands, Quebec, Canada. *For. Ecol. Manage.*, 274:210–221. doi: [10.1016/j.foreco.2012.02.020](https://doi.org/10.1016/j.foreco.2012.02.020).

- Prévost, M., Raymond, P., and Lussier, J. M., 2010. Regeneration dynamics after patch cutting and scarification in yellow birch - Conifer stands. *Can. J. For. Res.*, 40(2):357–369. doi: [10.1139/X09-192](https://doi.org/10.1139/X09-192).
- Prévost, M. and Pothier, D., 2003. Partial cuts in a trembling aspen conifer stand: effects on microenvironmental conditions and regeneration dynamics. *Can. J. For. Res.*, 33(1):1–15. doi: [10.1139/x02-147](https://doi.org/10.1139/x02-147).
- Prévosto, B. and Balandier, P., 2007. Influence of nurse birch and Scots pine seedlings on early aerial development of European beech seedlings in an open-field plantation of Central France. *Forestry*, 80(3):253–264. doi: [10.1093/forestry/cpm017](https://doi.org/10.1093/forestry/cpm017).
- Pukkala, T., Becker, P., Kuuluvainen, T., and Okerblom, P., 1991. Predicting Spatial-Distribution of Direct-Radiation Below Forest Canopies. *Agric. For. Meteorol.*, 55(3-4):295–307. doi: [10.1016/0168-1923\(91\)90067-Z](https://doi.org/10.1016/0168-1923(91)90067-Z).
- Pukkala, T., Kuuluvainen, T., and Stenberg, P., 1993. Below-canopy distribution of photosynthetically active radiation and its relation to seedling growth in a boreal *Pinus sylvestris* stand: a simulation approach. *Scand. J. For. Res.*, 8(3):313–325. doi: [10.1080/02827589309382780](https://doi.org/10.1080/02827589309382780).
- R Core Team, 2013. R: A Language and Environment for Statistical Computing.
- Rameau, J.-C., 1999. Accrus, successions végétales et modèles de dynamique linéaire forestière. In *Boisement naturels des espaces agricoles*, pages 33–48. Ingénieries EAT, Nancy.
- Rey, H., Dauzat, J., Chenu, K., Barczi, J.-F., Dosio, G. A. A., and Lecoœur, J., 2008. Using a 3-D virtual sunflower to simulate light capture at organ, plant and plot levels: contribution of organ interception, impact of heliotropism and analysis of genotypic differences. *Ann. Bot.*, 101(8):1139–1151. doi: [10.1093/aob/mcm300](https://doi.org/10.1093/aob/mcm300).
- Reyes, G. P., Kneeshaw, D., De Grandpré, L., and Leduc, A., 2010. Changes in woody vegetation abundance and diversity after natural disturbances causing different levels of mortality. *J. Veg. Sci.*, 21(2):406–417. doi: [10.1111/j.1654-1103.2009.01152.x](https://doi.org/10.1111/j.1654-1103.2009.01152.x).
- Ross, J., 1981. *The radiation regime and architecture of plant stands*, volume 3 of *Tasks for vegetation sciences*. Springer, Boston. doi: [10.1007/978-94-009-8647-3](https://doi.org/10.1007/978-94-009-8647-3).
- Rugani, T., Diaci, J., and Hladnik, D., 2013. Gap dynamics and structure of two old-growth beech forest remnants in slovenia. *PloS one*, 8(1):1–13. doi: [10.1371/journal.pone.0052641](https://doi.org/10.1371/journal.pone.0052641).
- Scharnweber, T., Manthey, M., Criegee, C., Bauwe, A., Schröder, C., and Wilmking, M., 2011. Drought matters—Declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north-eastern Germany. *For. Ecol. Manage.*, 262(6):947–961. doi: [10.1016/j.foreco.2011.05.026](https://doi.org/10.1016/j.foreco.2011.05.026).

- Schütz, J.-P., 1997. La sylviculture proche de la nature face au conflit economic-ecologie: panacee ou illusion? *Biotechnol. Agron. Soc. Environ.*, 1(4):239–247.
- Schütz, J.-P., 1999. Close-to-nature silviculture: is this concept compatible with species diversity? *Forestry*, 72(4):359–366. doi: [10.1093/forestry/72.4.359](https://doi.org/10.1093/forestry/72.4.359).
- Schütz, J.-P., Pukkala, T., Donoso, P., and Gadow, K., 2012. Historical Emergence and Current Application of CCF. In Pukkala, T. and Gadow, K., editors, *Continuous Cover Forestry*, volume 23 of *Continuous Cover Forestry*, pages 1–28. Springer, Netherlands. doi: [10.1007/978-94-007-2202-6\\_1](https://doi.org/10.1007/978-94-007-2202-6_1).
- Shinozaki, K., Yoda, K., Hozumi, K., and Kira, T., 1964. A quantitative analysis of plant form—the pipe model theory: I. Basic analyses. *Jpn. J. Ecol.*, 14(3): 97–105.
- Sinoquet, H., Varlet-Grancher, C., and Bonhomme, R., 1993. Modelling radiative transfer within homogeneous canopies: basic concepts. In Varlet-Grancher, C., Bonhomme, R., and Sinoquet, H., editors, *Crop structure and light microclimate*, pages 207–228. INRA, Lusignan, France.
- Sinoquet, H., Le Roux, X., Adam, B., Ameglio, T., and Daudet, F. A., 2001. RATP: a model for simulating the spatial distribution of radiation absorption, transpiration and photosynthesis within canopies: application to an isolated tree crown. *Plant Cell Environ.*, 24(4):395–406. doi: [10.1046/j.1365-3040.2001.00694.x](https://doi.org/10.1046/j.1365-3040.2001.00694.x).
- Sinoquet, H., Sonohat, G., Phattaralerphong, J., and 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(9):1158–1170. doi: [10.1111/j.1365-3040.2005.01353.x](https://doi.org/10.1111/j.1365-3040.2005.01353.x).
- Smith, T. and Huston, M., 1989. A theory of the spatial and temporal dynamics of plant communities. *Vegetatio*, 83(1-2):49–69. doi: [10.1007/BF00031680](https://doi.org/10.1007/BF00031680).
- Sprugel, D. G., Rascher, K. G., Gersonde, R., Dovciak, M., Lutz, J. A., and Halpern, C. B., 2009. Spatially explicit modeling of overstory manipulations in young forests: Effects on stand structure and light. *Ecol. Model.*, 220(24):3565–3575. doi: [10.1016/j.ecolmodel.2009.07.029](https://doi.org/10.1016/j.ecolmodel.2009.07.029).
- Stadt, K. J. and Lieffers, V. J., 2000. MIXLIGHT: a flexible light transmission model for mixed-species forest stands. *Agric. For. Meteorol.*, 102(4):235–252. doi: [10.1016/S0168-1923\(00\)00128-3](https://doi.org/10.1016/S0168-1923(00)00128-3).
- Stancioiu, P. T. and O'Hara, K. L., 2006a. Morphological plasticity of regeneration subject to different levels of canopy cover in mixed-species, multiaged forests of the Romanian Carpathians. *Trees*, 20(2):196–209. doi: [10.1007/s00468-005-0026-2](https://doi.org/10.1007/s00468-005-0026-2).

- Stancioiu, P. T. and O'Hara, K. L., 2006b. Leaf area and growth efficiency of regeneration in mixed species, multiaged forests of the Romanian Carpathians. *For. Ecol. Manage.*, 222(1-3):55–66. doi: 10.1016/j.foreco.2005.10.018.
- Stancioiu, P. and O'Hara, K., 2006. Regeneration growth in different light environments of mixed species, multiaged, mountainous forests of Romania. *Eur. J. For. Res.*, 125(2):151–162. doi: 10.1007/s10342-005-0069-3.
- Thérézien, M., Palmroth, S., Brady, R., and Oren, R., 2007. Estimation of light interception properties of conifer shoots by an improved photographic method and a 3D model of shoot structure. *Tree Physiol.*, 27(10):1375–1387. doi: 10.1093/treephys/27.10.1375.
- Tian, H., Chen, G., Liu, M., Zhang, C., Sun, G., Lu, C., Xu, X., Ren, W., Pan, S., and Chappelka, A., 2010. Model estimates of net primary productivity, evapotranspiration, and water use efficiency in the terrestrial ecosystems of the southern United States during 1895–2007. *For. Ecol. Manage.*, 259(7):1311–1327. doi: 10.1016/j.foreco.2009.10.009.
- Timbal, J., Gelpe, J., and Garbaye, J., 1990. Preliminary study of the depressive effect of *Molinia caerulea* (L.) Moench on early growth and mycorrhizal status of *Quercus rubra* seedlings. *Ann. For. Sci.*, 47(6):643–649. doi: 10.1051/forest:19900609.
- Touzet, G., 1996. La sylviculture proche de la nature: polémique actuelle, vieux débats. *Rev. For. Fr.*, sp.:23–30. doi: 10.4267/2042/26798.
- Turbang, J., 1954. Contribution à l'étude de la régénération naturelle du chêne en Lorraine belge. *Bull. Inst. Agron. Gembloux*, 22(1/2):90–133.
- Tychon, B., 2000. Prévention des productions végétales à l'échelle nationale basée sur un système intégré "modèle agrométéorologique-télé-détaction": analyse de sensibilité et domaine de validité en tant qu'outil d'aide à la décision en politique agricole. Technical report, Fondation Universitaire Luxembourgeoise (FUL), Vlaamse Instelling voor Onderzoek (VITO) et Centre de Recherches Agronomiques (CRA).
- Tyler, G., 1992. Tree species affinity of decomposer and ectomycorrhizal macrofungi in beech (*Fagus sylvatica* L.), oak (*Quercus robur* L.) and hornbeam (*Carpinus betulus* L.) forests. *For. Ecol. Manage.*, 47(1-4):269–284. doi: 10.1016/0378-1127(92)90279-I.
- Valladares, F. and Niinemets, U., 2008. Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences. *Annu. Rev. Ecol., Evol., Syst.*, 39(1): 237–257. doi: 10.1146/annurev.ecolsys.39.110707.173506.
- Van Couwenberghe, R., Gégout, J.-C., Lacombe, E., and Collet, C., 2013. Light and competition gradients fail to explain the coexistence of shade-tolerant *Fagus sylvatica* and shade-intermediate *Quercus petraea* seedlings. *Ann. Bot.*, 112(7):1421–1430. doi: 10.1093/aob/mct200.

- von Lüpke, B., 1998. Silvicultural methods of oak regeneration with special respect to shade tolerant mixed species. *For. Ecol. Manage.*, 106(1):19–26. doi: [10.1016/S0378-1127\(97\)00235-1](https://doi.org/10.1016/S0378-1127(97)00235-1).
- von Lüpke, B. and Hauskeller-Bullerjahn, K., 1999. Production forestry without clear felling: will oak become marginalized? *Forst und Holz*, 54(18): 563–568.
- von Lüpke, B. and Hauskeller-Bullerjahn, K., 2004. A contribution to modelling juvenile growth exemplified by mixed oak-beech regeneration. *Allgemeine Forst Und Jagdzeitung*, 175(4-5):61–69.
- Wagner, S., Collet, C., Madsen, P., Nakashizuka, T., Nyland, R., and Sagheb-Talebi, K., 2010. Beech regeneration research: from ecological to silvicultural aspects. *For. Ecol. Manage.*, 259(11):2172–2182. doi: [10.1016/j.foreco.2010.02.029](https://doi.org/10.1016/j.foreco.2010.02.029).
- Walters, M. B. and Reich, P. B., 1996. Are shade tolerance, survival, and growth linked? Low light and, nitrogen effects on hardwood seedlings. *Ecology*, 77(3):841–853. doi: [10.2307/2265505](https://doi.org/10.2307/2265505).
- Wang, Y. P. and Jarvis, P. G., 1990. Description and validation of an array model: MAESTRO. *Agric. For. Meteorol.*, 51(3):257–280. doi: [10.1016/0168-1923\(90\)90112-J](https://doi.org/10.1016/0168-1923(90)90112-J).
- Webb, W. L. and Ungs, M. J., 1993. Three dimensional distribution of needle and stem surface area in a Douglas-fir. *Tree Physiol.*, 13(2):203–212. doi: [10.1093/treephys/13.2.203](https://doi.org/10.1093/treephys/13.2.203).
- Weiss, M., Baret, F., Smith, G. J., Jonckheere, I., and Coppin, P., 2004. Review of methods for *in situ* leaf area index (LAI) determination Part II. Estimation of LAI, errors and sampling. *Agric. For. Meteorol.*, 121(1-2):37–53. doi: [10.1016/j.agrformet.2003.08.001](https://doi.org/10.1016/j.agrformet.2003.08.001).
- Welander, N. T. and Ottosson, B., 1998. The influence of shading on growth and morphology in seedlings of *Quercus robur* L. and *Fagus sylvatica* L. *For. Ecol. Manage.*, 107(1-3):117–126. doi: [10.1016/S0378-1127\(97\)00326-5](https://doi.org/10.1016/S0378-1127(97)00326-5).
- Williams, D. L., 1991. A comparison of spectral reflectance properties at the needle, branch, and canopy level for selected conifer species. *Remote Sens. Environ.*, 35(2-3):79–93. doi: [10.1016/0034-4257\(91\)90002-N](https://doi.org/10.1016/0034-4257(91)90002-N).