Dissertationes Forestales 22

Radiative transfer, interception and scattering in coniferous forests: models and applications for production ecology and remote sensing

Sampo Smolander
Department of Mathematics and Statistics
Faculty of Science
University of Helsinki

Academic dissertation

To be presented, with the permission of the Faculty of Science
of the University of Helsinki, for public criticism in Auditorium B123,
Exactum (Gustaf Hällströmin katu 2b), on June 16th, 2006, at 12 o’clock.

Radiative transfer, interception and scattering in coniferous forests: models and applications for production ecology and remote sensing

Author: Sampo Smolander

Dissertationes Forestales 22

Supervisors:
Docent Pauline Stenberg
Department of Forest Ecology
University of Helsinki
Finland

Professor Elja Arjas
Department of Mathematics and Statistics
University of Helsinki
Finland

Pre-examiners:
Professor Yuri Knyazikhin
Department of Geography
Boston University
USA

Professor Olevi Kull
Institute of Botany and Ecology
University of Tartu
Estonia

Opponent:
Professor Ranga B. Myneni
Department of Geography
Boston University
USA

Cover drawing by Petri Hiltunen

ISSN 1795-7389
ISBN-13: 978-951-651-132-3 (PDF)
ISBN-10: 951-651-132-5 (PDF)

Paper copy printed:
Yliopistopaino
Helsinki 2006

Publishers:
The Finnish Society of Forest Science
Finnish Forest Research Institute
Faculty of Agriculture and Forestry of the University of Helsinki
Faculty of Forestry of the University of Joensuu

Editorial Office:
The Finnish Society of Forest Science
Unioninkatu 40A, 00170 Helsinki, Finland
http://www.metla.fi/dissertationes/

Smolander, Sampo 2006. Radiative transfer, interception and scattering in coniferous forests: models and applications for production ecology and remote sensing. University of Helsinki. Department of Mathematics and Statistics.

ABSTRACT

This work develops methods to account for shoot structure in models of coniferous canopy radiative transfer. Shoot structure, as it varies along the light gradient inside canopy, affects the efficiency of light interception per unit needle area, foliage biomass, or foliage nitrogen. The clumping of needles in the shoot volume also causes a notable amount of multiple scattering of light within coniferous shoots. The effect of shoot structure on light interception is treated in the context of canopy level photosynthesis and resource use models, and the phenomenon of within-shoot multiple scattering in the context of physical canopy reflectance models for remote sensing purposes.

Light interception. A method for estimating the amount of PAR (Photosynthetically Active Radiation) intercepted by a conifer shoot is presented. The method combines modelling of the directional distribution of radiation above canopy, fish-eye photographs taken at shoot locations to measure canopy gap fraction, and geometrical measurements of shoot orientation and structure. Data on light availability, shoot and needle structure and nitrogen content has been collected from canopies of Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) and Norway spruce (*Picea abies* (L.) Karst.). Shoot structure acclimated to light gradient inside canopy so that more shaded shoots have better light interception efficiency. Light interception efficiency of shoots varied about two-fold per needle area, about four-fold per needle dry mass, and about five-fold per nitrogen content. Comparison of fertilized and control stands of Norway spruce indicated that light interception efficiency is not greatly affected by fertilization.

Light scattering. Structure of coniferous shoots gives rise to multiple scattering of light between the needles of the shoot. Using geometric models of shoots, multiple scattering was studied by photon tracing simulations. Based on simulation results, the dependence of the scattering coefficient of shoot from the scattering coefficient of needles is shown to follow a simple one-parameter model. The single parameter, termed the recollision probability, describes the level of clumping of the needles in the shoot, is wavelength independent, and can be connected to previously used clumping indices. By using the recollision probability to correct for the within-shoot multiple scattering, canopy radiative transfer models which have used leaves as basic elements can use shoots as basic elements, and thus be applied for coniferous forests. Preliminary testing of this approach seems to explain, at least partially, why coniferous forests appear darker than broadleaved forests in satellite data.

Keywords: shoot structure, light interception, leaf area index, forest reflectance model, multiple scattering, photon recollision probability

PREFACE

This work begun in 1997, when I – then a second year biology student – was working as a summer trainee for Pauline Stenberg. She had the dataset of paper **II** and had outlined the method described in paper **I**. I spent the summer developing the method, programming, and analysing the data. Pauline introduced me to the study of light and canopy structure, and especially to the problem of describing and modelling the coniferous shoots. Her continuing guidance and support has made this work possible.

In 2000, Ranga Myneni invited me to visit his group in Boston. There, he and Yuri Knyazikhin introduced me to the radiative transfer theory. After all the work with Pauline to describe light interception at the shoot level, it was natural for me to think the scattering process at the shoot level as well. One afternoon we had a long discussion with Yuri on the definitions of the basic scattering element and the elementary volume in numerical radiative transfer computations. Papers **IV** and **V** are basically a late argument to supplement that discussion. I am sorry it took me such a long time to explicate my thoughts.

Discussions with and writings by the old Estonian masters of vegetation radiative transfer, late Juhan Ross, Tiit Nilson and Andres Kuusk, have been a great source of information and inspiration.

I wish to thank my supervisors Pauline Stenberg and Elja Arjas, and all my coauthors. Comments from the pre-examiners Yuri Knyazikhin and Olevi Kull were valuable and really helped to improve the composition of the summary part, for which I am thankful. My father, an ecologist himself, has been a great support and given me lots help and advice.

Financial support from the Graduate School in Computational Biology, Bioinformatics, and Biometry (ComBi), the MaDaMe research programme of the Academy of Finland, the University of Helsinki, the Ella and Georg Ehrnrooth foundation, the Emil Aaltonen foundation, and the Niemi foundation is gratefully acknowledged.

LIST OF ARTICLES

This thesis is based on the following original articles:

I **Smolander, S.** and Stenberg, P. 2001. A method for estimating light interception by a conifer shoot. Tree Physiology 21(12/13):797-803.
(Errata: On page 799 some units are wrong. Both kJ and KJ should always be MJ.)

II Stenberg, P., Smolander, H., Sprugel, D., and **Smolander, S.** 1998. Shoot structure, light interception and distribution of nitrogen in an *Abies amabilis* canopy. Tree Physiology 18(11): 759-767.

III Palmroth, S., Stenberg, P., **Smolander, S.**, Voipio, P. and Smolander, H. 2002. Fertilization has little effect on light-interception efficiency of *Picea abies* shoots. Tree Physiology 22(15/16): 1185-1192.

IV **Smolander, S.** and Stenberg, P. 2003. A method to account for shoot scale clumping in coniferous canopy reflectance models. Remote Sensing of Environment 88(4): 363-373.
(Errata: on page 367, in the line following Eq. 9, ω_L should be leaf scattering coefficient, not reflectance.)

V **Smolander, S.** and Stenberg, P. 2005. Simple parameterizations of the radiation budget of uniform broadleaved and coniferous canopies. Remote Sensing of Environment 94(3): 355-363.

The articles are reproduced with the kind permission of the journals concerned, including permission for electronic distribution under University of Helsinki web pages.

Author's contribution

I am fully responsible for the summary part of this thesis. In paper **I** I did model development, implementation and computations and a major part of the writing. In paper **II** I did the computations applying the model described in paper **I**, and a minor part of the writing. In paper **III** I did part of the field work and part of the computations. In papers **IV** and **V** I did model development, implementation and computations and an equal part of the writing.

CONTENTS

1 INTRODUCTION

Mathematical modelling of radiative transfer and photosynthesis in plant canopies is generally seen to date back to the seminal paper by Monsi and Saeki (1953). Solar radiation provides energy for plant photosynthesis, and the energy and carbon derived from photosynthesis, the primary production, drive most of the biological processes in Earth's biosphere. Canopy structure determines the part of the available light that plants are able to absorb. Other factors, such as water and nutrient conditions, may limit the capacity with which plants are able to utilize absorbed light in photosynthesis, but the description of the amount of absorbed light is of prime importance in studies of canopy photosynthesis and production ecology.

Since the light response of leaf photosynthesis is non-linear, and generally varies in shape in different parts of a canopy (Larcher 2003), knowing only the total amount of light absorbed by a canopy is sufficient only for rather approximate estimates of canopy photosynthesis (Friend 2001). If we assume canopy geometrical structure and incoming light to be known, we can, in principle at least, calculate the distribution of absorbed light in the canopy. If we also assume the photosynthetic light response in different parts of the canopy as known, using this and the distribution of light, we can calculate canopy photosynthesis. In practice all of the three problems (measuring and modelling canopy structure, calculating canopy radiation regime when structure is known, and measuring and modelling the distribution of photosynthetic capacity in different parts of a canopy) are nontrivial, and empirical and theoretical research of these problems has proceeded iteratively.

Canopy structure, together with the properties of the underlying ground, also determines how vegetation reflects radiation. Understanding the process of radiation reflection, in different wavelengths, from vegetation forms physical basis for the interpretation of vegetation properties from satellite images and other remotely sensed signals (such as satellite radars and lidar). Since in the PAR[1]-wavelengths reflectance and transmittance of leaves and needles is low[2], the models of radiative transfer in plant canopies that have been developed for the purposes of light absorption and photosynthesis usually neglect light scattering and concentrate only on the penetration of direct sunlight and skylight into the canopy. In the radiative transfer models for canopy reflectance, on the other hand, scattered radiation is the main interest and accurate values for leaf or needle optical properties in different wavelengths are important input data.

In their current state of development, canopy reflectance models assume canopy structure and element optical properties to be known, and aim to solve the radiation field inside canopy (e.g. Knyazikhin et al. 1998b, 1999, Gobron et al. 1999, Kuusk and Nilson 2000). The upward radiation leaving the top of the canopy constitutes then the canopy reflectance. The estimation of vegetation properties from remote sensing data is then based on either comparing the observed signal to a database of previously computed reflectances for a wide selection of different canopies, and choosing the closest matches (Knyazikhin et al. 1998b, 1999, Gobron et al. 1999), or iteratively optimizing model input parameters to match the observed signal as closely as possible (Kuusk and Nilson 2000).

Several aspects of the structure of coniferous trees distinguish them from broadleaved plants. The leaves of conifers are needles in shape, not planar like those of broadleaved plants. The needles of conifers are closely grouped together as shoots. While there is shoot

---

[1] Photosynthetically Active Radiation, 400-700 nm

[2] Generally less than 10%, except for a peak in green that may reach over 20% in a narrow waveband (Walter-Shea and Norman 1991, Middleton et al. 1997)

level grouping also in broadleaved canopies (e.g. Kull and Tulva 2002), the phenomenon is much more pronounced in conifers (Oker-Blom 1986, Oker-Blom et al. 1991, Nilson 1992). Also higher level grouping, shoots in branches and branches in tree crowns, is usually more pronounced in conifers than in broadleaved trees.

The mathematical description of radiative transfer in an interacting medium has traditionally been based on the so called turbid medium assumption (Chandrasekhar 1950, Ross 1981). This means that there should be a length scale in which the locations of absorbing and scattering elements (leaves) in the medium (canopy) are amenable to be described using the concept of statistical density distribution. This is indeed the case in the fields where the radiative transfer theory has been developed (astrophysics, atmospheric physics, nuclear physics). The assumption also holds true relatively well to facilitate describing the radiative regimes of broadleaved canopies (Ross 1981, Myneni et al. 1989).

However, if there is no such length scale, the concept of statistical density distribution is not good for describing the properties of the medium (Mandelbrot 1983). The main motivation of this work has been the notification that this is the case in coniferous canopies. The length scale of the size of the basic elements, needles, is in the order of centimeters. The density distribution of needles in the canopy also varies greatly at the essentially same length scale; needle density is high inside a shoot volume, and then within a distance of a couple of centimeters, outside of a shoot, it can be zero.

The first hierarchy level of grouping is the grouping (or clumping) of needles into shoots. In this work, the effect of shoot scale grouping and the variations in shoot structure on the processes of light absorption (papers **I**, **II** and **III**) and scattering (papers **IV** and **V**) are studied. The effect of grouping in higher hierarchy levels (branches, whorls, tree crowns) is outside the scope of this work and remains subject to further studies.

In paper **I**, a method for estimating light interception by conifer shoots is described. Shoot structure alone can introduce many-fold variation in the efficiency of light interception by unit needle surface or unit needle dry mass (papers **II** and **III**), so it clearly needs to be included in accurate models of canopy light absorption, photosynthesis and resource use. Papers **II** and **III** present empirical work describing the variation in shoot structure and physiology in relation to shoot light interception. Theories and models of canopy photosynthesis and resource use should confirm to this kind of empirical observations.

In paper **IV**, the phenomenon of multiple scattering of light within a coniferous shoot is described using a detailed simulation model. Based on the results of the simulations, a simple algebraic formula is presented that should describe the amount of within-shoot multiple scattering to a very good approximation, and could be used as an easy way to correct for the within-shoot scattering in the traditional leaf-based canopy radiative transfer models. The effect of including within-shoot multiple scattering into canopy level radiative transfer models is described in papers **IV** and **V**, albeit using only simple model canopies with homogeneous higher level structure. The effect is found to be notable, and in the right direction, to explain the observed higher absorption and lower reflectance of coniferous forests, when compared to broadleaved forests (Williams 1991, Zhang et al. 2002, Roberts et al. 2004).

2 RADIATIVE TRANSFER

Radiative transfer theory is the study of radiation inside a medium which absorbs, emits and scatters radiation. Historically, it was developed in the early 1900's by astrophysicists and meteorologists studying electromagnetic radiation in planetary, stellar and terrestrial atmospheres (Simpson 1928, Chandrasekhar 1950, Sobolev 1970, Thomas and Stamnes 1999). From the mid 1900's the theory has also been applied and developed by physicists and engineers studying neutron radiation in nuclear reactors (Case and Zweifel 1967, Bell and Glasstone 1970). Transfer theory is also known by the name transport theory.

A more complete description of interaction of radiation with matter would include the Maxwell equations and the wave nature of photons (Ishimaru 1999), or also quantum mechanical behavior of particles. However, in the areas where radiative transfer theory is applied (e.g. atmospheric physics, nuclear reactor theory, radiative transfer in plant canopies), wave nature, polarization, etc. are usually not important and photons, or neutrons, can be treated as point particles.

The theory of radiative transfer inside vegetative canopies started with the interest in modelling canopy photosynthesis (Ross 1981, Hirose 2005), and for that purpose radiation scattering is relatively unimportant and can be mostly ignored. The advent of satellite imaging and remote sensing (Campbell 1996) has made the scattering of photons by vegetation an important area of study.

The radiative transfer equation describes the propagation and scattering of point particles inside an absorbing and scattering medium (Chandrasekhar 1950, Bell and Glasstone 1970, Ross 1981, Myneni et al. 1989, Myneni and Ross 1991). It is based on the following assumptions: (i) that there is a sufficient number of particles so that mean particle flux, as described by the radiation field, is a sufficient description and statistical fluctuations can be ignored, (ii) the particles do not interact with each other, and do not alter the properties of the medium, and (iii) the medium can be described as a continuous turbid medium.

2.1 Basic definitions

A position in space is described by vector $\mathbf{r} = (x, y, z)$. A direction is described by unit vector $\mathbf{\Omega}$. A direction can also be specified in polar coordinates by polar angle θ and azimuth angle ϕ. In this case $\mathbf{\Omega} = (\sin\theta\cos\phi, \sin\theta\sin\phi, \cos\theta)$. Particle angular density $N(\mathbf{r}, \mathbf{\Omega}, E, t)$ gives the density of particles in point $\mathbf{r}$ propagating to direction $\mathbf{\Omega}$ with energy E at time t. Thus,

$$N(\mathbf{r}, \mathbf{\Omega}, E, t)\, dV\, d\mathbf{\Omega}\, dE \tag{1}$$

is the number of particles in the volume element dV about $\mathbf{r}$, having directions within solid angle $d\mathbf{\Omega}$ about $\mathbf{\Omega}$, energies within dE about E, at time t. If polar coordinates are used for directions, the differential element of solid angle $d\mathbf{\Omega} = \sin\theta\, d\theta\, d\phi$.

Particle angular flux I is the particle angular density N multiplied by the particle velocity v. Another view of the particle flux is that

$$I(\mathbf{r}, \mathbf{\Omega}, E, t)\, dA\, d\mathbf{\Omega}\, dE\, dt \tag{2}$$

gives the number of particles having directions within $d\mathbf{\Omega}$ about $\mathbf{\Omega}$ and energies within dE about E that cross area dA, being perpendicular to $\mathbf{\Omega}$, in time interval dt about t. In photometric terminology (Bell and Rose 1981), angular photon flux is also called radiance.

Radiation traversing a medium will be weakened by its interaction with matter. The total interaction cross section σ is the probability that a particle will undergo an interaction, per distance traversed, for differentially small distances. Using differential notation, flux I becomes $I + dI$ after traversing a distance ds, and

$$dI = -\sigma I \, ds. \tag{3}$$

σ can depend on location and also on the direction of incoming radiation. A part of the radiation interacting with the medium is absorbed, this is given by the absorption cross section σ_a. Another part is scattered to other directions, this is given by the scattering cross section σ_s. These two constitute the total interaction cross section, $\sigma = \sigma_\mathrm{a} + \sigma_\mathrm{s}$. The ratio σ_s/σ gives the probability of scattering for one interaction, and is called the scattering coefficient.[3] The scattering coefficient is here denoted by ω. A scattered particle shall appear in a new direction. This is described by a probability distribution $f(\mathbf{r}, \mathbf{\Omega}' \to \mathbf{\Omega})$, giving the probability density that a particle coming from $\mathbf{\Omega}'$ and scattered at $\mathbf{r}$ shall continue to direction $\mathbf{\Omega}$. Naturally,

$$\int_{4\pi} f(\mathbf{r}, \mathbf{\Omega}' \to \mathbf{\Omega}) \, d\mathbf{\Omega} = 1 \tag{4}$$

since f is a probability distribution. Here integration over all directions (all vectors $\mathbf{\Omega}$ on the surface of the unit sphere) is denoted by 4π. The directional distribution f multiplied by the scattering coefficient ω is called the scattering phase function. Some authors (e.g. Chandrasekhar 1950) prefer to normalize f to 4π rather than to 1. This has the advantage that $f \equiv 1$ for uniform scatterers, and the disadvantage that a term $\frac{1}{4\pi}$ has to be included in the scattering term in the equations.

The term $\sigma(\mathbf{r}, \mathbf{\Omega}') \, \omega(\mathbf{r}, \mathbf{\Omega}') \, f(\mathbf{r}, \mathbf{\Omega}' \to \mathbf{\Omega})$ is written together as $\sigma_\mathrm{s}(\mathbf{r}, \mathbf{\Omega}' \to \mathbf{\Omega})$ for brevity. In this form it is called the differential scattering cross section. In the case of f normalized to 4π, the differential scattering cross section gives the probability per length traversed and per solid angle, for differentially small length and solid angle, that a particle traversing a unit length to direction $\mathbf{\Omega}'$ shall be scattered to direction $\mathbf{\Omega}$.

2.2 The radiative transfer equation

The general form of the radiative transfer equation is

$$\frac{1}{v}\frac{\partial I}{\partial t} = -\mathbf{\Omega} \cdot \nabla I - \sigma I + \int_0^\infty \int_{4\pi} \sigma \omega f I \, d\mathbf{\Omega}' \, dE' + Q. \tag{5}$$

Here v denotes particle velocity, $I(\mathbf{r}, \mathbf{\Omega}, E, t)$ is the flux of particles in point $\mathbf{r}$ to direction $\mathbf{\Omega}$ with energy E at time t. The total interaction cross section $\sigma(\mathbf{r}, \mathbf{\Omega}, E)$ describes the rate at which particles in point $\mathbf{r}$ traversing to direction $\mathbf{\Omega}$ are removed (absorbed or scattered) from the beam. The scattering coefficient $\omega(\mathbf{r}, \mathbf{\Omega}, E)$ describes the proportion of interactions that lead to scattering, and $f(\mathbf{r}, \mathbf{\Omega}' \to \mathbf{\Omega}, E)$ describes the probability density that a scattered particle will continue to direction $\mathbf{\Omega}$. The term $Q(\mathbf{r}, \mathbf{\Omega}, E, t)$ describes particle source. The del operator ∇ operates only on the spatial coordinates $\mathbf{r}$. Boundary conditions can be included in the terms for source, interaction and scattering, or given separately.

---

[3] This probabilistic interpretation is valid here with photons, as collisions do not produce new particles. A more general interpretation is used with neutron scattering, when the production of new particles is possible.

2.3 Time-independent form

In photon-vegetation interactions the particle velocity, the speed of light, is so great that the radiation field can usually (with some exceptions, like lidar studies, e.g. Kotchenova et al. 2003) be assumed to be in a steady state, that is $\frac{\partial}{\partial t}I = 0$. The collisions can be assumed not to change photon energies, so the steady state solution can be constructed for different photon energies independently. Additionally, instead of energy, photons are usually characterized by their wavelength. Photon wavelength λ is completely determined by photon energy by $E = hc/\lambda$, where h is the Planck's constant and c is the speed of light. The time-independent form of the radiative transfer equation is

$$\mathbf{\Omega} \cdot \nabla I_\lambda(\mathbf{r}, \mathbf{\Omega}) = -\sigma(\mathbf{r}, \mathbf{\Omega}) I_\lambda(\mathbf{r}, \mathbf{\Omega}) + \int_{4\pi} \sigma_{\mathrm{s}\lambda}(\mathbf{r}, \mathbf{\Omega}' \rightarrow \mathbf{\Omega})\, d\mathbf{\Omega}' + Q_\lambda(\mathbf{r}, \mathbf{\Omega}). \tag{6}$$

When defining the boundary conditions, a canopy is usually considered infinite in horizontal directions. The assumption that σ does not depend on wavelength is well justified in plant canopies.

2.4 Limitations of the turbid medium assumption

When the traditional radiative transfer theory, as developed for astrophysical, atmospheric and nuclear engineering applications, is applied for plant canopies, three complications appear: anisotropy, spatial inhomogeneity and the large size of the scattering elements.

A good description of plant canopy anisotropy and inhomogeneity is given by Ross (1981). In many areas of application, the properties of the scattering medium are isotropic, i.e. the scattering properties of the medium in a point do not depend on the direction. However, numerical methods for anisotropic scattering also have been developed e.g. in nuclear reactor theory (Bell and Glasstone 1970).

It has been common to assume plant canopies to be horizontally homogeneous. For example the review by Myneni et al. (1989) mainly describes computational methods based on this assumption. At that time available computer resources may indeed have limited feasible numerical methods to horizontally homogeneous cases. Later there has been numerical work also covering horizontally inhomogeneous canopies (Knyazikhin et al. 1997, 1998a,b).

The first two of the above mentioned complications, anisotropy and inhomogeneity, are not inherent limitations in the turbid medium approach, they just have somewhat limited the direct applicability of numerical methods developed in other fields of radiative transfer.

A more serious limitation of the turbid medium approach is encountered with the large size of the scattering elements in plant canopies. In atmospheric and nuclear reactor applications the scattering elements are usually single atoms or molecules. In these cases the element size is many orders of magnitude smaller than the length scale in which the properties of the medium change. This kind of medium is well amenable to the statistical description. In plant canopies the element (leaf, needle) size is in the order of centimeters, and the density and distribution of these elements may change along distances of decimeters or meters. This phenomenon is especially pronounced in conifers, where needles are grouped together as shoots. The geometry of conifers is further discussed in section 3.2. In conifers, the element density varies from high, inside shoot volume, to zero, outside shoot volume, at essentially the same length scale as the element (needle) size. In this case, there is no length scale in which the medium could be considered continuous enough to warrant the use of the turbid medium approximation. Work based on this observation is further discussed in section 5 and in papers **IV** and **V**.

2.5 Photon tracing

The method of photon tracing involves generating photons at the light sources and following their paths as they interact with the elements of the scene (Glassner 1995, Jensen 2001). Photon tracing[4] falls under a family of simulation methods called Monte Carlo ray tracing (Disney et al. 2000).

In photon tracing, photons are generated to enter the scene from a specified directional distribution. Their paths are traced until they escape out of the scene, or until an interaction happens. The outcome of an interaction may be absorption, reflection or transmission, and for a particular interaction the outcome is randomly sampled from the respective probabilities. In the case of scattering (i.e. reflection and transmission), the new direction is sampled from a directional distribution describing the scattering properties of the target object, and the path is traced further. The scene can consist of solid objects, as was the case with the shoot level simulation in paper **IV**. In this case the point of first interaction along a photon path is solved by geometric means. The scene can also include objects filled with random turbid medium. In this case the length of the path penetrating into the medium before first collision is sampled from the exponential distribution. This method was used in the canopy level simulations in papers **IV** and **V**.

Since the first publication on the Monte Carlo methods (Metropolis and Ulam 1949), they have developed into a versatile tool in a large variety of applications. An interesting piece of history, as described by Metropolis (1987), is that the Monte Carlo methods were first developed and applied specifically for problems in radiative transfer theory.

3 CANOPY ARCHITECTURE AND RADIATION REGIME

The photosynthetic production of a vegetated area is determined by the total amount of foliage, and its photosynthetic performance. If we assume the spatial distribution of the parameters that govern photosynthesis locally to be known, calculating the whole vegetation stand photosynthetic production is reduced to the problem of describing the distribution of light on the photosynthetic surfaces (e.g. Ross 1981, Oker-Blom 1986, Oker-Blom et al. 1991, Gutschick 1991). On the other hand, if we assume that the radiation regime is known, we can ask the question which distribution of photosynthetic resources over different parts of foliage would maximize photosynthetic production (e.g. Kull 2002, and references therein). The matter is further complicated by that fact that plants can alter the total amount of foliage in a canopy, and they can alter the radiation penetration to the lower parts of the canopy by controlling the structure of the higher parts of the canopy (e.g. Anten et al. 1995b, Stenberg 1996b). Also, competition between individuals seems to add the condition that the optimal solution for maximal photosynthetic production is not evolutionary stable strategy (Schieving and Poorter 1999, Anten and Hirose 2001).

---

[4] Some sources (such as Disney et al. 2000) use the term forward ray tracing instead of photon tracing. However, Foley et al. (1990) point out that that term may be misleading, since usually ray tracing involves tracing the paths of photons from camera to the light sources. Thus the method of tracing photon paths from light sources to camera has also been called backward ray tracing, while it is also know to some as forward ray tracing. To avoid this confusion, I follow the terminology of Glassner (1995) and Jensen (2001) and use the term photon tracing here.

3.1 Development of canopy radiation regime models

The now classical mathematical model of canopy light regime and photosynthesis was published by Monsi and Saeki (1953). They measured light attenuation, under overcast sky, in herbaceus plant communities, and found that it was well described by the Beer's law, equation:

$$I(L) = I_0 e^{-kL}, \tag{7}$$

where I is the photosynthetic photon flux density (PPFD) on a horizontal plane, I_0 is the PPFD at the top of canopy, L is the leaf area index (LAI) cumulated from the top of the canopy and k is the attenuation coefficient per unit cumulated leaf area. Monsi and Saeki (1953) noted that for randomly located horizontal leaves k should be equal to 1. If leaf distribution is more even than random, it increases k, and if leaves are clumped together, it decreases k. The amount of light that leaves in a certain infinitesimal layer receive, is given by the derivative of Eq. 7.

The light response $A(I)$ of photosynthetic carbon assimilation was described by a Michaelis-Menten (or rectangular hyperbola) type equation (Michaelis and Menten 1913),

$$A(I) = \frac{bI}{1 + aI} - r, \tag{8}$$

where a and b are some parameters describing photosynthesis light response (b gives the initial slope for small values of I, b/a gives the saturated value for large I) and r is the respiration rate. Combining 8 and the derivative of 7, and integrating from 0 to maximum LAI ($L_{\max}$), Monsi and Saeki got productivity P as

$$\begin{aligned} P &= \int_0^{L_{\max}} \left(\frac{bkI_0 e^{-kL}}{1 + akI_0 e^{-kL}} - r \right) dL \\ &= \frac{b}{ka} \ln \left(\frac{1 + akI_0}{1 + akI_0 e^{-kL_{\max}}} \right) - rL_{\max}. \end{aligned} \tag{9}$$

An important observation form Eq. 9 is that under some fixed light conditions, there will be some $L_{\max}$ for which the productivity is maximized.

This model of Monsi and Saeki (1953) is perhaps the simplest canopy photosynthesis model that one can think of. For example, the light intercepted by leaves in layer $L + \Delta L$ is assumed to be distributed evenly on the leaf surfaces. This assumption is clearly non-realistic. In reality the light available at a certain depth in a canopy consists of an interplay of spots of sunlight, shadow and penumbra. Leaf orientation, as it usually departs from the horizontal, also effects the irradiance on the surface of a leaf. Additionally, all leaves of the canopy are assumed to have the same photosynthetic capacity, and also this assumption contradicts general empirical knowledge (e.g. Larcher 2003).

The main determinant of the leaf photosynthetic capacity is the leaf nitrogen content[5] (Mooney and Gulmon 1979, Field and Mooney 1986, Evans 1989, Evans and Seeman 1989, Hirosaka and Terashima 1996). Usually, leaves developed in low-light conditions are thinner, and have a smaller amount of photosynthetic apparatus and nitrogen per unit area. Leaves developed in full sunlight are thicker, and have more of photosynthetic apparatus and nitrogen per unit area. Studies on leaf level light acclimation have shown both light saturated photosynthesis rates and respiration rates to be higher in sun leaves than in shade

---

[5] Leaf nitrogen content = amount of nitrogen per leaf area

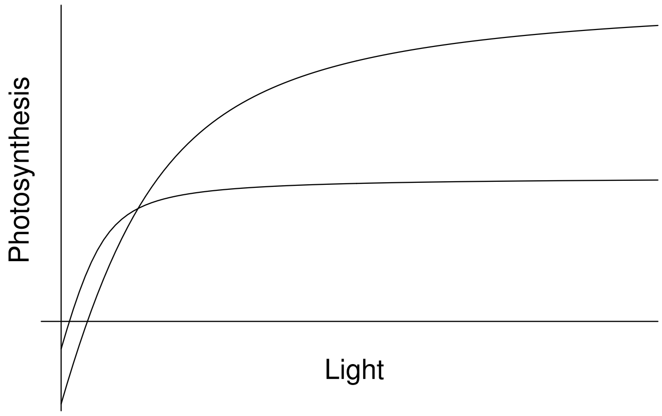

Figure 1: A schematic illustration of the typical photosynthesis light response curves of sun and shadow leaves. A sun leaf (higher curve) has higher photosynthesis when there is abundant light, but at low light levels the higher respiration cost causes the sun leaf to photosynthetize less than a shadow leaf (lower curve). The curves follow the form of a widely used model for photosynthesis light response, the non-rectangular hyperbola

$$P = \frac{\phi I + P_{\max} - \sqrt{(\phi I + P_{\max})^2 - 4\theta\phi I P_{\max}}}{2\theta} - r$$

(Thornley 1976). Here, P is photosynthesis, I is light, $P_{\max}$ is the maximum level of photosynthesis, ϕ is the initial slope of the photosynthesis light response, and θ controls the convexity of the curvature between the initial slope and the final saturation.

leaves (e.g. Hollinger 1989, Marek et al. 1989, Ellsworth and Reich 1993, Bassow and Bazzaz 1998). This difference in the photosynthetic light response curves of sun and shade leaves is illustrated in Fig. 1.

The seminal work of Monsi and Saeki has resulted in theories being developed on the optimal distribution of nitrogen in plant canopies, and in experimental work testing the theories. Mooney and Gulmon (1979) proposed a framework of cost-benefit analysis in plant resource use studies. The idea is that sequestering nitrogen (and also other nutrients, but nitrogen is the most important one) and synthesizing proteins for building the photosynthetic apparatus consumes energy, and the energy gain from photosynthesis by this apparatus should exceed the energy invested in its construction.

Field (1983) formulated leaf nitrogen allocation as a variational problem. The optimal distribution of nitrogen among the leaves would be such that no redistribution could increase productivity. Charles-Edwards et al. (1987) and Farquhar (1989) made the assumption that photosynthetic capacity is linearly related to nitrogen content and thus proposed that the optimal nitrogen distribution would be linearly related to intercepted light. Leaf nitrogen distribution has been studied extensively (e.g. Field 1983, DeJong and Doyle 1985, Field and Mooney 1986, Hirose and Werger 1987a,b, Evans 1989, Hirose et al. 1989, Hollinger 1989, Pons et al. 1990, Leuning et al. 1991, Werger and Hirose 1991, Schieving et al. 1992, Ellsworth and Reich 1993, Evans 1993, Kull and Niinemets 1993, Anten et al. 1995a, Hollinger 1996, Dang et al. 1997, Bond et al. 1999, Wilson et al. 2000, Meir et al. 2002, Han et al. 2004) and in nearly all cases nitrogen per unit leaf area varies in parallel with light availability. However, it does not decrease sharply enough to remain proportional to light at lower levels of canopies (Kull 2002, Anten 2005). A more detailed theory of nitrogen allocation should also take into account the partitioning of leaf nitrogen into different components of the photosynthetic machinery (e.g. Laisk et al. 2005, Eichelmann et al. 2005).

3.2 Structural properties of conifers

The geometrical structure of trees has been studied from many viewpoints, including biomechanics (e.g. Niklas 1992), water relations (e.g. Kramer 1995, Kirkham 2005) and light conditions (e.g. Ross 1981, Myneni and Ross 1991). For the study of radiative transfer in vegetative canopies, the main interest lies in the spatial and angular distribution of phytoelements (plant parts: leaves, branches, stems).

Coniferous trees have a geometrical structure that is hierarchical in several levels (e.g. Oker-Blom 1986, Oker-Blom et al. 1991, Nilson 1992, Stenberg et al. 1995b, Bégin and Filion 1999). The space filled by the foliage and the branches of a tree is called a tree crown. It is quite normal for coniferous tree species to have rather distinct tree crowns (Gelderen and Van Hoey Smith 1996). This is especially pronounced in species which have conical crown shapes, such as spruces (genera *Picea*) and firs (genera *Abies*), and somewhat less pronounced in species which have more ellipsoidal crown shape, such as pines (genera *Pinus*). In general, the division of the space of a forest stand into tree crowns filled with foliage, and the empty space between the tree crowns, is important in determining the light conditions of the stand (Anderson 1966, Oker-Blom et al. 1991).

Within a crown, the foliage is divided into branches. Usually most first order lateral branches (lateral branches extending from the main stem) developed in a certain year start growth from the trunk at the same height. This collection of branches attached to tree trunk at the same height is called a whorl (Zimmerman and Brown 1971).

In the context of the conifer species that are treated in this work (*Abies amabilis* (Dougl.) Forbes), *Picea abies* (L.) Karst., and *Pinus sylvestris* L.), the basic unit of one year's growth is called a shoot. In these species, there usually is no branching within a single shoot, but branching takes place when new shoots grow from the buds at the end of previous year's shoots. However, it is also possible that some buds form along the length of a shoot, and new shoots can start to grow from these. The buds can even stay dormant for several years before a new shoot starts to elongate from them (Ishii and Ford 2001). The grouping of shoots into spatially distinct branches can be very pronounced, with empty spaces between the branch volumes, as in many spruces. Or the spaces of individual branches can join together to form a rather continuous crown, as is many pines (Gelderen and Van Hoey Smith 1996).

Perhaps the most distinct structural property of conifers is the aggregation of narrow needles into shoots (e.g. Norman and Jarvis 1974, Leverenz and Jarvis 1980, Carter and Smith 1985, Smith and Carter 1988). Because of the mutual shading of the needles in shoots, a certain amount of needle area, when clumped together into shoots, intercepts less light than would be the case when an equal amount of leaf area were independently distributed in canopy space[6]. Models of coniferous canopy light interception have thus used shoots as the basic elements, and described the canopy structure in terms of the spatial and angular distribution of shoots (Oker-Blom and Kellomäki 1983, Stenberg et al. 1993, Cescatti 1998, Nilson et al. 1999). This requires specifying how shoot silhouette areas, and thus the shoot level attenuation coefficient, depend on the amount of needle area in the shoot and the shoot

---

[6] That is, following a spatial Poisson process with constant intensity.

structure.

Norman and Jarvis (1974) may have been the first to measure shoot silhouette areas. They also sampled comprehensively from the directions of hemisphere. They called it the attached needle area, projected at an angle. Later, Carter and Smith (1985) defined the silhouette to total area ratio (STAR) as the silhouette area of the shoot divided by the total surface area of needles in the shoot. Since the shoot silhouette area varies as a function of the view direction, so should the STAR, but apparently Carter and Smith (1985) used only one view direction, directly from above the dorsal ("upper") side of the shoot, in their measurements. Measurement from this direction, but normalized to projected rather than total needle area, was later termed $\mathrm{R}_{\mathrm{max}}$ by Leverenz and Hinckley (1990) and $\mathrm{SPAR}_{\mathrm{max}}$ by Stenberg et al. (1995a), but as noted in paper **II** it usually does not represent the true maximum.

Next, Oker-Blom and Smolander (1988) explicitly noted the dependence of STAR on the angle between shoot axis and view direction. They worked with Scots pine (*Pinus sylvestris*) and assumed that the shoot structure is cylinder symmetric. They defined the spherical average of STAR as $\overline{\mathrm{STAR}}$ and calculated it for shoots that they had measured from several different view directions. For Scots pine, the assumption of cylinder symmetry in the shoots is rather good, but not perfect, as can be seen from Fig. 5 in paper **I**. For other species, such as Pacific silver fir (*Abies amabilis*) (Fig. 1 in paper **II**), or Norway spruce (*Picea abies*), it does not hold true at all.

Generally, to be able to estimate the value of the average silhouette area of an irregularly shaped object, silhouette area measurements from the directions of half of the the full sphere are required. Since the silhouette area is the same for a direction and its opposite direction, the full sphere is not required. Smolander and Oker-Blom (1989), Smolander et al. (1994) and Stenberg et al. (1995a) included also different angles of rotation of shoot axis in their measurements but they took measurements from one half (Smolander and Oker-Blom 1989, Smolander et al. 1994) or one fourth (Stenberg et al. 1995a) of the hemisphere only. Paper **II** may be the first work since Norman and Jarvis (1974) to present measurements of shoot silhouette areas with comprehensive sampling of all the hemisphere.

The level of needle clumping in shoots, as quantified by STAR, is generally higher in the topmost parts of canopy, and decreases with decreasing light availability (e.g. Sprugel 1989, Leverenz and Hinckley 1990, Schoettle and Smith 1991, Smolander et al. 1994, Niinemets and Kull 1995, Sprugel et al. 1996, Stenberg et al. 2001, paper **II**, paper **III**). Since projected needle area[7] is somewhat easier to measure than total needle surface area, it is sometimes used instead. In this case instead of STAR we have SPAR (silhouette to projected area ratio) (Stenberg et al. 1995a).

In a similar manner, usually needle thickness also decreases with the decreasing light availability from the top to the bottom of the canopy (e.g. Kellomäki and Oker-Blom 1981, Sprugel 1989, Niinemets and Kull 1995, Sprugel et al. 1996, paper **II**, paper **III**). This is illustrated in Fig. 1 of paper **III**.

As STAR increases and needle thickness decreases with the decreasing light availability, they both have the effect of decreasing the amount of needle dry mass per unit shoot silhouette area. We can think that there is more dry biomass "behind" a certain amount of shoot silhouette area in the top, better illuminated, parts of the canopy than in the lower, more shaded, parts.

---

[7] Area of the projection of needles when they are detached and laid non-overlapping on a flat surface.

4 RADIATION INTERCEPTION AND PHOTOSYNTHESIS

The theoretical models of canopy light interception and photosynthesis, as mentioned in section 3.1, are based on several simplifying assumptions on canopy structure and the process of light interception. To facilitate the comparison of theories to nature, we have developed a method to estimate seasonal light interception by real conifer shoots (paper **I**). Papers **II** and **III** describe studies on the effect of needle and shoot structure and shoot light interception efficiency to distributions of light and nitrogen in coniferous canopies, and on how shoot structure and light interception efficiency differ in canopies of different nutritional status.

4.1 Light interception at shoot level

The amount of photosynthetically active radiation (PAR) intercepted by leaves or shoots cannot be directly measured by the traditional method of placing horizontal sensors in the canopy (Anderson 1966). Only in the case of strictly horizontal leaves, the reading of a horizontal sensor would correspond to the amount of energy a leaf would receive. In the general case of non-horizontal leaves, or 3-dimensional objects such as shoots, the amount of intercepted radiation depends on the shape and orientation of the object, and the directional distribution of the incoming radiation field. While directional measurements of incoming radiation fields are technically possible (Kuusk et al. 2002), they require lots of effort and special equipment. This kind of directional data are very rare to date.

Our approach in paper **I** was to simulate the directional distribution of incoming radiation from sky during a growing period, based on the equations of motion for the sun, the Beer's law for atmospheric attenuation, and an assumption of simple uniform distribution for the diffuse radiation. The simulated distribution was calibrated to agree with total amounts on direct and diffuse radiation obtained from meteorological field data.

The radiation fields at the locations of shoots were reconstructed by taking a fish-eye photographs at the specific shoot locations, and using these to analyze gap fraction (fraction of visible sky) in different directions as seen from the shoot location. An example is shown in Fig. 3 of paper **I**. In paper **III**, a simpler method was used: The gap fraction of the whole fish-eye photo taken at the location of a shoot was analyzed. This parameter, termed openness (Eq. 1 in paper **III**), provides an indirect measure that correlates strongly with available light.

To describe the shoot geometry, the shoot orientation was measured before detaching the shoot from the tree. Then the shoot silhouette area from different directions was photographically measured in laboratory, and appropriate interpolation and coordinate rotation procedures were applied to reconstruct the shoot silhouette area as it would have been seen from different directions of the sky.

Finally, to calculate the amount of light intercepted by the shoot, the simulated directional distribution of skylight, the directional gap fractions as analyzed from the fish-eye photograph, and the directional distribution of shoot silhouette area were combined.

The main motivation in paper **I** was to describe the process of light interception of a coniferous shoot in a, hopefully, realistic way by including shoot geometry and the directionality of the radiation field in the description. This is done in order to demonstrate that the process of light interception is, especially in conifers, more complex than models of the type described in section 3.1 assume. The model by Monsi and Saeki (1953) is half a century old, but similar models are also currently used in canopy photosynthesis modelling (e.g. Thornley 2002, Medlyn et al. 2003). When modelling large scale processes, model properties such as simplicity and easy integrability with remote sensing information are of course desirable properties. However, also simpler models for upscaling purposes benefit from comparisons with more detailed models. Our description of the shoot level light interception is hopefully useful when estimating the accuracy of the simpler large scale models.

The shoot seasonal light interception data in paper **II**, as obtained by the method described in paper **I**, is to my knowledge the first to consider both the directionality of the incoming radiation field and shoot geometry. This level of detail is required when testing the theories which predict the relation of leaf nitrogen to intercepted light. Many earlier works have compared sampled leaf nitrogen content with some indirect measure that correlates with the seasonal light interception. For example, Hirose et al. (1989) have used measurements from horizontal light sensors, Hollinger (1989) height in canopy, Ellsworth and Reich (1993) cumulative LAI and Kull and Niinemets (1993) canopy openness.

The theories on nitrogen use optimization describe how nitrogen should be distributed in relation with intercepted light, but they do not usually specify further e.g. the time interval and illumination conditions for light interception. In paper **II** the amount of light intercepted by shoots during one growth period was chosen as the level of detail for comparison with the theories. A more complete description of shoot photosynthesis would also include the distribution of irradiance on the needle surface of the shoot (Oker-Blom 1985, Smolander et al. 1987, Oker-Blom et al. 1992, Cescatti and Zorer 2003) and the effect of penumbra (Stenberg 1995). As the light response of leaf photosynthesis is non-linear (see Fig. 1), similar amounts of seasonal light interception can lead to different amounts of photosynthetic production if their spatial, temporal, or both distributions are different (Lappi and Smolander 1984, Smolander 1984). It remains unknown whether light interception at shoot scale and during one growth period is an adequate level of detail for comparing with the theories, or whether describing light interception at needle level, and accounting for different illumination conditions (e.g. clear and overcast days), would be essential in this context.

4.2 Morphology and physiology along light gradient

The study in paper **II** describes variation in shoot and needle structure and their effect on the distributions of light and nitrogen in the canopy of a Pacific silver fir (*Abies amabilis*) stand. Shoots were collected from different heights in the canopy, shoot seasonal light interception was modelled using the method described in paper **I**, shoot and needle structure was measured, and shoot nitrogen content was analyzed.

The radiation regime around the shoots, as obtained by modelling, was clearly multidirectional (Figs. 2, 3 and 4 in paper **II**), also for the shoots from lower locations. This makes accounting for shoot orientation and shape necessary when aiming for accurate estimates of intercepted light. The amount of light available to shoots was quantified by the amount of seasonal interception by a spherical surface if it had been at the place of a shoot. The seasonal light interception of a spherical surface, $\mathrm{SLI_O}$ (Eq. 4 in paper **I**, Eq. 3 in paper **II**), as averaged at the locations of the five most sunlit shoots was about 40 times greater than that averaged at the locations of five most shaded shoot. This is indicative of the variation of available light inside the canopy.

From the top to the bottom of the canopy, SPAR increased about 1.5-fold (Fig. 5A in paper **II**). This, together with the interplay of shoot orientations and the radiation fields surrounding the shoots (Fig. 8 in paper **II**), reduced the 40-fold variation in $\mathrm{SLI_O}$ to about 20-fold variation in shoot seasonal light interception (SLI), expressed in this case on projected needle area basis. Needle thickness decreased about two-fold from top to bottom (Fig. 6A in paper **II**), resulting in a corresponding increase in specific needle area[8] (SNA) (Fig. 6B in paper **II**). The responses in SPAR, shoot orientation and specific projected needle area together resulted in about four-fold response in shoot silhouette area per dry weight (Fig. 6C in paper **II**) and in reducing the initial 40-fold variation in available light (as measured by $\mathrm{SLI_O}$) to about 10-fold variation in the intercepted light per dry mass.

Needle nitrogen content[9] increased linearly with seasonal light interception (Fig. 9 in paper **II**), albeit with a positive intercept at zero light interception. On mass basis, needle nitrogen concentration (nitrogen per dry mass) increased about 1.5-fold from the bottom to top of the canopy in the dominant and codominant trees. However, the largest nitrogen concentrations were observed in the suppressed trees, which had foliage only in the shaded parts of the canopy. Thus, in the data as a whole, there was no correlation between light availability and needle nitrogen concentration (Fig. 7A in paper **II**). The lowest observed nitrogen concentrations were about 5.5 – 7.5 mg/g. In a survey of 21 species of C_3 plants, Field and Mooney (1986, p. 37) present a rough approximate value of 0.5 mmol/g = 7 mg/g for the point where photosynthesis (in abundant light) just compensates for respiration, but commenting that there is much variation in the data between species.

Paper **III** presents a study on shoot and needle morphology and nitrogen concentration along light gradient in Norway spruce (*Picea abies*), with the added dimension that these properties were compared between trees from an irrigated and fertilized and a control ("natural") stand. Generally, shoot silhouette to dry mass ratio (SMR) increased three-fold from the most sunlit to the most shaded shoots in the data (Fig. 7 in paper **III**). However, in the irrigated and fertilized stand more of the variation in SMR resulted from variation in specific needle area (SNA), and less from variation in STAR. In the control stand, STAR caused more variation in SMR than SNA (Figs. 5 and 6 in paper **III**). The proximate reason for this was that the shoots in the control stand had smaller needles and lower needle density. Foliar nitrogen concentration was consistently higher in the irrigated and fertilized stand, and it increased with increasing openness about 1.3-fold in the irrigated and fertilized stand and about 1.2-fold in the control stand (Fig. 3 in paper **III**). The lowest new shoots were found at 2% openness in the irrigated and fertilized stand, and at 10% openness at the control stand.

4.3 Discussion and conclusions

It is important to note the difference between available light and intercepted light. There is theoretical (e.g. Stenberg 1996b) and experimental (among others, papers **II** and **III**) evidence that it may be advantageous for trees to have smaller light interception efficiency in the higher parts of canopy so that more light penetrates to the lower parts. In this way, a higher total leaf area can be maintained. The data in papers **II** and **III** suggest that the shoot light interception efficiency can vary about two-fold per needle area, about four-fold per dry mass, and about five-fold per nitrogen. This plasticity is not limited to conifers, also broadleaved trees can control the amount of intercepted light by altering leaf angle and branch structure (e.g. Kull and Tulva 2002). Branch structure at the higher level than shoot structure supposedly also has an effect in conifers, but studies on this are rare.

---

[8] (In this case, projected) needle area divided by needle dry weight

[9] Amount of nitrogen per (projected) needle area

It is also notable that the spherically averaged shoot silhouette area is not an accurate measure of shoot light interception efficiency (Fig. 8 in paper **II**). Especially in the lower part of canopy the radiation field, while not unidirectional, is concentrated near the top part of the hemisphere (Figs. 3B and 4 in paper **II**). At the same time, the shoots in species like *Abies amabilis* and *Picea abies* in the lower canopy tend to be flat and horizontal, which makes the shoot orientation more favourable to light interception than a spherically distributed orientation would be.

Direct measurement of light intercepted by shoots in natural conditions is a technical problem that has not yet been solved. The work in paper **I** presents a solution combining modelling and relatively easy measurements to achieve the result without direct measurements. As the intercepted light is the concept which is used in the nitrogen-use optimization theories, obtaining measured values for it is needed for direct comparison between theories and nature.

The basic prediction of the nitrogen-use optimization theories is that trees should distribute nitrogen in relation to intercepted light. The details of the distribution vary somewhat between different theories. Papers **II** and **III** detail the mechanisms (changes in shoot structure, needle structure, and nitrogen concentration) controlling the nitrogen distribution and that they can lead up to five-fold difference in the amount of nitrogen per unit of light intercepting shoot silhouette area in the observed canopies.

5 RADIATION SCATTERING AND REMOTE SENSING

In coniferous canopies the density of scattering elements changes in the shoot scale, and also in larger scales (branches, tree crowns). It is not feasible to include such small scale variation into the leaf area density function, when formulating the radiative transfer problem for coniferous canopies, since that would require specifying the location of each shoot in the canopy. For example, Knyazikhin et al. (1997) used a density function that is piecewise constant in a mesh of 0.5 m sided cubes. When the leaf area density function varies in a length scale that is larger than the length scale in which needles are clumped into shoots, we need an additional method to account for the shoot scale clumping in the models.

If we assume no scattering, i.e. that the canopy elements are optically black, the description of radiation inside canopy is reduced from Eq. 6 to Eq. 3. This assumption is rather common when modelling radiation penetration into canopy for the purposes of photosynthesis modelling or leaf area index measurements. In these models, the phenomenon of needle grouping into shoots has been dealt with by introducing a grouping (or clumping) coefficient (e.g. Oker-Blom and Kellomäki 1983, Oker-Blom 1986, Stenberg 1996a, Chen et al. 1997, Nilson 1999). This coefficient, STAR (see section 3.2) or something similar, has the effect of decreasing the total interaction cross section σ (see section 2) for a given amount of needle area density. Using this kind of correction coefficient for shoot level clumping is conceptually equivalent to using shoots as the basic units (scattering elements), and the statistical density function then describes shoot density, not needle density (Nilson and Ross 1997). Some recent canopy reflectance models (Knyazikhin et al. 1998b, Kuusk and Nilson 2000) have used this kind of parameterization.

What seemingly has gone unnoticed in previous models, is that when a shoot level grouping index is used to reduce the area interaction cross section, meaning that shoots, not needles, are treated as the basic scattering elements, optical properties (usually transmittance and reflectance) measured from needles can no longer be used to describe the scattering properties of the basic elements.

In paper **IV**, the process of light scattering from coniferous shoots is studied using photon tracing and a geometric model of shoot structure, and a simple wavelength dependent correction to scattering is proposed. In paper **V** the consequences of this correction at canopy scale are explored using simple model canopies.

5.1 The recollision probability

The key concept in papers **IV** and **V** is the recollision probability. It is defined as the probability that a photon inside a canopy, after being scattered, will collide with the canopy again. A similar definition is applied for recollisions within a shoot, in this case regarding the shoot as a mini-canopy. The probability of hitting the canopy again is supposedly different for photons in different locations and flying to different directions. However, the methods developed in this work are based on the simplifying assumption that these differences do not matter much, and that we can use just one value of recollision probability when modelling the amount of multiple scattering that takes place within a certain canopy (or a shoot). It turns out that this simplifying assumption gives very good results.

Similar ideas have been used in nuclear reactor theory. The key objective in nuclear engineering is to keep the number of neutrons in a reactor stable. Neutrons are lost to absorption, and new neutrons are created in collisions (that is, scattering events). In this process, the changes in the number of neutrons in successive generations is of interest. In nuclear reactor theory literature, the ratio of the number of neutrons in two successive generations is known as the “multiplication factor” or the “multiplication factor eigenvalue” (see sec. 1.5 in Bell and Glasstone 1970), albeit it is not really an eigenvalue in the usual linear algebra sense. For a photon flying inside a canopy to pass from one generation to the next one, both recollision and a subsequent scattering are required. Thus, recollision probability multiplied by scattering probability gives the multiplication factor.

In thermal engineering, the concept of recollision probability is known as view factor or shape factor, giving the proportion of radiation emitted by a body that hits the body again (e.g. Holman 1986). It is important when calculating the capacity of cooling elements to lose heat by thermal radiation. The idea of radiation from one needle hitting the neighboring needles within the same shoot, in the context of heat transfer, has been mentioned by Gates and Benedict (1963).

Knyazikhin et al. (1998b) used the concept of multiplication factor eigenvalue, calling it the “unique positive eigenvalue of the radiative transfer equation”, to develop a simple formula for relating canopy absorption in one wavelength to that in another, when leaf absorption was assumed to be known in both wavelengths. Panferov et al. (2001) noted that when the multiplication factor is divided by the element scattering coefficient, the remaining term should be independent of wavelength, and thus be related only to the geometrical structure of a canopy. They termed this factor as the “canopy spectral invariant p_{i}”. This is the same concept that is termed the recollision probability here.

The recollision probability is applied to calculate multiple scattering within a canopy as follows. In this example, ground reflectance is assumed to be zero. The part of photons passing through the canopy without colliding is called zero order transmission (t_0). The part of photons that collide is called zero order interception (i_0). Together, $i_0 + t_0 = 1$. Following the fates of the collided photons (i_0), part of them will be absorbed in the first collision (a_1). The part of the photons that are scattered at least once before absorption is called the scattered component of absorption (a_{s}). Photons that are scattered at least once and then escape the canopy downwards, are the scattered component of transmission (t_s), and photons that escape upwards constitute the reflection (r). Naturally there is no uncollided component in the reflection. Noting that the components are wavelength dependent, except i_0, we get

$$a_1(\lambda) + a_\mathrm{s}(\lambda) + r(\lambda) + t_\mathrm{s}(\lambda) + t_0 = 1. \tag{10}$$

Under the simplifying assumption that the recollision probability is constant in successive scatterings, we can write the total absorptions as a series

$$\begin{aligned} a &= i_0 \left[(1-\omega) + \omega p\,(1-\omega) + \omega^2 p^2\,(1-\omega) + \ldots\right] \\ &= i_0\,\frac{1-\omega}{1-\omega p}, \end{aligned} \tag{11}$$

where ω is the element scattering coefficient, and p the recollision probability for the canopy. (The dependence of a and ω on λ is not written, to shorten the notation). The fraction of photons that are absorbed at the first collision, a_1, is given by $i_0\,(1-\omega)$. Thus, we can write Eq. 11 also as

$$\begin{aligned} a &= a_1 + i_0 \left[\omega p\,(1-\omega) + \omega^2 p^2\,(1-\omega) + \ldots\right] \\ &= a_1 + i_0\,\frac{\omega p\,(1-\omega)}{1-\omega p} \end{aligned} \tag{12}$$

and here the last term gives the multiply scattered part of absorption, a_s. Now we see that the multiply scattered part of the total absorption simplifies to

$$\frac{a_\mathrm{s}}{a} = \frac{\omega p\,(1-\omega)}{1-\omega p} \Bigg/ \frac{1-\omega}{1-\omega p} = \omega p. \tag{13}$$

The approach of Eq. 11 can also be interpreted as a Markov chain, and it is illustrated in Fig. 1 in paper **V**.

The above parameterization was based on a simple probabilistic model of multiple scattering. Knyazikhin et al. (1998b) and Panferov et al. (2001) used different methods (they expanded the solution to the radiative transfer equation (Eq. 6) in series of orthogonal functions and truncated the series focusing on the coefficient of the first, dominating term) and arrived at a similar parameterization.

Knyazikhin et al. (1998b) and Panferov et al. (2001) also presented a similar parameterization for the fraction of scattered radiation in canopy transmission. This parameterization was later formulated by Shabanov et al. (2003) into the form

$$\frac{t_\mathrm{s}}{t} = \omega p_\mathrm{t}, \tag{14}$$

where $t = t_0 + t_\mathrm{s}$ is the total canopy transmission, and p_t is a wavelength independent, canopy structure related parameter describing canopy transmittance.

Both Eqs. 13 and 14 assume that the scattered part in total canopy absorption and transmission depends linearly on the element scattering coefficient. The coefficients p (termed p_i by Panferov et al. (2001)) and p_t are postulated to be related to the canopy structure. The following sections, and papers **IV** and **V**, show that the parameterization for absorption, at both shoot scale and canopy scale, conforms well with results from simulations, while the parameterization for transmission does not conform with the simulations.

5.2 Multiple scattering at shoot level

In paper **IV**, measured data and a geometric model of a Scots pine (*Pinus sylvestris*) shoot structure by Stenberg et al. (2001) is used. An illustration of the model shoot is shown in Fig. 1 in paper **IV**. The main assumptions in the light scattering simulations were the following: needles were cylindrical in shape, needles followed a Fibonacci phyllotactic arrangement, needle reflectance and transmittance were always equal to each other, and both reflected and transmitted light followed the Lambert distribution. The idea of recollision probability was applied here at shoot level, and the recollision probability was denoted by p_{sh}.

The scattering properties of the model shoot was studied using the photon tracing technique (see section 2.5). The constructed scattering phase functions for a model shoot are shown in Fig. 3 in paper **IV**. Multiple scattering within a shoot was found to be considerable. For example, using the value $p_{\mathrm{sh}} = 0.6$ from Fig. 6 in paper **IV** (this is for a shoot from top canopy) in Eq. 5 in paper **IV**, and using needle scattering coefficient $\omega_{\mathrm{L}} = 0.9$ to represent near infrared (NIR) radiation, we get the result that a photon hitting the shoot will interact with it 2.17 times on the average. Or, for the shoot illustrated in Fig. 1 (which was taken from the middle canopy) in paper **IV**, $p_{\mathrm{sh}} = 0.47$ and the average number of NIR interactions is 1.73.

The recollision probability was used to construct a very simple model of multiple scattering as a geometric series (Eqs. 4 and 5 in paper **IV**) to relate shoot scattering coefficient to needle scattering coefficient at the same wavelength. This simple formula agreed remarkably well at all wavelengths with the values of shoot scattering coefficient obtained from photon tracing simulations (Fig. 5 in paper **IV**). Further, the shoot level recollision probability (p_{sh}) was shown to be approximately equal to $1 - 4\,\overline{\mathrm{STAR}}$. This means that the values of $\overline{\mathrm{STAR}}$ already reported in the literature for several species (papers **II** and **III**, Stenberg et al. 1999, 2001, Cescatti and Zorer 2003) can be directly utilized in parameterizing within-shoot multiple scattering.

5.3 Multiple scattering at canopy level

The consequences on canopy level of accounting for the within-shoot shoot multiple scattering (previous section, paper **IV**) are explored briefly in paper **IV** and in more detail in paper **V**. Simple model canopies with homogeneous structure were constructed with either leaves or shoots as the basic scattering elements. In the simulations, photons were fired into the canopy, and the absorption and scattering processes were sampled accordingly. With leaf canopy, scattering was sampled from the scattering phase function for spherically oriented leaves (Eq. 9 in paper **IV**). With shoot canopy, the scattering process was simulated by using the shoot level photon tracing model of paper **IV** as a sub-model for the canopy level simulations.

The fates of the photons were followed and statistics were collected of the number of photons that (i) went through the canopy with no interactions, (ii) were absorbed after zero, one or more interactions, or (iii) were scattered out of the canopy (either upwards or downwards) after one or more interactions (see Fig. 2 in paper **V** for an example). These simulations were performed for canopies of several leaf area indices, and with varying leaf/needle scattering coefficients (which represented different wavelengths).

With these statistics, the idea by Panferov et al. (2001) of using one parameter to describe the wavelength dependency of canopy absorption was tested, and found to be good with both leaf and shoot canopies. This parameter, the canopy level recollision probability, was shown to be decomposable between shoot level and higher level multiple scattering (Eq. 5 and Fig. 5 in paper **V**).

Knyazikhin et al. (1998b) and Panferov et al. (2001) have also proposed a parameter similar to p_i (which describes wavelength dependent canopy absorption), the p_t, to describe wavelength dependent canopy transmission. With absorption and transmission known, the most relevant property from the remote sensing point of view, reflection, is easy to calculate as 1–absorption–transmission. The p_t-parameterization, when compared with the simulations, performed relatively well with the leaf canopies, but not well with the shoot canopies.

As an example of including the shoot level correction for a general radiative transfer model, a simple two-stream model by Ross (1981, section II.6.4) was chosen. With this correction included, Ross' model compared rather well with all the simulations (Figs. 7 and 8 in paper **V**).

5.4 Implications for remote sensing

As already implemented in some canopy reflectance models (Knyazikhin et al. 1998b, Kuusk and Nilson 2000), the effect of shoot level clumping for the amount of light a canopy intercepts can be implemented by multiplying the leaf area density of the canopy by a clumping index. In this way we get an "effective leaf area density" that describes the efficiency of shoot silhouette area to intercept and attenuate light traversing inside the canopy. In this work I propose that such a correction should logically be accompanied by a wavelength dependent correction for the degree of within-shoot multiple scattering.

For example, if a canopy consists of shoots with a clumping index STAR = 0.133, the effective leaf area index of the canopy is reduced by 4 STAR = 0.532. When performing radiative transfer modelling for this canopy at, say, NIR wavelengths with a needle scattering coefficient of 0.9, we should – since we have chosen shoots as the scattering elements in the model – use shoot level scattering coefficient in the model. The shoot scattering coefficient obtained using values $\omega_\mathrm{L} = 0.9$ and $p_\mathrm{sh} = 1 - 4\,\mathrm{STAR}$ in Eq. 6 in paper **IV** is 0.829, instead of the needle level value of 0.9.

This correction for the shoot level multiple scattering causes a wavelength dependent increase in canopy absorption (Fig. 3 in paper **V**) and an accompanying decrease in reflection and transmission (Fig. 7 in paper **V**). The increase in canopy absorption is largest when scattering is high but not perfect, corresponding to needle scattering coefficients of around 0.7 – 0.9. This is the situation in NIR wavelengths.

Interestingly, when Kuusk and Nilson (2000, 2001) compared their canopy radiative transfer model to measured data, they note that it specifically seems to underestimate the NIR and MIR (middle infrared) absorption in coniferous canopies, and discuss that this could be related to the inadequacy of their algorithm to calculate multiple scattering when canopies contain clustered structures.

5.5 Discussion and conclusions

The specific values chosen for needle reflectance and transmittance in paper **IV** may not be the most realistic. Especially the assumption that needle reflectance always equals transmittance was made more in order to achieve simplicity than realism. Measuring these values for conifer needles is somewhat complicated technically (Daughtry et al. 1989, Mesarch et al. 1999), but some values have been reported (Daughtry et al. 1989, Williams 1991, Rock et al.

1994, Middleton et al. 1997, Mesarch et al. 1999) and generally needle reflectance is larger than transmittance. Additionally, I think that the concepts of needle reflectance and transmittance – needles mostly not being even remotely planar shaped objects – would benefit from careful definition. This would help to clarify what is actually being measured, and whether light escaping from the sides of needles is counted as reflectance, transmittance, or whether it escapes from the measurement system is such a way that it is not included in either. I am not aware of any reported measurements of the specular reflectance of needle surface. However, measurements by Brakke (1994) on some broadleaved species indicate that specular reflectance may not be negligible. The existence of the phenomenon of needle specular reflection is also easy to qualitatively verify by visually observing needles. An improved model of shoot level scattering would include realistic values for needle optical properties, and needle surface specular reflectance.

The recollision probability holds potential to be the single parameter needed to describe how canopy spectral absorption depends on the absorption of canopy elements (leaves, needles). Present results show this approach to adequately describe absorption in homogeneous canopies, and with the inclusion of shoot level clumping when the higher level structure remains homogeneous. The final usefulness of the concept depends on whether the same approach can be successfully used to describe absorption in canopies with several intermediate levels of hierarchical grouping.

The results in paper **V** (Fig. 8) show that while the p_t-parameterization of Panferov et al. (2001) performs well in the simple case of homogeneous leaf canopy, the introduction of shoot level clumping in the canopy causes the p_t-based description to deviate from the simulation results. This gives reason to assume that the p_t-parameterization might not perform well with canopies with grouping in several hierarchy levels. Also, the assumptions behind p_t as seen from Eq. 14 seem suspicious since it is assumed that the fraction of scattered radiation in total canopy transmission depends linearly on the element scattering coefficient. This assumption is not supported by the simulations (Fig. 2 in paper **V**). Still, Fig. 8D in paper **V** indicates regularity in the fractions of upwards and downwards scattered radiation. Perhaps it would be possible to develop another simple parameterization for this process.

Satellites mostly measure reflectances from a single direction, or from a limited set of directions. The models in this work have mostly considered the total reflection to the upper hemisphere. Forest directional reflectance varies for different measurement and solar directions, and is also influenced by crown structure (e.g. Rautiainen et al. 2004) and, according to simulations by Disney et al. (2006), by needle shape and shoot structure.

To conclude, papers **IV** and **V** demonstrate that accounting for multiple scattering at the shoot scale is important for accurate models of coniferous canopy radiative transfer and scattering. One way to handle clumped structures in modelling is to simulate their spectral scattering properties in isolation (paper **IV**) and use the results to derive parameterizations for scattering to be used in models of higher structural level (papers **IV** and **V**). Another way, as has recently been demonstrated by Disney et al. (2006), is to model complete forest canopies to needle level precision, and directly simulate light scattering in the model canopies by photon tracing techniques. Using any approach, the effect that the canopy structural properties at different hierarchy levels have on the canopy reflectance should be described in a way that is helpful in model inversion, i.e. estimating LAI or other structural information from canopies with varying level of clumping using reflectance data.

REFERENCES

Anderson, M.C. 1966. Stand structure and light penetration, II. A theoretical analysis. Journal of Applied Ecology 3: 41–54.

Anten, N.P.R. 2005. Optimal photosynthetic characteristics of individual plants in vegetation stands and implications for species coexistence. Annals of Botany 95: 495–506.

— & Hirose, T. 2001. Limitations on photosynthesis of competing individuals in stands and the consequences for canopy structure. Oecologia 129: 186–196.

— , Schieving, F. & Werger, M.J.A. 1995a. Patterns of light and nitrogen distribution in relation to whole canopy carbon gain in C_3 and C_4 mono- and dicotyledonous species. Oecologia 101: 504–513.

— , Schieving, F., Medina, E., Werger, M.J.A. & Schuffelen, P. 1995b. Optimal leaf area indices in C_3 and C_4 mono- and dicotyledonous species at low and high nitrogen availibility. Physiologia Plantarum 95: 541–550.

Bassow, S.L. & Bazzaz, F.A. 1998. How environmental conditions affect canopy leaf-level photosynthesis in four deciduous tree species. Ecology 79: 2660–2675.

Bégin, C. & Filion, L. 1999. Black spruce (*Picea marianna*) architecture. Canadian Journal of Botany 77: 664–672.

Bell, C.J. & Rose, D.A. 1981. Light measurement and the terminology of flow. Plant, Cell and Environment 4: 89–96.

Bell, G.I. & Glasstone, S. 1970. Nuclear Reactor Theory. Robert E. Krieger Publishing Company, Malabar, Florida.

Bond, B.J., Farnsworth, B.T., Coulombe, R.A. & Winner, W.E. 1999. Foliage physiology and biochemistry in response to light gradients in conifers with varying shade tolerance. Oecologia 120: 183–192.

Brakke, T.W. 1994. Specular and diffuse components of radiation scattered by leaves. Agricultural and Forest Meteorology 71: 283–295.

Campbell, J.B. 1996. Introduction to Remote Sensing. 3 edn. Taylor & Francis, London.

Carter, G.A. & Smith, W.K. 1985. Influence of shoot structure on light interception and photosynthesis in conifers. Plant Physiology 79: 1038–1043.

Case, K.M. & Zweifel, P.F. 1967. Linear transport theory. Addison-Wesley, Reading, MA.

Cescatti, A. 1998. Modelling the radiative transfer in discontinuous canopies of asymmetric crowns I. Model structure and algorithms. Ecological Modelling 101: 263–274.

— & Zorer, R. 2003. Structural acclimation and radiation regime of silver fir (*Abies alba* Mill.) shoots along a light gradient. Plant, Cell and Environment 26: 429–442.

Chandrasekhar, S. 1950. Radiative Transfer. Clarendon Press, Oxford. Reprinted by Dover Publications, New York, 1960.

Charles-Edwards, D.A., Stutzel, H., Ferraris, R. & Beech, D.F. 1987. An analysis of spatial variation in the nitrogen content of leaves from different horizons within a canopy. Annals of Botany 60: 421–426.

Chen, J.M., Rich, P.M., Gower, S.T., Norman, J.M. & Plummer, S. 1997. Leaf area index of boreal forests: Theory, techniques and measurements. Journal of Geophysical Research D 102: 29 429–29 443.

Dang, L.D., Margolis, H.A., Sy, M., Coyea, M.R., Collatz, G.J. & Walthall, C.L. 1997. Profiles of photosynthetically active radiation, nitrogen and photosynthetic capacity in the boreal forest: Implications for scaling from leaf to canopy. Journal of Geophysical

Research D 102: 28 845–28 859.

Daughtry, C.S.T., Biehl, L.L. & Ranson, K.J. 1989. A new technique to measure the spectral properties of conifer needles. Remote Sensing of Environment 27: 81–91.

DeJong, T.M. & Doyle, J.F. 1985. Seasonal relationships between leaf nitrogen content (photosynthetic capacity) and leaf canopy light exposure in peach (*Prunus persica*). Plant, Cell and Environment 8: 701–706.

Disney, M., Lewis, P. & North, P.R.J. 2000. Monte Carlo ray tracing in optical canopy reflectance modelling. Remote Sensing Reviews 18: 163–196.

— , Lewis, P. & Saich, P. 2006. 3D modelling of forest canopy structure for remote sensing simulations in the optical and microwave domains. Remote Sensing of Environment 100: 114–132.

Eichelmann, H., Oja, V., Rasulov, B., Padu, E., Bichele, I., Petta, H., Kull, O. & Laisk, A. 2005. Adjustment of leaf photosynthesis to shade in a natural canopy: reallocation of nitrogen. Plant, Cell and Environment 28: 389–401.

Ellsworth, D.S. & Reich, P.B. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. Oecologia 96: 169–178.

Evans, J.R. 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78: 9–19.

— 1993. Photosynthetic acclimation and nitrogen partitioning within a lucerne canopy. I. Canopy charasteristics. Australian Jounal of Plant Physiology 20: 55–67.

— & Seeman, J.R. 1989. The allocation of protein nitrogen in the photosynthetic apparatus: costs, consequences and control. In: W.R. Briggs (ed.) Photosynthesis. Alan R. Liss, New York, pp. 183–205.

Farquhar, G.D. 1989. Models of integrated photosynthesis of cells and leaves. Philosophical transactions of the Royal Society of London, Series B 323: 357–367.

Field, C. 1983. Allocating leaf nitrogen for the maximization of carbon gain: Leaf age as a control on the allocation program. Oecologia 56: 341 – 347.

— & Mooney, H.A. 1986. The photosynthesis-nitrogen relations in wild plants. In: T. Givnish (ed.) On the Economy of Plant Form and Function. Cambridge University Press, Cambridge, pp. 25–55.

Foley, J.D., van Dam, A., Feiner, S.K. & Hughes, J.F. 1990. Computer Graphics: Principles and Practice. 2 edn. Addison-Wesley, Reading, Massachusetts.

Friend, A.D. 2001. Modelling canopy CO_2 fluxes: are 'big-leaf' simplifications justified? Global Ecology & Biography 10: 603–619.

Gates, D.M. & Benedict, C.M. 1963. Convection phenomena from plants in still air. American Journal of Botany 50: 536–573.

Gelderen, D.M.V. & Van Hoey Smith, J.R.P. 1996. Conifers: The Illustrated Encyclopedia. Timber Press, Oregon.

Glassner, A.S. 1995. Principles of Digital Image Synthesis. Morgan Kaufmann, San Francisco.

Gobron, N., Pinty, B., Verstraete, M. & Govaerts, Y. 1999. The MERIS Global Vegetation Index (MGVI): description and pleriminary application. International Journal of Remote Sensing 20: 1917–1927.

Gutschick, V.P. 1991. Joining leaf photosynthesis models and canopy photon-transport models. In: R. Myneni & J. Ross (eds.) Photon-Vegetation Interactions. Springer-Verlag, Berlin, pp. 501–535.

Han, Q.M., Kawasaki, T., Nakano, T. & Chiba, Y. 2004. Spatial and seasonal variability of temperature responses of biochemical photosynthesis parameters and leaf nitrogen content within a *Pinus densiflora* crown. Tree Physiology 24: 737–744.

Hirosaka, K. & Terashima, I. 1996. Nitrogen partitioning among photosynthetic components and its consequence in sun and shade plants. Functional Ecology 10: 335–343.

Hirose, T. 2005. Development of the Monsi–Saeki theory on canopy structure and function. Annals of Botany 95: 483–494.

— & Werger, M.J.A. 1987a. Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. Oecologia 72: 520–526.

— & Werger, M.J.A. 1987b. Nitrogen use efficiency in instantaneous and daily photosynthesis of leaves in the canopy of a *Solidaga altissima* stand. Physiologia plantarum 70: 215–222.

— , Werger, M.J.A. & van Rheenen, J.W.A. 1989. Canopy development and leaf nitrogen distribution in a stand of *Carex acutiformis*. Ecology 70: 1610–1618.

Hollinger, D.Y. 1989. Canopy organization and foliage photosynthetic capacity in a broad leaved evergreen montane forest. Functional Ecology 3: 53–62.

— 1996. Optimality and nitrogen allocation in a tree canopy. Tree Physiology 16: 627–634.

Holman, J.P. 1986. Heat Transfer. 6 edn. McGraw-Hill, New York.

Ishii, H. & Ford, E.D. 2001. The role of epicormic shoot production in maintaining foliage in old *Pseudotsuga menziesii* (Douglas-fir) trees. Canadian Journal of Botany 79: 251–264.

Ishimaru, A. 1999. Wave Propagation and Scattering in Random Media. Wiley-IEEE Press, New York.

Jensen, H.W. 2001. Realistic Image Synthesis Using Photon Mapping. AK Peters, Wellesley, Massachusetts.

Kellomäki, S. & Oker-Blom, P. 1981. Specific needle area of Scots pine and its dependence on light conditions inside the canopy. Silva Fennica 15: 190–198.

Kirkham, M.B. 2005. Principles of Soil and Plant Water Relations. Elsevier Academic Press, San Diego, California.

Knyazikhin, Y., Mießen, G., Panfyorov, O. & Gravenhorst, G. 1997. Small-scale study of three-dimensional distribution of photosynthetically active radiation in a forest. Agricultural and Forest Meteorology 88: 215–239.

— , Kranigk, J., Myneni, R.B., Panfyorov, O. & Gravenhorst, G. 1998a. Influence of small-scale structure on radiative transfer and photosynthesis in vegetation canopies. Journal of Geophysical Research D 103: 6133–6144.

— , Martonchik, J.V., Myneni, R.B., Diner, D. & Running, S.W. 1998b. Synergistic algorithm for estimating vegetation canopy leaf area index and fraction of absorbed photosynthetically active radiation from MODIS and MISR data. Journal of Geophysical Research D 103: 32 257–32 276.

— , Glassy, J., Privette, J.L., Tian, Y., Lotsch, A., Zhang, Y., Wang, Y., Morisette, J.T., Votava, P., Myneni, R.B., Nemani, R.R. & Running, S.W. 1999. MODIS Leaf Area Index (LAI) and Fraction of Photosynthetically Active Radiation Absorbed by Vegetation (FPAR) Product (MOD15) Algorithm Theoretical Basis Document. Tech. rep., NASA Goddard Space Flight Center, Greenbeld, Maryland.

Kotchenova, S.Y., Shabanov, N.V., Knyazikhin, Y., Davis, A.B., Dubayah, R. & Myneni, R.B. 2003. Modeling lidar waveforms with time-dependent stochastic radiative transfer theory for remote estimation of forest structure. Journal of Geophysical Research D 108: 4484–4496.

Kramer, P.J. 1995. Water Relations of Plants and Soil. Academic Press, San Diego, California.

Kull, O. 2002. Acclimation of photosynthesis in canopies: models and limitations. Oecologia 2002: 267–279.

— & Niinemets, Ü. 1993. Variations in leaf morphometry and nitrogen concentration in *Betula pendula, Corylus avellana* and *Lonicera xylosteum.* Tree Physiology 12: 311–318.

— & Tulva, I. 2002. Shoot structure and growth among a vertical profile within a *Populus-Tilia* canopy. Tree Physiology 22: 1167–1175.

Kuusk, A. & Nilson, T. 2000. A directional multispectral forest reflectance model. Remote Sensing of Environment 72: 244–252.

— & Nilson, T. 2001. Testing directional properties of a forest reflectance model. Journal of Geophysical Research D 106: 12 011–12 021.

— , Nilson, T. & Paas, M. 2002. Angular distribution of radiation beneath forest canopies using a CCD-radiometer. Agricultural and Forest Meteorology 110: 259–273.

Laisk, A., Eichelmann, H., Oja, V., Rasulov, B., Padu, E., Bichele, I., Petta, H. & Kull, O. 2005. Adjustment of leaf photosynthesis to shade in a natural canopy: rate parameters. Plant, Cell and Environment 28: 375–388.

Lappi, J. & Smolander, H. 1984. Integration of the hyperbolic radiation-response function of photosynthesis. Photosynthetica 18: 402–410.

Larcher, W. 2003. Physiological Plant Ecology. 4 edn. Springer, Berlin.

Leuning, R., Cromer, R.N. & Rance, S. 1991. Spatial distributions of foliar nitrogen and phosphorus in crowns of *Eucalyptus grandis*. Oecologia 88: 504–510.

Leverenz, J.W. & Hinckley, T.M. 1990. Shoot structure, leaf area index, and productivity of evergreen conifer stands. Tree Physiology 6: 135–149.

— & Jarvis, P.G. 1980. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.). IX. the relative contribution made by needles at various positions in the shoot. Journal of Applied Ecology 17: 59–68.

Mandelbrot, B.B. 1983. The Fractal Geometry of Nature. Freeman, New York.

Marek, M., Masarovicová, E., Kratochvíla, I., Eliás, P. & Janous, D. 1989. Stand microclimate and physiological activity of tree leaves in an oak-hornbeam forest. II. Leaf photosynthetic activity. Trees 4: 234–240.

Medlyn, B., Barrett, D., Landsberg, J. & Clement, P.S.R. 2003. Conversion of canopy intercepted radiation to photosynthate: a review of modelling approaches for regional scales. Functional Plant Biology 30: 153–169.

Meir, P., Kruijt, B., Broadmeadow, M., Barbosa, E., Kull, O., Carswell, F., Nobre, A. & Jarvis, P.G. 2002. Acclimation of photosynthetic capacity to irradiance in tree canopies in relation to leaf nitrogen concentration and leaf mass per unit area. Plant, Cell and Environment 25: 343–357.

Mesarch, M.A., Walter-Shea, E.A., Asner, G.P., Middleton, E.M. & Chan, S.S. 1999. A revised measurement methodology for conifer needles spectral optical properties: Evaluating the influence of gaps between elements. Remote Sensing of Environment 68: 177–192.

Metropolis, N. 1987. The beginning of the Monte Carlo method. Los Alamos Science 15: 125–130.

— & Ulam, S. 1949. The Monte Carlo method. Journal of American Statistical Association 44: 335–341.

Michaelis, L. & Menten, M.L. 1913. Die Kinetik der Invertinwirkung. Biochemische Zeitschrift 49: 334–336.

Middleton, E.M., Chan, S.S., Rusin, R.J. & Mitchell, S.K. 1997. Optical properties of black spruce and jack pine needles at BOREAS sites in Saskatchewan, Canada. Canadian Journal of Remote Sensing 23: 108–119.

Monsi, M. & Saeki, T. 1953. Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. Japanese Journal of Botany 14: 22–55. English translation, On the factor of light in plant communities and its importance for matter production, published in Annals of Botany (2005) 95: 549-567.

Mooney, H.A. & Gulmon, S.L. 1979. Environmental and evolutionary constraints on the photosynthetic characteristics of higher plants. In: O.T. Solbrig, S. Jain, G.B. Johnson & P.H. Raven (eds.) Topics in plant population ecology. Columbia University Press, New York, pp. 316–337.

Myneni, R.B. & Ross, J. (eds.) 1991. Photon-Vegetation Interactions. Springer-Verlag, Berlin.

— , Ross, J. & Asrar, G. 1989. A review on the theory of photon transport in leaf canopies. Agricultural and Forest Meteorology 45: 1–153.

Niinemets, Ü. & Kull, O. 1995. Effects of light availibility and tree shape on the architecture of assimilative surface in the canopy of *Picea abies*: variation in shoot structure. Tree Physiology 15: 791–798.

Niklas, K.J. 1992. Plant Biomechanics: An Engineering Approach to Plant Form and Function. University of Chicago Press, Chicago.

Nilson, T. 1992. Radiative transfer in nonhomogeneous plant canopies. In: G. Stanhill (ed.) Advances in Bioclimatology 1. Springer Verlag, Berlin, pp. 59–88.

— 1999. Inversion of gap frequency data in forest stands. Agricultural and forest meteorology 98-99: 437–448.

— & Ross, J. 1997. Modeling radiative transfer through forest canopies: Implications for canopy photosynthesis and remote sensing. In: H.L. Gholz, K. Nakane & H. Shimoda (eds.) The use of remote sensing in the modeling of forest productivity. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 23–60.

— , Anniste, J., Lang, M. & Praks, J. 1999. Detemination of needle area indices of coniferous forests canopies in the NOPEX region by ground-based optical measurements and satellite images. Agricultural and Forest Meteorology 98-99: 449–462.

Norman, J.M. & Jarvis, P.G. 1974. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.). III. Measurements of canopy structure and interception of radiation. Journal of Applied Ecology 11: 375–398.

Oker-Blom, P. 1985. Photosynthesis of a Scots pine shoot: Simulation of the irradiance distribution and photosynthesis of a shoot in different radiation fields. Agricultural and Forest Meteorology 34: 31–40.

— 1986. Photosynthetic radiation regime and canopy structure in modelled forest stands. Acta Forestalia Fennica 197: 1–44.

— & Kellomäki, S. 1983. Effect of grouping of foliage on the within-stand and within-crown light regime: Comparison of random and grouping canopy models. Agricultural Meteorology 28: 143–155.

— & Smolander, H. 1988. The ratio of shoot sihouette area to total needle area in Scots pine. Forest Science 34: 894–906.

— , Lahti, T. & Smolander, H. 1992. Photosynthesis of a Scots pine shoot: A comparison of two models of shoot photosynthesis in direct and diffuse radiation fields. Tree Physiology 10: 111–125.

— , Lappi, J. & Smolander, H. 1991. Radiation regime and photosynthesis of coniferous stands. In: R. Myneni & J. Ross (eds.) Photon-Vegetation Interactions. Springer-Verlag, Berlin, pp. 469–499.

Panferov, O., Knyazikhin, Y., Myneni, R.B., Szarzynski, J., Engwald, S., Schnitzler, K.G. & Gravenhorst, G. 2001. The role of canopy structure in the spectral variation of transmission and absorption of solar radiation in vegetation canopies. IEEE Transaction on Geosciences and Remote Sensing 39: 241–253.

Pons, T.L., Schieving, F., Hirose, T. & Werger, M.J.A. 1990. Optimization of leaf nitrogen allocation for canopy photosynthesis in *Lysimachia vulgaris*. In: H. Lambers, M.L. Cambridge, H. Konings & T.L. Pons (eds.) Causes and consequences of variation in growth rate and productivity of higher plants. SPB Academic Publishing, Hague, pp. 175–186.

Rautiainen, M., Stenberg, P., Nilson, T. & Kuusk, A. 2004. The effect of crown shape on the reflectance of coniferous stands. Remote Sensing of Environment 89: 41–52.

Roberts, D., Ustin, S., Ogunyemiyo, S., Greenberg, J., Dobrowski, S., Chen, J. & Hinckley, T. 2004. Spectral and structural measures of northwest forest vegetation at leaf to landscape scales. Ecosystems 7: 545–562.

Rock, B.N., Williams, D.L., Moss, D.M., Lauten, G.N. & Kim, M. 1994. High-spectral resolution field and laboratory optical reflectance measurements of red spruce and eastern hemlock needles and branches. Remote Sensing of Environment 47: 176–189.

Ross, J. 1981. The Radiation Regime and Architecture of Plant Stands. Kluwer, Hague.

Schieving, F. & Poorter, H. 1999. Carbon gain in a multispecies canopy: the role of specific leaf area and photosynthetic nitrogen use efficiency in the tragedy of the commons. New Phytologist 143: 201–211.

— , Pons, T.L., Werger, M.J.A. & Hirose, T. 1992. Vertical distribution of nitrogen and photosynthetic activity at different plant densities in *Carex acutiformis*. Plant and Soil 142: 9–17.

Schoettle, A.W. & Smith, W.K. 1991. Interaction between shoot characteristics and solar irradiance in the crown of *Pinus contorta* ssp. *latifolia*. Tree Physiology 9: 245–254.

Shabanov, N.V., Wang, Y., Buermann, W., Dong, J., Hoffman, S., Smith, G., Tian, Y., Knyazikhin, Y. & Myneni, R.B. 2003. The effect of spatial heterogeneity in validation of the MODIS LAI and FPAR algorithm over broadleaf forests. Remote Sensing of Environment 85: 410–423.

Simpson, G.C. 1928. Some studies in terrestrial radiation. Memoirs of the Royal Meteorological Society 2: 69–95.

Smith, W.K. & Carter, G.A. 1988. Shoot structural effects on needle temperatures and photosynthesis in conifers. American Journal of Botany 75: 496–500.

Smolander, H. 1984. Measurement of fluctuating irradiance in field studies of photosynthesis. Acta Forestalia Fennica 187: 1–56.

— & Oker-Blom, P. 1989. The effect of nitrogen content on the photosynthesis of Scots pine needles and shoots. In: E. Dreyer et al (eds.) Annales des Sciences Forestieres 46 suppl. Forest Tree Physiology. pp. 473–475.

— , Stenberg, P. & Linder, S. 1994. Dependence of light interception efficiency of Scots pine shoots on structural parameters. Tree Physiology 14: 971–980.

— , Oker-Blom, P., Ross, J., Kellomäki, S. & Lahti, T. 1987. Photosynthesis of a Scots pine shoot: Test of a shoot photosynthesis model in a direct radiation field. Agricultural and Forest Meteorology 39: 67–80.

Sobolev, V.V. 1970. Light Scattering by Planetary Atmospheres. Pergamon Press, New York.

Sprugel, D. 1989. The relationship of evergreennes, crown architecture, and leaf size. American Naturalist 133: 465–479.

— , Brooks, J.R. & Hinckley, T.M. 1996. Effects of light on shoot geometry and needle morphology in *Abies amabilis*. Tree Physiology 16: 99–108.

Stenberg, P. 1995. Penumbra in within-shoot and between-shoot shading in conifers and its significance for photosynthesis. Ecological Modelling 77: 215–231.

— 1996a. Correcting LAI-2000 estimates for the clumping of needles in shoots of conifers. Agricultural and Forest Meteorology 79: 1–8.

— 1996b. Simulations on the effects of shoot structure and orientation on vertical gradients in intercepted light by conifer canopies. Tree Physiology 16: 99–108.

— , Linder, S. & Smolander, H. 1995a. Variation in the ratio of shoot silhouette area to needle area in fertilized Norway spruce trees. Tree Physiology 1995: 705–712.

— , Smolander, H. & Kellomäki, S. 1993. Description of crown structure for light interception models: Angular and spatial distribution of shoots in young Scots pine. Studia Forestalia Suecica 191: 843–50.

— , DeLucia, E.H., Schoettle, A.W. & Smolander, H. 1995b. Photosynthetic light capture and processing from cell to canopy. In: W.K. Smith & T.M. Hinckley (eds.) Resource Physiology of Conifers: Acquisition, Allocation, and Utilization. Academic Press, San Diego, California, pp. 3–38.

— , Kangas, T., Smolander, H. & Linder, S. 1999. Shoot structure, canopy openness, and light interception in Norway spruce. Plant, Cell and Environment 22: 1133–1142.

— , Palmroth, S., Bond, B.J., Sprugel, D.G. & Smolander, H. 2001. Shoot structure and photosynthetic efficiency along the light gradient in a Scots pine canopy. Tree Physiology 21: 805–814.

Thomas, G.E. & Stamnes, K. 1999. Radiative Transfer in the Atmosphere and Ocean. Cambridge University Press, Cambrigde.

Thornley, J.H.M. 1976. Mathematical Models in Plant Physiology. Academic Press.

— 2002. Instantaneous canopy photosynthesis: Analytical expressions for sun and shade leaves based on exponential light decay down the canopy and an acclimated non-rectangular hyperbola for leaf photosynthesis. Annals of Botany 89: 451–458.

Walter-Shea, E.A. & Norman, J.M. 1991. Leaf optical properties. In: R. Myneni & J. Ross (eds.) Photon-Vegetation Interactions. Springer-Verlag, Berlin, pp. 229–251.

Werger, M.J.A. & Hirose, T. 1991. Leaf nitrogen distribution and whole canopy photosynthetic carbon gain in herbaceous stands. Vegetatio 97: 11–20.

Williams, D. 1991. A comparison of spectral reflectance properties at the needle, branch, and canopy level for selected conifer species. Remote Sensing of Environment 35: 79–93.

Wilson, K.B., Baldocchi, D.D. & Hanson, P.J. 2000. Spatial and seasonal variability of photosynthesis parameters and their relationship to leaf nitrogen in a deciduous forest. Tree Physiology 20: 565–587.

Zhang, Y., Tian, Y., Myneni, R.B., Knyazikhin, Y. & Woodcock, C.E. 2002. Assessing the information content of multiangle satellite data for mapping biomes I: Statistical analysis. Remote Sensing of Environment 80: 418–434.

Zimmerman, M.H. & Brown, C.L. 1971. Trees: Structure and Function. Springer-Verlag, New York.