Crown structure, radiation absorption, 
photosynthesis and transpiration

by

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DECLARATION

This thesis has been composed by myself and it has not been submitted in any previous application for a degree. The work reported within this thesis was executed by myself unless otherwise stated.

Yingying Wang
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Abstract

A complex simulation model, MAESTRO, has been developed and validated against field measurements in plantations in both Scotland and Australia. It has been shown that MAESTRO can reasonably predict the daily course of PAR (photosynthetically active radiation) transmittance at points below the canopies of radiata pine and Sitka spruce plantations.

1. Four structural properties of the Sitka spruce tree crown have been identified and evaluated in relation to PAR absorption, photosynthesis, and transpiration. They are: the total amount of leaves within the tree crown, leaf inclination angle distribution and crown shape. The total area of leaves and their spatial distribution within the tree crown are ranked as the two most significant properties.

2. Among the four different structural properties studied, crown shape is least important for PAR absorption, photosynthesis, and transpiration. For the Sitka spruce stand studied, transpiration was most sensitive to the total area of leaves within the tree crown, whereas photosynthesis can be significantly affected by the leaf angle distribution. The influence of crown structure also depends on the beam fraction, radiance of diffuse radiation, incident angle of beam radiation.

3. Application of MAESTRO has shown the importance of the spatial distribution of leaf area density distribution and the age structure of the leaf population within a dense Sitka spruce canopy for the radiation regime and for photosynthesis. It has been found that the non-uniform canopy structure results in a more uniform radiation regime within the canopy, and hence a higher PAR use efficiency than a uniform canopy structure. The actual leaf age structure within a dense Sitka spruce canopy has been compared with the leaf age structure that is optimal for maximizing the PAR use efficiency of the canopy and it has been found that PAR use efficiencies of both canopies are very close.

4. The non-uniform structure of a tree crown has been described using a two-dimensional leaf area density distribution function within the tree crown. It was found that the spatial distribution of leaf area density and the age structure of the leaf population within the crowns of radiata pine trees were significantly affected by water stress and nutrient deficiency during the growing season.

5. The radiance distribution of diffuse radiation from the sky and the beam fraction of the incident radiation also affect PAR absorption, photosynthesis, and transpiration by altering the uniformity of the radiation regime within the tree crown. The light use efficiency of the canopy decreases with the increase in beam fraction.

6. The stomatal and photosynthetic properties of the shoots of Sitka spruce were measured in an open path gas exchange system to parameterize a biochemical photosynthesis model. It was found that co-limitation of photosynthesis plays an important role in the PAR
responses of both an isolated shoot and of a canopy. It was shown that co-limitation of canopy photosynthesis enables the canopy to use a high flux density of incident PAR efficiently.

7. The dry matter production of the above-ground biomass of a Sitka spruce stand was studied in relation to PAR absorption to test the Monteith hypothesis. It was found that the relationship between the above-ground dry matter production and PAR absorption is approximately linear. The slope of this linear relationship is affected by nitrogen fertilization, but not by thinning for the Sitka spruce stands studied.

Crown structure plays an important role in the processes of radiation transfer, photosynthesis and transpiration within the tree crown. Detailed descriptions of the important structural properties of the tree crown are necessary for adequate understanding of canopy processes, such as photosynthesis. Co-limitation of crown photosynthesis, determined by the structure of all the tree crowns in the stand, results in an efficient use of the incident solar radiation by the trees in the stand. Photosynthesis of the forest canopy is roughly proportional to the incident PAR, PAR absorption is the primary determinant of dry matter production of the above-ground biomass for the Sitka spruce stand studied.
Preface

Canopy structure has been extensively studied in relation to radiation interception, photosynthesis and dry matter production by means of simulation models. (e.g. Monsi and Saeki 1953, Duncan et al 1967, Norman and Jarvis 1974, 1975, McMurtrie et al 1985). Lemeur and Blad (1974) reviewed the major types of radiation models before the 1970's. A wide range of radiation models has since been developed in connection with the advent of powerful computing facilities, but little development has been made of the basic theory underpinning these models since the 1970's. However, Ross (1981) has provided a comprehensive treatise of radiation penetration in plant stands.

Horizontal homogeneity is usually assumed in modelling radiation penetration in plant canopies, but this is hardly realistic for many canopies and in particular for widely spaced stands of trees. A geometric crown model is more appropriate for taking the horizontal discontinuity of a tree canopy into account (Norman and Welles 1983). Furthermore, there are large variations of leaf area density within a tree crown and spatial heterogeneity at this scale may also influence the radiation regime, and hence photosynthesis within the tree crown. However, this has not been studied, and a uniform canopy structure is still assumed in many geometric models (Charles-Edwards and Thornley 1974, Whitfield and Connor 1980).

Radiation absorption and photosynthesis depend not only on the crown structure and the positions of all trees in a stand, but also on the incident radiation, and their respective influences may also be interactive. Only few systematic evaluations of different structural properties of a tree crown or a plant canopy have so far been made in relation to radiation absorption, photosynthesis and transpiration (Jarvis and Leverenz 1983, Rook et al 1985, Campbell and Norman 1987).

It would be a vain attempt to consider all different structural properties of the tree crown, as such an approach would be too complex to be realistic. Discriminative study using a simulation model should enable us to pinpoint the important characteristics of the tree crown.

The dry matter production of the above-ground biomass of a stand may also be linearly related to the amount of radiation absorbed by the stand as hypothesized by Monteith (1972, 1977). This has been demonstrated for a number of agricultural crops (e.g. Gallagher and Biscoe 1978, Coulson 1985), but only few such studies have so far been made on stands
of trees (Linder 1984, Cannell et al 1986).

Such a simple linear relationship between dry matter production and radiation absorption provides an excellent overall summary of the complex processes of dry matter production. Factorial analysis of the slope of that linear relation should enable identification of the important partial processes on which further research should be concentrated in order to increase the productivity of forest plantations. Study of the partial processes and the development of process-based submodels should eventually allow that linear relationship to be modelled.

Therefore I am going to

1. study the leaf area density distribution within the crowns of radiata pine and Sitka spruce trees (Chapter 1).

2. develop the model, MAESTRO and validate it against measurement of PAR transmittances at different locations below canopies (Chapter 2).

3. investigate the influence of crown structure, crown shape and tree spacing on radiation absorption, photosynthesis and transpiration of a tree crown (Chapter 3).

4. investigate the influence of the incident radiation on radiation absorption, photosynthesis and transpiration (Chapter 3).

5. study shoot structure and its influence on photosynthesis of a shoot and a canopy (Chapter 4).

6. study the relation between radiation absorption and dry matter production of the aboveground biomass of a Sitka spruce stand (Chapter 5).
1. THE NEEDLE AREA DENSITY DISTRIBUTION AND ITS INFLUENCE ON RADIATION TRANSMISSION AND PHOTOSYNTHESIS

1.1. Introduction

Since Stephens's earlier work (1969) on the vertical distribution of needle area within the crowns of 50 red pine (*Pinus resinosa*) trees, similar studies have been made for several other coniferous species, such as Scots pine (*Pinus sylvestris*) (Whitehead 1978, Kellomaki et al 1980, Halldin 1985), Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*Pinus lambertiana*) (Massman 1982) and Japanese cypress (*Chamaecyparis obtusa*) (Hagihara and Hozumi 1986), but only a very few studies have been made on the two-dimensional distribution of leaf area density (LAD) within the tree crown. Earlier work by Philip (1969) was based on data collected by the point quadrat method for Atriplex bushes, and later work by Kurachi (1986) and Koike (1986) was based on data collected by stratified samples or from photographs for *Photinia serrulata* and *Aucuba japonica*. In this investigation I describe the two-dimensional needle area density (NAD) distribution within the crowns of radiata pine (*Pinus radiata* D. Don) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) trees. The NAD in the vertical was normalized with respect to the length of the live crown and the total needle area within the tree crown; the NAD distribution in the horizontal was normalized with respect to the crown radius at each whorl and the total area of needles within the tree crown. A function with six parameters was used to describe the two-dimensional distribution of NAD within a tree crown.

Clumping of the foliage is a structural characteristic of coniferous forest canopies, and can enhance the radiation flux density within and below tree crowns. Norman and Jarvis (1975) used a non-random theory to simulate the clumping of needles in a Sitka spruce canopy and got good agreement between theoretical predictions and measurements. One disadvantage of their non-random theory is that the assumption of horizontal continuity of a plant canopy breaks down for a widely spaced stand.

I have considered clumping by describing the two-dimensional NAD distribution within the tree crown, as NAD can be well-defined, and is easily understood. Clumping at a location within the tree crown is expressed as the ratio of the actual NAD within the non-uniform crown to the hypothetical NAD within an assumed uniform tree crown.

A complex leaf age structure is another structural characteristic of coniferous forest canopies. The total photosynthetic rate of a tree crown is determined by the area of needles within the tree crown, the age distribution of the needles and their photosynthetic activities. As needles of different age may have different photosynthetic activities, an
optimal needle age distribution would maximize the total rate of canopy photosynthesis for the same flux density of PAR absorbed (i.e. light use efficiency).

1.2. Definitions

In this study, I define

**Light use efficiency**: the ratio of photosynthetic rate of a canopy to the flux density of PAR absorbed by the canopy.

**Current needles**: the needles that emerged during the last growing season before the tree harvest.

**One-year-old needles**: the needles that emerged during the growing season just before the current needles emerged.

**Other older needles**: the needles that emerged before the one-year-old needles emerged.

**Needle area density**: the area of needles within a unit crown volume.

**Needle age distribution**: the NAD distribution of needles in different age classes within a tree crown or canopy.

**Needle age structure**: the relative proportions by plan area of needles in different age classes within a tree crown or canopy.

**Needle age transition function**: a function that defines the relative proportion of all needles in age class $i$ to all needles in age class $i-1$ within a tree crown or canopy ($i=1, 2$ for one-year-old and other older needles, respectively, in this study).

**Clumping factor**: the ratio of the actual NAD at a location within the tree crown or canopy to the hypothetical NAD within an assumed uniform tree crown or canopy.

1.3. The NAD distribution within the forest canopy and its influence on PAR transmission and on photosynthesis

Empirical equations are frequently used in studies of radiation interception by canopies (Allen et al 1965, Federer 1971, Cohent et al 1987). Even though they may provide adequate predictions of the radiation intercepted by the canopy, they include some empirical coefficients which contain both errors and compensating factors. In seeking a better understanding of the influences of canopy structure on both radiation transmission
and photosynthesis, I have taken account of the variation of NAD in the vertical within the canopy: this can provide a more adequate simulation of the radiation transmission within the forest canopy, and of the influence of the needle age structure in the vertical on canopy photosynthesis.

1.3.1. Influence of vertical NAD distribution on the PAR transmission within the forest canopy

As the NAD varies vertically within the canopy, the PAR regime within the canopy differs from that within a uniform canopy. Near the middle of the canopy, the NAD is very large, and a large proportion of PAR is absorbed; near the top or bottom of the canopy, a large proportion of PAR will be transmitted as the NAD is very small. As a result, the PAR regime within the canopy is dependent on the vertical NAD distribution.

Assumptions and definitions

1. The canopy is homogeneous in the horizontal.
2. Either the NAD is uniform (canopy I), or
3. The NAD varies vertically within the canopy (canopy II). The following relation between the NAD in the vertical \((L_d)\) and the relative canopy height \((h)\) is used: \(L_d = B_1h^{B_2}(1-h)^{B_3}/H_c\), where \(H_c\) and \(L_c\) are canopy height and needle area index of the canopy, respectively.

Table 1.3.1.1 Parameters of the vertical distributions of NAD in canopy II for Sitka spruce (SS) and radiata pine (RP)

<table>
<thead>
<tr>
<th>Species</th>
<th>(B_1)</th>
<th>(B_2)</th>
<th>(B_3)</th>
<th>M.S.</th>
</tr>
</thead>
<tbody>
<tr>
<td>SS</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T</td>
<td>77.37</td>
<td>2.46</td>
<td>2.77</td>
<td>0.16</td>
</tr>
<tr>
<td>C</td>
<td>92.47</td>
<td>3.04</td>
<td>3.00</td>
<td>0.003</td>
</tr>
<tr>
<td>C+1</td>
<td>44.45</td>
<td>2.62</td>
<td>3.20</td>
<td>0.003</td>
</tr>
<tr>
<td>C+2</td>
<td>61.80</td>
<td>2.60</td>
<td>4.29</td>
<td>0.003</td>
</tr>
<tr>
<td>RP</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T</td>
<td>6.84</td>
<td>0.57</td>
<td>1.90</td>
<td>1.28</td>
</tr>
<tr>
<td>C</td>
<td>3.51</td>
<td>1.04</td>
<td>1.41</td>
<td>0.20</td>
</tr>
<tr>
<td>C+1</td>
<td>4.65</td>
<td>1.03</td>
<td>2.53</td>
<td>0.25</td>
</tr>
<tr>
<td>C+2</td>
<td>13.07</td>
<td>0.89</td>
<td>5.67</td>
<td>0.36</td>
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T: all needles together; C: current needles; C+1: one-year-old needles; C+2: other older needles. M.S. mean square error.
Figure 1.3.1.1 The vertical NAD distribution of all needles within the Sitka spruce canopy (solid curve) and radiata pine canopy (broken curve). The canopy needle area index is 10.0, and canopy depth is 10.0 m for both canopies.

Figure 1.3.1.2 The profiles of diffuse transmittances within a uniform canopy (solid curve), a radiata pine canopy (broken curve with shorter intervals) and a Sitka spruce canopy (broken curve with longer intervals).

Figure 1.3.1.3 The cumulative NAI of a uniform canopy (solid curve), a radiata pine canopy (broken curve with the shorter intervals) and a Sitka spruce canopy (broken curves with the longer intervals). The NAI of three canopies is assumed to be 10.0.
Figure 1.3.3.1 The cumulative photosynthetic rate \( P_c(h) \) and flux density of PAR intercepted \( Q_g(h) \) in relation to the relative canopy height \( h \) of a Sitka spruce canopy. The flux density of incident PAR above the canopy is 2000 umol m\(^{-2}\) s\(^{-1}\).

Figure 1.3.3.2 The actual (broken curves) and optimal (solid curves) needle age distributions within a dense Sitka spruce canopy. The canopy needle area index is 10.0 and the canopy depth is 10.0 m. The relation between the needle area index of the canopy \( L_c \) and relative canopy height \( h \) is: \( L_c = B_1 h^{B_2} (1.0 - h)^{B_3} \) and parameters \( B_1, B_2 \) and \( B_3 \) are different for needles of different age classes.

Figure 1.3.3.3 Photosynthetic rate of a canopy with different needle age structures defined by parameters \( B_2 \) and \( B_3 \) (see text for details). Parameter \( B_3 \) was varied from 1.0 to 5.0 in steps of 0.5. As \( B_2 \) increases or \( B_3 \) decreases, the vertical NAD distribution of current needles is skewed towards the canopy top. The vertical NAD distributions of one-year-old and other older needles within the canopy are determined by parameters \( B_2 \) and \( B_3 \) together with needle age transition functions.

Figure 1.3.3.4 The simulated light responses of an optimal (solid curve) and actual (broken curve with the shorter intervals) canopy and of a canopy with the uniform needle age structure (broken curve with the longer intervals).
Parameters have been determined from biomass data for Sitka spruce in Scotland and radiata pine in Australia (see 1.4.3 and 1.4.4 for details). The values of the parameters for needles of different age classes and for all the needles together are tabulated in Table 1.3.1.1, and the distributions are also shown in Figure 1.3.1.1 for both species.

The transmittance of beam PAR within a canopy is:

\[ \exp(-k_b L_c (1-h)/\cos(\theta)) \] for canopy I, and

\[ \exp(k_b L_c Y/\cos(\theta)) \] for canopy II

where \( Y = \int_0^1 B_1 x B_2 (1-x) B_3 dx \) is the cumulative relative vertical NAD from the canopy top to relative canopy height \( h \), \( \theta \) is the zenith angle of the sun, \( k_b \) is beam extinction coefficient.

As the NAD within the canopy I is \( L_c/H_c \), the clumping factor \( c \) at a location within canopy II is given by \( B_1 h B_2 (1-h) B_3 \).

Providing that at a height of \( p \) within the canopy, PAR transmittances are equal within canopies I and II, then

\[ (1-p)^{-1} \int_0^\phi \cdh = 1 \]

\( p \) is equal to 0.48 and 0.10 for Sitka spruce and radiata pine canopies, respectively. Above height \( p \), the clumping factor is less than 1.0, and greater than 1.0 below this height. The average PAR flux density of beam PAR impinging on the upper surface of the needle is calculated as

\[ F_b l_0 k_b/(1-\tau) \] for canopy I, and

\[ F_b l_0 h_b/(1-\tau) \] for canopy II,

where \( F_b \), \( l_0 \), \( \rho \) and \( \tau \) are beam fraction, flux density of the incident PAR above the canopy, reflectance and transmittance of needles of PAR.

Results

As the profiles of diffuse and beam PAR are very similar within the horizontal homogeneous canopy, I have plotted only the profile of diffuse PAR within Canopy I and Canopy II in Fig. 1.3.1.2 and the cumulative needle area fractions from the top of the canopies in Figure 1.3.1.3.
The flux density of PAR absorbed by the canopy is independent of the NAD distribution in the vertical, but the PAR regime within the canopy is determined by the vertical NAD distribution within the canopy, and this is shown in Figure 1.3.1.3, for Sitka spruce and radiata pine, respectively; 60% and 90% of the needles receive higher PAR flux densities above the relative canopy height of 0.48 and 0.27, the remainder receive lower PAR flux densities than in Canopy I (see Fig. 1.3.1.2). This results in a more efficient use of incident PAR, as the needles are physiologically more active near the top of the canopy. Below the foliage (i.e. h=0), the PAR transmittance is the same for both canopies, and therefore the flux density of PAR absorbed is also the same.

Conclusions

The flux density of PAR absorbed by the canopy is independent of the NAD distribution in the vertical, but the PAR regime is determined by the vertical NAD distribution within the canopy. Variations of NAD in the vertical within Sitka spruce and radiata pine canopy result in 60% and 90% of its needles receiving higher PAR flux density than the needles at the same height within a uniform canopy.

1.3.2. The needle age distribution and its influence on photosynthesis

Unlike most crops and deciduous trees, coniferous trees have a very complex age structure. For example, Sitka spruce needles can remain on the tree crown for up to eight years (Ford 1982). The photosynthetic activities of needles decrease with age (Jarvis and Sandford 1986). Therefore the spatial arrangement of needles of different ages within the canopy may have a major influence on the utilization of the flux density of absorbed PAR by the canopy.

Schulze et al (1977a, 1977b) studied the carbon balance within the crown of Norway spruce (Picea abies) in relation to the age and positions of needles and found that sun needles produced about 70% of the total carbon gain, while only 32% of the annual carbon gain was contributed by the current year needles and one-year-old needles. However most of the canopy photosynthesis of Sitka spruce is contributed by the current and one-year-old needles (Jarvis et al 1976, Jarvis and Sandford 1986). A similar needle age structure is found within canopies of a number of coniferous species (Schulze et al 1977a, Beadle et al 1982, Borghetti, et al 1986). The needle age structure can also influence the light use efficiency of the canopy, and consequently the productivity of a tree stand (Monteith 1977).

If all needles within the canopy have the same physiological properties, the canopy photosynthetic rate is independent of the needle age structure within the canopy, and
utilization of incident PAR by canopy II is not any more efficient than by canopy I. Based on the assumptions made in 1.3.1 and ignoring the interception of scattered PAR flux, the flux density of PAR absorbed by the canopy is:

\[ F_b (1 - \exp(-k_b L_c / \cos \theta)) + (1 - F_b)(1 - \exp(-k_d L_c)) \frac{I_o}{(1 - \tau)} \]

and the photosynthetic rate of the canopy is:

\[ L_c \int_0^L \exp(-k_b L_c Y / \cos \theta) F(i_1) dY + L_c \int_0^L \int \exp(-k_b L_c Y / \cos \theta) \Gamma(i_2) dY \]

where \( F(i_1), \Gamma(i_2) \) are the light response functions of photosynthesis of sunlit and shaded needles; \( i_1, i_2 \) are the average light flux densities impinging on the surface of the sunlit and shaded needles, and are given by

\[ i_1 = (k_b F_b + k_d (1 - F_b) \exp(-k_d L_c Y)) \frac{I_o}{(1 - \tau)} \]

and

\[ i_2 = k_d I_o (1 - F_b) \exp(-k_d L_c Y)/(1 - \tau) \]

Thus on the assumption that \( k_d \) is constant, the total rate of canopy photosynthesis is independent of the vertical NAD distribution within the canopy, as was shown earlier by Duncan et al (1967) for corn.

However, needles within the canopy may have very different physiological properties. The maximum photosynthetic rate of current needles within the canopy of Sitka spruce may be 50% larger than that of one-year-old needles. At low PAR flux densities, their light use efficiencies are very similar (Jarvis and Sandford 1986), but very different at high PAR flux densities. It is, therefore, advantageous for the current needles to predominate near the top of the canopy. At the bottom of the canopy, where the PAR flux density has been much attenuated, the older needles predominate, older needles can utilize this light nearly as efficiently as the current needles. The relative height of the maximum NAD of different age needles decreases with the age of needles (Beadle et al 1982, Schulze et al 1977a), but the relative height of the maximum NAD for all needles together is very close to the middle of the canopy for several coniferous canopies (Schulze et al 1977a, Beadle et al 1982, Borghetti et al 1986).
1.3.3. The optimal needle age distribution

As the photosynthetic properties of needles vary with the needle age, the photosynthetic rate and the light use efficiency of the canopy are dependent on the needle age distribution within the canopy. If a needle age structure can maximize the total photosynthetic rate of the canopy, it can also use the PAR absorbed most efficiently, as the flux density of PAR absorbed is little dependent on the needle age structure.

In this analysis, it is assumed that the photosynthetic light response can be represented by a non-rectangular hyperbola (Thornley 1976). This simple empirical function is adequate for the purpose of illustrating the optimal needle age distribution, even though it might be better to use a mechanistic model (Farquhar and Von Caemmerer 1983).

The needle age structure can be determined from the needle age distribution. The NAD in the vertical is $f_0'(h), f_1'(h)$ and $f_2'(h)$ for current, one-year-old and other older needles, and the needle age structure is $f_0'(h):f_1'(h):f_2'(h)$ at relative height $h$. The needle age structure can also be described by the needle transition function. This age transition function has been widely used for this in population biology (Barlette 1960).

For a dynamic but steady needle population in which the production of new needles and abscission of old needles are balanced, the transition functions within the canopy should also be steady. The parameters in the transition function can be regarded as constants with values that depend on the species and the particular surrounding environment. The needle transition functions used in this study are:

\[
\begin{align*}
  f_1'(h) &= f_1'(h)/f_0'(h) = C_{21} h^{C_{22}} (1-h)^{C_{23}} \\
  f_2'(h) &= f_2'(h)/f_1'(h) = C_{31} h^{C_{32}} (1-h)^{C_{33}}.
\end{align*}
\]

As the ageing process is different for young and old stands and for sparse and dense stands, the parameters $C_{i,j}$ ($i=2,3; j=i-1$) might also be expected to be different.

Assumptions

1. There is no discrimination between sunlit and shaded needles. The average PAR flux density at relative canopy height $h$ within the canopy is calculated as $k_b \left[ b \exp(-k_{b}l_{v}Y)/(1-\bar{Y}) \right]$. 

2. The photosynthetic light response of all needles is $\frac{\theta_{n}}{\left( P_{n}-R_{n} \right)^{2}}(\alpha_{n} \left( P_{n}-R_{n} \right)(P_{n}-R_{n})+\alpha_{n} \left( P_{nmi}-R_{n} \right)=0.00$, where $\alpha_{n}$ is the quantum efficiency of the needles, $P_{n}$ the net photosynthetic rate of the needles, $R_{n}$ the dark respiratory rate of the needles, $P_{nmi}$ the maximum photosynthetic rate of the needles at...
age class \( i \) and \( \theta_{ni} \) the convexity of the photosynthetic light response curve of the needles at age class \( i \). \( \theta_{ni} \) and \( P_{mni} \) are different for needles in different age classes.

3. Incident PAR is the only primary variable limiting photosynthesis of the canopy.

4. The total rate of canopy photosynthesis is \( P_{ci} \) for the needles in age class \( i \) (\( i=0,1,2 \)) and the inequality relation holds: \( P_{c0} \leq 0.555P_{c} \). The factor 0.555 is the simulated proportion of photosynthetic rate by the current year needles in the actual canopy of Sitka spruce. \( P_{c} \) is the canopy photosynthetic rate of all needles at different age classes.

If assumption 3 holds over a long period, the optimal needle age distribution is a product of the long term interaction between the PAR regime within the canopy and the canopy itself. Therefore it is appropriate not to discriminate between beam and diffuse PAR or sunlit and shaded needles, as they can be taken as stochastic variables.

**Optimization**

The total photosynthetic rate of the canopy, \( \int_{0}^{L} P_{c}(h)dh \), is:

\[
P_{c0} + P_{c1} + P_{c2} = L_{c} \int_{0}^{L} [f_{i}(h)F(I)dh]
\]

where \( P_{c0} \), \( P_{c1} \) and \( P_{c2} \) are the total photosynthetic rate of current, one-year-old and other older needles. The average flux density of PAR impinging on the surface of needles at canopy height \( h \), \( I \), is given by

\[
k_{b}L_{b}\exp(-k_{b}L_{c})\int_{0}^{L} (f_{0}(x)+f_{1}(x)+f_{2}(x))dx/(1-\tau).
\]

\( F(I) \) is the non-rectangular response of photosynthesis to light of needles in age class \( i \) (\( i=0,1,2 \)).

The aim of this optimization is to maximize \( \int_{0}^{L} (P_{c}(h)dh) \) under the following constraints:

1. \( \int_{0}^{L} (f_{0}(h)-f_{1}(h)+f_{2}(h))dh = L_{c} \)

2. \( P_{c0} \leq 0.555P_{c} \)
Table 1.3.3.1 The values of all parameters assumed in the optimization

<table>
<thead>
<tr>
<th>Parameter</th>
<th>LAI</th>
<th>$k_b$</th>
<th>$R_n$</th>
<th>$P_{nm0}$</th>
<th>$P_{nm1}$</th>
<th>$P_{nm2}$</th>
<th>$\theta_{n0}$</th>
<th>$\theta_{n1}$</th>
<th>$\theta_{n2}$</th>
<th>$\alpha_n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>unit</td>
<td></td>
<td></td>
<td></td>
<td>umol m$^{-2}$ s$^{-1}$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>0.5</td>
<td>0.7</td>
<td>8.65</td>
<td>6.38</td>
<td>3.63</td>
<td>0.9</td>
<td>0.86</td>
<td>0.82</td>
<td>0.055</td>
</tr>
</tbody>
</table>

and also

$f'_{10}(h)=0.4807h^{-1.27}(1-h)^{0.26}$

$f'_{21}(h)=1.3415h^{-0.02}(1-h)^{1.09}$

Typical values of $P_{nm}$, $\theta_n$ for Sitka spruce (Ludlow and Jarvis 1971, Neilson et al 1972) and for $f'_{10}(h)$, $f'_{21}(h)$ are presented in Table 1.3.3.1

The parameters in the needle age transition functions are derived from $f'_{0}(h)$, $f'_{1}(h)$, $f'_{2}(h)$, and have been obtained from the biomass measurements (see Table 1.3.3.1). In this optimization, the needle age transition functions of the optimal needle age distribution within the canopy are assumed to be the same as those in the actual canopy, if the LAI of the canopy is not less than 8.0 (in which case I assume that the NAD in the horizontal is uniform). If this optimization is not constrained by the needle age transition, the optimal needle age structure will be a canopy sandwich with all current, one-year-old and other needles in the upper, middle and lower part of the canopy, respectively; and the needle age structure will be discontinuous within the canopy. Canopy with this discontinuous age structure is highly unstable and this contradicts my assumption of a dynamic, steady canopy.

The total rate of canopy photosynthesis ($P_c$) is proportional to the flux density of PAR absorbed by the canopy ($Q_g$), if the incident flux density of PAR ($I_0$) is not more than 200 umol m$^{-2}$ s$^{-1}$, i.e.

$$\int_S dP_c(h)dh/\int_S dQ_gc(h)dh=\alpha_n=0.05$$ for Sitka spruce.

In this instance, the total rate of canopy photosynthesis is nearly independent of the needle age distribution. This is because the photosynthetic machinery of most needles within the canopy is operating in the linear region of the photosynthetic light response curve. In this case, the optimal needle age distribution is meaningless. Therefore in the optimization, the incident PAR flux density is varied from 200 to 2000 umol m$^{-2}$ s$^{-1}$.

When the flux density of incident PAR is greater than 200 umol m$^{-2}$ s$^{-1}$, the average light use efficiency $(a)$ and needle age distribution change with $I_{max}$, the maximum flux density of incident PAR. The average light use efficiency decreases with
$I_{max}$, as more needles within the canopy are light-saturated at higher $I_{max}$. The distribution of current needles tends to skew towards the top of the canopy, with the result that a large PAR flux density is absorbed by the current needles. The skewness factors of the distributions of current needles are 0.23, 0.20, 0.17 and 0.15 for an $I_{max}$ of 2000, 1500, 1000 and 500 umol m$^{-2}$ s$^{-1}$ (see Table 1.3.3.2).

Table 1.3.3.2 The optimal needle age structure and its light use efficiency

<table>
<thead>
<tr>
<th>$I_{max}$(umol/(m$^2$*s))</th>
<th>2000</th>
<th>1500</th>
<th>1000</th>
<th>500</th>
</tr>
</thead>
<tbody>
<tr>
<td>$B_1$</td>
<td>4.35</td>
<td>4.64</td>
<td>4.18</td>
<td>3.14</td>
</tr>
<tr>
<td>$B_2$</td>
<td>1.9</td>
<td>1.9</td>
<td>1.8</td>
<td>1.6</td>
</tr>
<tr>
<td>$B_3$</td>
<td>1.1</td>
<td>1.2</td>
<td>1.2</td>
<td>1.1</td>
</tr>
<tr>
<td>$a$</td>
<td>0.014</td>
<td>0.017</td>
<td>0.022</td>
<td>0.033</td>
</tr>
<tr>
<td>Skewness</td>
<td>0.23</td>
<td>0.20</td>
<td>0.17</td>
<td>0.15</td>
</tr>
</tbody>
</table>

The skewness factor was calculated as $2.0(B_2-B_3)/(B_2+B_3+4)$.

If the flux density of incident PAR is fixed, $L\int_{Q_g}(h)dh$ is constant, and the total rate of canopy photosynthesis is maximized when the rate of reduction of $\int_{P_c}(h)dh$ is equal to the rate of attenuation of the flux density of PAR absorbed ($\int_{Q_g}(h)dh$) by the needles within the canopy, that is:

$$\partial \int_{P_c}(h)/\partial h = a \partial \int_{Q_g}(h)/\partial h$$

The relations between $\int_{P_c}(h)dh$, $\int_{Q_g}(h)dh$ and $h$ are presented in Figure 1.3.3.1 for the canopy with the optimal needle age distribution (see Table 1.3.3.2) at an $I_{max}$ of 2000 umol m$^{-2}$ s$^{-1}$. As is shown in Figure 1.3.3.1, above the relative height 0.4, both $\int_{P_c}(h)dh$ and $\int_{Q_g}(h)dh$ increase with the depth of the canopy, and become relatively constant with the canopy depth when the PAR flux density is too low for the needles to photosynthesize below the relative height of 0.4. Both $\partial \int_{P_c}(h)dh/\partial h$ and $\partial \int_{Q_g}(h)dh/\partial h$ decrease with the canopy depth; the reduction rates are approximately proportional.

For a Sitka spruce stand with a LAI of 10.0, and variation in the incident PAR flux density from 200 to 2000 umol m$^{-2}$ s$^{-1}$, the function $f_0(h)$ obtained from the optimization is $4.35h^{1.89}(1-h)^{1.10}$. This has been plotted against the relative canopy height together with the measured $f_0(h)$ obtained from the biomass measurements in Figure 1.3.3.2.
Discussion

In this optimization, the objective function, $P_c(h)$, in which $f_0(h)$ is unknown is maximized. This function has three parameters, $B_1$, $B_2$, $B_3$. $B_1$ can be obtained from the constraint 1, if $B_2$ and $B_3$ are known. Parameters $B_2$ and $B_3$ determine the vertical NAD distribution of current needles within the canopy. The relations among $P_c(h)$ and $B_2$, $B_3$ are shown in Figure 1.3.3.3 from which it can be derived that

1. For a fixed value of $B_3$, the total rate of canopy photosynthesis increases with the value of $B_2$ with a diminishing increment. This is because the proportion of current needles in the upper part of the tree crown increases as $B_2$ increases.

2. For a fixed value of $B_2$, the total rate of canopy photosynthesis increases with $B_3$ with a diminishing increment. This is because when $B_3$ is larger, the relative height of the maximum NAD of the current needles shifts further down towards the bottom of the canopy. As the relative height of the maximum NAD for needles in the different age classes decreases with needle age, the relative height of the maximum NAD of all needles together will shift further down the canopy, if the relative height of the maximum NAD of current needles moves towards the bottom of the canopy. When the relative height, $p$, above which the clumping factor is 1.0, is lower, a larger proportion of needles receive higher PAR flux density above $p$, and these needles are physiologically more active than needles below $p$, therefore the canopy photosynthetic rate increases with $B_3$.

3. For the range of values of $B_2$ and $B_3$ studied here, the canopy photosynthetic rate is maximal when $B_2$ and $B_3$ are equal to 5.0, but this violates constraint 2 (see Figure 1.3.3.1).

As shown in Figure 1.3.3.2, the actual needle age distribution differs from the optimum, but the photosynthetic light response is very close to that of a canopy with the optimal needle age structure (see Figure 1.3.3.4). This indicates that solar PAR is not the only environmental variable that limits canopy photosynthesis in a dense stand of Sitka spruce in Scotland. The needle age distribution might also be determined by some other constraints, such as the allocation of nitrogen to needles of different ages and heights within the tree crown (Field 1983, Hirose and Werger 1987) so as to maximize photosynthesis of the canopy.

The photosynthetic light responses of the optimal and actual canopies are different from that of a canopy in which the proportions are 37%, 37% and 26% for current, one-year-old and other older needles through the canopy. The differences are about 8% (see Fig. 1.3.3.4).

From this optimization study, I conclude:
1. The proportions of needles in different age classes are 0.37, 0.37 and 0.26 for current, one-year-old and other older needles. The relative heights of the maximum NAD for needles in the different age classes decrease with needle age, and the NAD distribution of all needles together is approximately symmetrical in a Sitka spruce canopy. This is similar to a number of other coniferous canopies.

2. The needle age structure has a strong influence on the canopy photosynthesis. The photosynthetic light response of a Sitka spruce canopy is very close to the light response of the canopy with the optimal needle age structure. The photosynthetic rate of a canopy with uniform needle age structure is about 8% less than that of the actual Sitka spruce canopy.

1.4. The NAD distribution within an individual tree crown

When there are appreciable gaps among tree crowns, the canopy is discontinuous, and this has a large influence on PAR transmission within the stand. It is then necessary to describe the NAD distribution within individual tree crowns to be able to interpret the spatial variation of PAR within the canopy and to simulate canopy photosynthesis adequately.

1.4.1. Assumptions and definitions

If the total needle area within the tree crown is \( F_1 \), then

\[
F_1 = \int_{\theta_{\text{max}}}^{\theta_{\text{min}}} \int_{r'}^r \int_{h'}^h f(r', h', \theta) r' dr' dh' \]

where \( r' \), \( h' \) and \( \theta \) are the radial distance from the centre of the tree trunk, height within the crown from the crown base and the azimuthal angle at the crown height \( h' \), respectively. \( l_c \) and \( R'(h') \) are the total crown height and the radius of the tree crown at crown height \( h' \) and azimuthal direction \( \theta \), respectively.

If we assume that

1. the horizontal NAD distribution is independent of the vertical NAD distribution,
2. the horizontal NAD distributions are the same at different relative heights within the tree crown,
3. the horizontal NAD distribution is independent of the azimuthal angle,

then I can derive a simple relation between the NAD within the tree crown and the relative NAD in both the vertical and the horizontal.
$$F_i = 2\pi \int_0^1 \int_0^{\theta(k)} f(r', h') r' dr' dh' \text{ (assumption 3)}$$

and $f(r', h')$ is the NAD at height $h'$ from the base of the tree crown and a distance $r'$ from the tree trunk within the tree crown. On the other hand, if the relative NAD in the vertical and in the horizontal is $\Gamma(h)$ and $\Gamma(r)$, respectively, and the total area of needles within the tree crown has been normalized to be 1.0, then

$$1.0 = 2\pi \int_0^h \int_0^{R(h)} \Gamma(h) \Gamma(r) r dr dh,$$

and thus

$$F_i = F_i \cdot 2\pi \int_0^h \int_0^{R(h)} \Gamma(h) \Gamma(r) r dr dh.$$

Also $h' = h|_c$ and $r' = r|_c(h')$, then

$$\Gamma(h) = \frac{1}{L_c} \int_0^h \Gamma(h') (R(h'))^{-2} \int_0^{R(h')} \Gamma(r) r dr dh'$$

and, therefore,

$$f(r', h') = F_i \cdot \frac{1}{L_c} \int_0^h \Gamma(h') (R(h'))^{-2} f(h) \Gamma(r).$$

$F_i \cdot \frac{1}{L_c} \int_0^h \Gamma(h') (R(h'))^{-2}$ is a scaling factor and $\Gamma(h) \Gamma(r)$ is the relative NAD within the tree crown.

As the NAD within the tree crown is $F_i \cdot \frac{1}{L_c} \int_0^h \Gamma(h') (R(h'))^{-2}$ for a uniform tree crown, the NAD within a non-uniform tree crown is $F_i \cdot \frac{1}{L_c} \int_0^h \Gamma(h') (R(h'))^{-2} f(h) \Gamma(r)$. Therefore the clumping factor is $F_i \cdot \Gamma(h) \Gamma(r)$ (see 1.2).

If we approximate both the vertical and the horizontal relative NAD distributions with the beta function, then

$$\Gamma(h) = B_h \cdot (1-h) \cdot B_h$$

$$\Gamma(r) = B_r \cdot (1-r) \cdot B_r$$

The vertical NAD distributions are $f_0(h)$, $f_1(h)$ and $f_2(h)$ for current, one-year-old and other older needles; each of them may have different values of $B_1$, $B_2$ and $B_3$. The horizontal relative NAD distributions are $f_0'(r)$, $f_1'(r)$ and $f_2'(r)$ for current, one-year-old and other older needles. The needle age transition functions in the vertical, $f_{10}'(r)$ and $f_{21}'(h)$, are therefore defined as $f_1(h) f_0(h)$ and $f_2(h)/f_1(h)$, respectively. The needle age transition functions in the horizontal, $f_{10}'(r)$ and $f_{21}'(r)$, are defined as $f_1'(r)/f_0'(r)$ and $f_2'(r)/f_1'(r)$, respectively.
1.4.2. Description of the experimental sites

The radiata pine trees were sampled at the Biology of Forest Growth (BFG) site of the Division of Forest Research, CSIRO, Australia. The geographic location is 35°21'S, 149°56'E, the elevation 625m, and the climate Mediterranean. There are a number of experimental plots of 0.25 ha to which various irrigation and fertilization treatments have been applied. The trees within the plots were planted in 1973 and the stocking density was between 700 to 1000 trees ha⁻¹ with variation of the needle area index from 8.0 to 5.0 in June 1986 (McMurtrie et al 1988) for different plots.

Sixteen Sitka spruce trees were sampled from Fetteresso forest for studying the vertical NAD distribution. Fetteresso forest, a part of Forestry Commission, Forest of Mearons, is about 27 miles south-east of Aberdeen. The trees were planted in 1948. The average tree height was 11.5 m, and there were approximately 4100 trees per ha with a NAI of 9.8. More details were given by Norman and Jarvis (1974).

Eighteen branches were also sampled from three trees at the Tummel experimental site described in Chapter 2 in detail.

1.4.3. Data collection

A total of 31 radiata pine trees was sampled in 1983, 1984 and 1985 before the beginning of the growing season. Each sample tree was felled carefully and the tree height and the height to each whorl measured. Within each whorl, the angles of all branches were measured with a device designed by Brown (1967). The branch length was measured at the same time. All branches at each whorl were then cut off, weighed, and laid into one of two size classes. One branch was randomly taken from each size class for detailed needle area measurements.

For each sampled branch, the distance from the centre of each internode to the branch origin was calculated; the length of each internode was measured and its age recorded. Needles within an internode were separated into four different age classes, i.e. current, one-year-old, two-year-old and other older needles. These needles were dried and weighed. In the subsequent analysis, the last two classes were combined as there were very few needles older than two years.

Some needles of each age were sampled every year from the trees near the tower for measurement of specific needle areas every year. The average specific needle area was calculated for each age class of needles at different heights, from the data for thirty-four whorls in the upper crown and thirty-two whorls in the lower crown of sixteen trees.
The average specific needle areas are presented in Table 1.4.3.1. Of the 31 trees, five trees were not used in the analysis as there were some errors in the data. General information about 26 trees sampled is given in the Table 1.4.3.2.

Measurement of the vertical needle area distribution was described by Norman and Jarvis (1974) for sixteen Sitka spruce trees. Needles were separated into four age classes. As there were few needles that were older than two years, the needles older than one year have been treated as one age class in the data analysis.

Collection of data on the horizontal needle area distribution for Sitka spruce was the same as for the radiata pine trees for each sampled branch. The tree crown was divided by height into three slices, i.e. upper, middle and lower. Two branches were sampled within each slice. The number of branches at each height was also recorded.

1.4.4. Data analysis

The vertical and horizontal NAD distributions were analysed separately.

The vertical distribution

The average needle area of each age class per unit length of tree crown between a whorl and the whorl above was calculated, and taken as the NAD at the mid-point between the two. By assuming that the crown length is 1.0, the relative height at each mid-point was calculated and the NAD distribution in the vertical was normalized so that the total needle area within the tree crown is 1.0.

The horizontal distribution

For a sampled branch, the distance from the mid-point of each branch internode to the tree trunk was calculated. The appropriate needle area was uniformly distributed within this internode, and expressed per unit horizontal section area of the tree crown in m²/m². The horizontal NAD was calculated in the following way:
Figure 1.4.6.1. Parameters $B_2$ and $B_3$ of the vertical NAD distributions of all needles together within the crowns of twenty-six radiata pine trees (see 1.4.1 for details).
Table 1.4.3.1 The average specific needle areas (m² kg⁻¹) of radiata pine trees at BFG in 1983 - 1985 with standard deviations (S.D.)

<table>
<thead>
<tr>
<th></th>
<th>C</th>
<th>S.D.</th>
<th>C+1</th>
<th>S.D.</th>
<th>C+2</th>
<th>S.D.</th>
<th>Others</th>
<th>S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper</td>
<td>5.54</td>
<td>0.70</td>
<td>4.82</td>
<td>0.75</td>
<td>4.00</td>
<td>0.48</td>
<td>4.42</td>
<td>0.64</td>
</tr>
<tr>
<td>Lower</td>
<td>6.55</td>
<td>1.05</td>
<td>5.61</td>
<td>0.79</td>
<td>4.38</td>
<td>0.66</td>
<td>5.63</td>
<td>0.50</td>
</tr>
</tbody>
</table>

Table 1.4.3.2 General information about the 26 radiata pine trees sampled in 1983, 1984 and 1985 at BFG

- **IL**: represents irrigation and liquid fertilization.
- **IF**: represents irrigation and solid fertilization.
- **IG**: represents irrigation only.
- **SF**: represents solid fertilization only.
- **O**: represents control.

<table>
<thead>
<tr>
<th>Tree No.</th>
<th>Treatment</th>
<th>D₁</th>
<th>H</th>
<th>F₁₂</th>
<th>Year sampled</th>
</tr>
</thead>
<tbody>
<tr>
<td>116</td>
<td>O</td>
<td>12.5</td>
<td>9.76</td>
<td>23.82</td>
<td>1983</td>
</tr>
<tr>
<td>117</td>
<td>O</td>
<td>14.1</td>
<td>10.79</td>
<td>38.56</td>
<td>1983</td>
</tr>
<tr>
<td>118</td>
<td>O</td>
<td>15.9</td>
<td>11.09</td>
<td>49.62</td>
<td>1983</td>
</tr>
<tr>
<td>119</td>
<td>O</td>
<td>16.7</td>
<td>9.74</td>
<td>61.25</td>
<td>1983</td>
</tr>
<tr>
<td>120</td>
<td>O</td>
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<td>12.96</td>
<td>70.38</td>
<td>1983</td>
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<tr>
<td>122</td>
<td>O</td>
<td>14.6</td>
<td>10.20</td>
<td>58.06</td>
<td>1983</td>
</tr>
<tr>
<td>125</td>
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<td>86.24</td>
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</tr>
<tr>
<td>126</td>
<td>O</td>
<td>8.6</td>
<td>7.45</td>
<td>17.28</td>
<td>1983</td>
</tr>
<tr>
<td>127</td>
<td>O</td>
<td>14.2</td>
<td>12.27</td>
<td>50.13</td>
<td>1983</td>
</tr>
<tr>
<td>128</td>
<td>O</td>
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<td>10.40</td>
<td>82.42</td>
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</tr>
<tr>
<td>130</td>
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<td>18.3</td>
<td>10.82</td>
<td>55.21</td>
<td>1983</td>
</tr>
<tr>
<td>131</td>
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<td>20.7</td>
<td>12.23</td>
<td>64.62</td>
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<tr>
<td>132</td>
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<td>19.5</td>
<td>11.87</td>
<td>69.44</td>
<td>1984</td>
</tr>
<tr>
<td>133</td>
<td>IF</td>
<td>22.6</td>
<td>12.98</td>
<td>95.82</td>
<td>1984</td>
</tr>
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<td>134</td>
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<td>68.99</td>
<td>1984</td>
</tr>
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<td>14.1</td>
<td>10.28</td>
<td>34.36</td>
<td>1984</td>
</tr>
<tr>
<td>136</td>
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<td>16.0</td>
<td>10.22</td>
<td>52.01</td>
<td>1984</td>
</tr>
<tr>
<td>137</td>
<td>IL</td>
<td>20.7</td>
<td>15.05</td>
<td>94.46</td>
<td>1985</td>
</tr>
<tr>
<td>138</td>
<td>IL</td>
<td>18.4</td>
<td>13.08</td>
<td>57.36</td>
<td>1985</td>
</tr>
<tr>
<td>140</td>
<td>IF</td>
<td>21.3</td>
<td>12.02</td>
<td>99.87</td>
<td>1985</td>
</tr>
<tr>
<td>141</td>
<td>IG</td>
<td>14.0</td>
<td>11.76</td>
<td>42.72</td>
<td>1985</td>
</tr>
<tr>
<td>142</td>
<td>IG</td>
<td>20.4</td>
<td>13.48</td>
<td>74.18</td>
<td>1985</td>
</tr>
<tr>
<td>143</td>
<td>O</td>
<td>18.7</td>
<td>14.48</td>
<td>67.55</td>
<td>1985</td>
</tr>
<tr>
<td>144</td>
<td>O</td>
<td>15.3</td>
<td>10.46</td>
<td>56.76</td>
<td>1985</td>
</tr>
<tr>
<td>145</td>
<td>SF</td>
<td>17.5</td>
<td>13.70</td>
<td>69.89</td>
<td>1985</td>
</tr>
<tr>
<td>146</td>
<td>SF</td>
<td>21.3</td>
<td>13.81</td>
<td>108.74</td>
<td>1985</td>
</tr>
</tbody>
</table>
If the total area of needles within the internode AB is \( l \), the horizontal NAD is:

\[
\frac{\sum_{i=1}^{M} W_i}{\pi (OB' \times OB' - OA' \times OA')} W_s
\]

\( OA' < 1 \), \( OB' < 1 \)

Diagram 1.4.3.1 a branch and its horizontal projection.

where \( O \) is the branch origin and \( A' \) and \( B' \) are the horizontal projection of \( A \) and \( B \), respectively. \( AB \) represents an internode along the branch (see Diagram 1.4.3.1), \( W_s \) is the fresh weight of a sampled branch, \( W_i \) is the fresh weight of branch \( i \) in this branch size class, \( M \) is the total number of branches within this branch size class, \( l \) is the total needle area within the internode \( AB \).

At each whorl, the horizontal radius of the tree crown was divided into 50 equal intervals. The total needle area along the horizontal radius was calculated as the sum of the horizontal NAD of the branches in the different size classes in this whorl.

The procedure of branch length normalization and calculation of the distribution of needle area along the normalized branch was repeated for each whorl within the tree crown. The NAD at the same relative radial distance was accumulated from the top to the bottom whorl. The accumulated horizontal NAD along the horizontal branch was normalized with respect to the total needle area within the tree crown so that the total needle area in the horizontal is 1.0.

For Sitka spruce trees, the tree crown was divided into three different slices by height, and two branches were sampled from each slice. The horizontal NAD distribution along the branch at each slice was calculated in the way described previously. The average horizontal distribution was calculated from the horizontal distribution along the branches at different heights, i.e. for the relative radial distance \( r \), the average horizontal NAD within the tree crown is calculated as:

\[
(1.6) \sum_{i=1}^{2} \sum_{r} N_i(\text{wt})(r)
\]
where $l_{ij}$ is the average needle area of the sampled branch $i$ at height $j$, $N_j$ the number of branches at height $j$, $i=1, 2$ and $j=1,2,3$

The horizontal NAD distribution was also normalized with respect to the total needle area within the tree crown.

1.4.5. The curve fitting

The normalized data were fitted to a beta function in both the vertical and the horizontal using the optimization procedure in GENSTAT. The average value of each parameter is presented in Table 1.4.5.1 together with the mean square errors (M.S.) of the fitted functions.

Table 1.4.5.1 The parameters of the NAD distributions for radiata pine (RP) and Sitka spruce (SS) trees

<table>
<thead>
<tr>
<th>Distribution</th>
<th>$D_1/D_4$</th>
<th>$D_2/D_3$</th>
<th>$D_3/D_4$</th>
<th>M.S.</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>RP horizontal</td>
<td>0.15</td>
<td>1.10</td>
<td>1.38</td>
<td>0.01</td>
<td>26</td>
</tr>
<tr>
<td>vertical</td>
<td>6.84</td>
<td>0.87</td>
<td>1.90</td>
<td>1.79</td>
<td>26</td>
</tr>
<tr>
<td>SS horizontal</td>
<td>1.96</td>
<td>0.86</td>
<td>2.34</td>
<td>0.01</td>
<td>3</td>
</tr>
<tr>
<td>vertical</td>
<td>79.21</td>
<td>2.46</td>
<td>2.77</td>
<td>0.16</td>
<td>16</td>
</tr>
</tbody>
</table>

1.4.6. Variation in the NAD distributions

There are large variations in the vertical NAD distributions among the trees. These variations can be attributed to the genetic differences between trees, microenvironmental variation within the stands, experimental treatments and so on. It is necessary to clarify the major sources of this variation, so that I can justify whether it is appropriate to apply the same vertical NAD distribution function to all trees in the stand, or whether the vertical NAD distribution depends on characteristics of the tree crowns, or whether different treatments should be taken into account.

Variation of the vertical NAD distribution among different trees

Figure 1.4.6.1 shows the relation between the pairs of parameters of the vertical NAD distribution for the twenty-six radiata pine trees. Most of these distribution functions are skewed towards the base of the tree crown as $D_2/D_3$ is less than 1.0. The values of some characteristic statistical parameters are also presented in Table 1.4.6.1.

The skewness factor ($V_s$) for most of the radiata pine trees ranges from -0.30 to -0.50, and the relative height of maximum NAD in the vertical ($V_x$) typically varies from 0.20 to
Table 1.4.6.1 Characteristic statistical parameters of the NAD distribution of all needles together for 26 trees of radiata pine

$V_x$ and $V_s$ are the relative height of maximum NAD in the vertical and skewness of the vertical NAD distribution; $H_x$ and $H_s$ are the relative radial distance of maximum NAD in the horizontal and skewness of the horizontal NAD distribution. These parameters do not exist for an exponential function. They were calculated as follows:

$V_x = \frac{B_2}{(B_2+B_3)}$

$V_s = \frac{2(B_2-B_3)}{(B_2+B_3+4)}$

$H_x = \frac{B_5}{(B_5+B_6)}$

$H_s = \frac{2(B_5-B_6)}{(B_5+B_6+4)}$

"*" indicates that this parameter does not exist as an exponential function was fitted to the data.

<table>
<thead>
<tr>
<th>Tree</th>
<th>$V_x$</th>
<th>$V_s$</th>
<th>$H_x$</th>
<th>$H_s$</th>
<th>Treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td>116</td>
<td>0.20</td>
<td>-0.42</td>
<td>0.37</td>
<td>-0.11</td>
<td>O</td>
</tr>
<tr>
<td>117</td>
<td>0.29</td>
<td>-0.63</td>
<td>0.42</td>
<td>-0.10</td>
<td>O</td>
</tr>
<tr>
<td>118</td>
<td>0.23</td>
<td>-0.76</td>
<td>0.47</td>
<td>-0.06</td>
<td>O</td>
</tr>
<tr>
<td>119</td>
<td>0.24</td>
<td>-0.46</td>
<td>0.44</td>
<td>-0.11</td>
<td>O</td>
</tr>
<tr>
<td>120</td>
<td>0.25</td>
<td>-0.48</td>
<td>0.51</td>
<td>0.02</td>
<td>O</td>
</tr>
<tr>
<td>122</td>
<td>0.25</td>
<td>-0.79</td>
<td>0.46</td>
<td>-0.05</td>
<td>O</td>
</tr>
<tr>
<td>125</td>
<td>0.33</td>
<td>-0.30</td>
<td>0.44</td>
<td>-0.11</td>
<td>O</td>
</tr>
<tr>
<td>126</td>
<td>0.21</td>
<td>-0.68</td>
<td>0.32</td>
<td>-0.18</td>
<td>O</td>
</tr>
<tr>
<td>127</td>
<td>0.25</td>
<td>-0.41</td>
<td>0.46</td>
<td>-0.09</td>
<td>O</td>
</tr>
<tr>
<td>128</td>
<td>0.15</td>
<td>-0.78</td>
<td>0.41</td>
<td>-0.14</td>
<td>O</td>
</tr>
<tr>
<td>130</td>
<td>0.32</td>
<td>-0.45</td>
<td>0.43</td>
<td>-0.14</td>
<td>O</td>
</tr>
<tr>
<td>131</td>
<td>0.26</td>
<td>-0.29</td>
<td>0.40</td>
<td>-0.17</td>
<td>IL</td>
</tr>
<tr>
<td>132</td>
<td>0.28</td>
<td>-0.31</td>
<td>0.57</td>
<td>0.07</td>
<td>SF</td>
</tr>
<tr>
<td>133</td>
<td>0.21</td>
<td>-0.34</td>
<td>0.41</td>
<td>-0.13</td>
<td>IF</td>
</tr>
<tr>
<td>134</td>
<td>0.14</td>
<td>-0.55</td>
<td>0.53</td>
<td>0.06</td>
<td>IL</td>
</tr>
<tr>
<td>135</td>
<td>*</td>
<td>-0.31</td>
<td>0.57</td>
<td>0.12</td>
<td>IG</td>
</tr>
<tr>
<td>136</td>
<td>*</td>
<td>-0.37</td>
<td>0.38</td>
<td>-0.18</td>
<td>IF</td>
</tr>
<tr>
<td>137</td>
<td>*</td>
<td>-0.37</td>
<td>0.38</td>
<td>-0.18</td>
<td>IL</td>
</tr>
<tr>
<td>138</td>
<td>0.32</td>
<td>-0.26</td>
<td>0.47</td>
<td>-0.05</td>
<td>IL</td>
</tr>
<tr>
<td>140</td>
<td>0.21</td>
<td>-0.30</td>
<td>0.36</td>
<td>-0.21</td>
<td>IF</td>
</tr>
<tr>
<td>141</td>
<td>0.30</td>
<td>-0.36</td>
<td>0.55</td>
<td>0.08</td>
<td>IG</td>
</tr>
<tr>
<td>142</td>
<td>0.04</td>
<td>-0.48</td>
<td>0.42</td>
<td>-0.11</td>
<td>IG</td>
</tr>
<tr>
<td>143</td>
<td>0.12</td>
<td>-0.36</td>
<td>0.43</td>
<td>-0.09</td>
<td>O</td>
</tr>
<tr>
<td>144</td>
<td>0.44</td>
<td>-0.06</td>
<td>0.42</td>
<td>-0.17</td>
<td>O</td>
</tr>
<tr>
<td>145</td>
<td>*</td>
<td>-0.17</td>
<td>0.42</td>
<td>-0.12</td>
<td>SF</td>
</tr>
<tr>
<td>146</td>
<td>0.48</td>
<td>-0.04</td>
<td>0.42</td>
<td>-0.16</td>
<td>SF</td>
</tr>
</tbody>
</table>
The regressions between $V_x$ or $V_s$ and the diameter of the tree trunk at breast height (1.3m) ($D_b$), tree height (H) and the total area of needles within the tree crown ($F_l$) are:

\begin{align*}
V_x &= -0.0005D_b + 0.1633 \quad r = -0.0045 \\
V_x &= 0.0009H + 0.2413 \quad r = 0.0009 \\
V_s &= -0.0002F_l + 0.1691 \quad r = -0.01 \\
V_s &= 0.0296D_b - 0.9444 \quad r = -0.43 \quad ** \\
V_s &= 0.0724H - 1.2943 \quad r = 0.52 \quad *** \\
V_s &= 0.0036F_l - 0.6667 \quad r = 0.37 \quad ** 
\end{align*}

** indicates that the correlation is significant at the 5% level, *** indicates that the correlation is significant at the 1% level.

The relative height of maximum NAD in the vertical is poorly correlated with $D_b$, H and $F_l$, but the skewness of the vertical NAD distribution is significantly correlated with $D_b$, H and $F_l$. All three of the latter correlation coefficients are positive, showing that the NAD distribution is more uniform in the vertical for bigger trees, as the skewness factor is closer to 0.0 for the bigger tree.

**Variation of the horizontal NAD distribution among different branches**

In analysing the data, it has been assumed that the horizontal NAD distributions are the same for all branches irrespective of their heights. This assumption has greatly simplified the description of the spatial NAD distribution, as there are both physiological and microenvironmental differences among branches at different heights within a tree crown. The horizontal NAD distribution along a branch might also be different to a significant extent, as shown in Figure 1.4.6.2 for radiata pine, and Figures 1.4.6.3 and 1.4.6.4 for Sitka spruce, but it is very doubtful whether it is worth taking it into account for the following reasons:

1. horizontal NAD distributions of the different branches are not any more variable than the vertical NAD distributions of different trees.

2. the horizontal NAD distribution is less important than the vertical NAD distribution for photosynthesis by the tree crown (see 1.6),

3. the applicability of a more complicated model would be limited.
Figure 1.4.6.2 Variations of the horizontal NAD along four different branches within the crown of a radiata pine tree.

Figure 1.4.6.3 Horizontal NAD distributions of current (*), one-year-old (O), other older needles (x) and all needles together (+) along a branch sampled near the middle of a Sitka spruce tree crown.

Figure 1.4.6.4 Horizontal NAD distributions of current (*), one-year-old (O), other older needles (x) and all needles together (+) along a branch sampled from the lower part of a Sitka spruce tree crown.
Variation of the horizontal NAD distribution among different trees

The average horizontal NAD distributions of the different radiata pine trees are very similar. If values of the NAD along the sampled branches of the twenty-six trees are plotted in Figure 1.4.6.5, a clear arch band pattern appears. Deviation from the average horizontal NAD decreases with relative radial distance from the tree trunk, and variations are much smaller than those among the different branches. This can be taken to indicate that differences in the horizontal NAD distribution among the branches are the major source of this variation.

The horizontal NAD distributions for three Sitka spruce trees, presented in Figure 1.4.6.6, also have a very similar pattern, even though the relative height of the maximum NAD in the horizontal is larger for the bigger tree. I can't extend this to other Sitka spruce trees because of the limited number of trees that were sampled.

The values of all the statistical parameters are similar for the different radiata pine trees, with variation in the skewness parameter the largest. In only one tree is the NAD distribution not skewed toward the tree trunk (see Table 1.4.6.1). On average for radiata pine trees, the relative radial distance of maximum NAD in the horizontal is 0.45, and the skewness is -0.08; this implies that the horizontal NAD distribution is approximately symmetrical.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Equation</th>
<th>r</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>H_x</td>
<td>0.0009D_b+0.4283</td>
<td>0.05</td>
<td>24</td>
</tr>
<tr>
<td>H_x</td>
<td>0.01173H+0.3065</td>
<td>0.32</td>
<td>24</td>
</tr>
<tr>
<td>H_x</td>
<td>-0.0003F+0.4640</td>
<td>-0.12</td>
<td>24</td>
</tr>
<tr>
<td>H_y</td>
<td>-0.0038D_b-0.0181</td>
<td>-0.14</td>
<td>24</td>
</tr>
<tr>
<td>H_y</td>
<td>-0.0091H+0.1919</td>
<td>-0.04</td>
<td>24</td>
</tr>
<tr>
<td>H_y</td>
<td>-0.0012F+0.0071</td>
<td>-0.31</td>
<td>24</td>
</tr>
</tbody>
</table>

The relative radial distance of maximum NAD (H_x) and the skewness factor of the horizontal NAD distribution (H_y) are poorly correlated with D_b, H and F for radiata pine trees.

The correlation between H_y and F is significant, and this indicates that the horizontal distribution is less uniform for a branch with a large area of needles. In this respect, the horizontal NAD distribution differs from the vertical NAD distribution. The average value of H_x for all 26 trees is 0.45 with a standard deviation of 0.06. As H_x is significantly correlated with H, the horizontal NAD distribution is more symmetrical for the taller trees. As the horizontal NAD distribution was obtained by averaging the relative horizontal NAD distribution at all whorls, variations of the horizontal NAD distributions within the crown
Figure 1.4.6.5 Variation of the relative horizontal NAD calculated from the normalization with the relative radial distance for 26 radiata pine trees (see text for more details). The relative horizontal NAD is expressed as needle area per unit horizontal area of the tree crown section. The total needle area within the tree crown is assumed to be 1.0.

Figure 1.4.6.6 Variations of the relative horizontal NAD calculated from the normalization for current (C), one-year-old (C+1), other older needles (C+2) and all needles together (T) with the relative radial distance, r, for three different Sitka spruce trees.

X: r
Y: Relative horizontal NAD
of a taller tree are better smoothed out and with a more symmetrical average horizontal NAD distribution, because a taller tree usually has more whorls.

The statistical parameters of the horizontal NAD distribution are less variable than the parameters of the vertical NAD distribution for the radiata pine trees. However, this does not mean that variations of horizontal NAD distributions among the different tree crowns are any smaller than variations of the vertical distributions, as the horizontal NAD distribution was averaged over all whorls within the tree crown. Nevertheless it does indicate that variability of the horizontal NAD distribution mainly derives from the different whorls within the tree crown.

1.4.7. The two-dimensional NAD distribution within the tree crown

As I showed earlier, the flux density of PAR absorbed is independent of the NAD distribution of a horizontally homogeneous canopy (see 1.3). By taking account of the variation of NAD in the horizontal, the flux density of PAR absorbed by a tree crown is determined by both the vertical and horizontal NAD distribution, i.e. the spatial variation of NAD within the tree crown.

Spatial variation of NAD within the tree crown may enhance the photosynthesis within the tree crown, as the light environment inside is more uniform. As a result, knowledge of the two-dimensional NAD distribution within a tree crown is of great importance in assessing the flux density of PAR absorbed by the tree crown and hence the photosynthesis.

Variation of NAD within the tree crown

Variations of NAD within a tree crown are dependent on crown shape, crown size and the values of all the parameters in the two-dimensional NAD distribution. The average NAD within the crown of many coniferous trees varies from 0.5 m\(^{-1}\) to 3.0 m\(^{-1}\), but the maximum NAD can be more than 12 m\(^{-1}\) within the crown of a Sitka spruce tree, as calculated by the two-dimensional NAD distribution function. This demonstrates that there can be large variations of NAD within the tree crown. The variations of the relative NAD within the crown are shown in Figs. 1.4.7.1 and 1.4.7.2 for Sitka spruce and radiata pine trees, respectively.

If the average radius at the base of the tree crown is R, the height of the tree crown is h, and the total area of needles within the tree crown is F, NAD is:
Table 1.4.7.1 The assumed dimensions of the crown of Sitka spruce (SS) and radiata pine (RP)

<table>
<thead>
<tr>
<th></th>
<th>R(m)</th>
<th>l_c(m)</th>
<th>P_f(m^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SS</td>
<td>1.5</td>
<td>8.5</td>
<td>40.0</td>
</tr>
<tr>
<td>RP</td>
<td>2.0</td>
<td>10.0</td>
<td>60.0</td>
</tr>
</tbody>
</table>

Table 1.4.7.2 The vertical and horizontal locations of the maximum NAD (L_d) and the maximum NAD within the tree crown

"***" means that a maximum does not exist.
h, r are dimensionless and L_d is in m^-1.

<table>
<thead>
<tr>
<th></th>
<th>Conical</th>
<th>Half ellipsoidal</th>
<th>Paraboloidal</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>h</td>
<td>r</td>
<td>L_d</td>
</tr>
<tr>
<td>Total</td>
<td>0.76</td>
<td>0.13</td>
<td>24.0</td>
</tr>
<tr>
<td>SS</td>
<td>C</td>
<td>0.79</td>
<td>0.44</td>
</tr>
<tr>
<td></td>
<td>C+2</td>
<td>0.53</td>
<td>0.11</td>
</tr>
<tr>
<td>RP</td>
<td>Total</td>
<td>***</td>
<td>0.45</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>***</td>
<td>0.56</td>
</tr>
<tr>
<td></td>
<td>C+2</td>
<td>0.65</td>
<td>0.44</td>
</tr>
<tr>
<td></td>
<td>C+2</td>
<td>0.19</td>
<td>0.29</td>
</tr>
</tbody>
</table>

Table 1.4.7.3 The average NAD within a tree crown

The proportions of current, one-year-old and other older needles within the crown are 0.37, 0.37 and 0.26 for Sitka spruce and 0.41, 0.28 and 0.31 for radiata pine. ELIP and PARB represent half ellipsoidal and paraboloid shapes, respectively.

<table>
<thead>
<tr>
<th></th>
<th>Sitka spruce</th>
<th>radiata pine</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total</td>
<td>C</td>
</tr>
<tr>
<td>Cone</td>
<td>2.0</td>
<td>0.7</td>
</tr>
<tr>
<td>ELIP</td>
<td>1.0</td>
<td>0.4</td>
</tr>
<tr>
<td>PARB</td>
<td>1.3</td>
<td>0.5</td>
</tr>
</tbody>
</table>
Figure 1.4.7.1 Two-dimensional contour mapping of the NAD of all needles together within the crown of a Sitka spruce tree. Numbers beside contour lines are relative NAD; this can be converted to NAD by multiplying by a scaling factor, \( F_l l_c R(h)^{-2} \), where \( F_l \) is the total area of needles within the tree crown \((m^2)\), \( l_c \) and \( R(h) \) are the crown length \((m)\) and the crown radius at the relative crown height \(h\) \((m)\).

Figure 1.4.7.2 Two-dimensional contour mapping of the NAD of all needles together within the crown of a radiata pine tree. Numbers beside contour lines are relative NAD (refer to Fig. 1.4.7.1).
\[
(F_{l}/(l_{z} R'(h) R'(h)))B_{1}r^{B_{2}} R(1-h)B_{3}r^{B_{5}}(1-r)^{B_{6}}.
\]

\( R'(h) \) is the crown radius at relative height \( h \), and depends on the assumed shape of the tree crown in the following way:

For a conical tree crown
\( R'(h) = R(1-h) \).

For a half ellipsoidal tree crown
\( R'(h) = R\sqrt{(1-h)(1-h)} \).

For a paraboloidal tree crown
\( R'(h) = R\sqrt{1-h} \).

Then let \( r' = r R'(h) \), and \( L_{d} = F_{l}r'(h)F''(r') \).

The solutions to the equations, \( \partial L_{d}/\partial h = 0.00 \) and \( \partial L_{d}/\partial r = 0.00 \), give the relative height \( h_{\text{max}} \) and the relative radial distance \( r_{\text{max}} \) at this height at which NAD is maximal.

For a conical tree crown,
\[
h_{\text{max}} = B_{2}/(B_{2} + B_{3} - 2)
\]
\[
r_{\text{max}} = B_{5}/(B_{5} + B_{6}).
\]

For a half ellipsoidal tree crown
\[
h_{\text{max}} = \sqrt{(2-B_{2}) + \sqrt{(2.0-B_{2})^2 + 4.0B_{2}(B_{2} - B_{3})}}/(2.0(B_{2} + B_{3}))
\]
\[
r_{\text{max}} = B_{5}/(B_{5} + B_{6}).
\]

For a paraboloidal tree crown
\[
h_{\text{max}} = B_{2}/(B_{2} + B_{3} - 1)
\]
\[
r_{\text{max}} = B_{5}/(B_{5} + B_{6}).
\]

To illustrate the consequence of crown shape and crown size for the distribution of NAD, the assumed crown properties presented in Table 1.4.7.1 were used.

The position of the maximum NAD and the maximum NAD within different crown shapes are presented in the Table 1.4.7.2. Parameters \( B_{1} \) to \( B_{9} \) in the NAD distributions are taken from Table 1.4.5.1 for radiata pine and Sitka spruce, respectively.

As shown in Tables 1.4.7.2 and 1.4.7.3, there are large variations of NAD within a tree crown. The maximum NAD is at least four times larger than the average NAD. Among the three crown shapes studied, the variations in NAD were largest within an assumed conical crown. The variation in NAD within the tree crown is different for the two species: it is much larger for Sitka spruce tree than for radiata pine tree.
1.5. Influence of irrigation and fertilization on the NAD distributions

1.5.1. Introduction

Needle area can be altered by many silvicultural treatments. Fertilization and irrigation are the two most important measures both for promoting needle growth and for increasing needle longevity. Needles of different age may also respond differently to drought and nutrient deficiency differently. Whether they also have a significant impact on the NAD distribution within the crown of forest trees has rarely been studied (Madgwick 1967).

As pointed out by Linder (1984), fertilization of coniferous trees can increase needle size, needle number per fascicle and shoot length. Drought has the opposite effects. At BFG it was very obvious that needle length and shoot length were much less and there are fewer needles per unit shoot length in the control plot after trees experienced from drought during a growing period. The effect of irrigation was most pronounced during a drought period (Linder et al 1987).

Several different treatments were applied to the plots at BFG and some of the trees sampled were from each treatment. I can therefore make comparisons of the differences in the NAD distributions within the crowns, in both the vertical and the horizontal, between the fertilized and irrigated trees and the untreated trees.

1.5.2. Data analysis and results

Over the years 1983 to 1985, twelve radiata pine trees were sampled from the control plots and seven from the irrigated and fertilized plots. The data have been combined for trees that received the same treatment, and the beta functions were fitted to the NAD distributions in the vertical and in the horizontal for all needles together, and for needles of different age classes separately for the treated and untreated trees. The values of all the parameters for these distributions are presented in Table 1.5.2.1

To test whether the parameters in the NAD distributions are significantly different between the two treatments, analyses of variances were made. Results are presented in Table 1.5.2.2. If the difference between the regressions is significant, different functions should be
Figure 1.5.2.1 Variation of the relative vertical NAD with relative crown height within the crowns of the control and treated radiata pine trees. The relative vertical NAD is calculated as needle area per unit length of tree crown and the total area of needles within the tree crown is normalized to be 1.0.

Figure 1.5.2.2 Variations of the relative horizontal NAD with the relative radial distance within the crowns of control and treated radiata pine trees.
Figure 1.5.2.3 Variations of the relative vertical NAD of current needles with the relative crown height within the crowns of control and treated radiata pine trees.

Figure 1.5.2.4 Variations of the relative vertical NAD of one-year-old needles with the relative crown height within the crowns of control and treated radiata pine trees.

Figure 1.5.2.5 Variations of the relative vertical NAD of other older needles with the relative crown height within the crowns of control and treated radiata pine trees.
Figure 1.5.2.6 Variations of the relative horizontal NAD of current needles with the relative radial distance within the crowns of control and treated radiata pine trees.

Figure 1.5.2.7 Variations of the relative horizontal NAD of one-year-old needles with the relative radial distance within the crowns of control and treated radiata pine trees.

Figure 1.5.2.8 Variations of the relative horizontal NAD of other older needles with the relative radial distance within the crowns of control and treated radiata pine trees.
Table 1.5.2.1 The values of all parameters in the NAD distribution functions of radiata pine trees

(see 1.4.1 for the definitions of all the parameters)

"V" is for the vertical distribution and "H" for the horizontal distribution.

<table>
<thead>
<tr>
<th>V/H</th>
<th>V1/B4 S.E.</th>
<th>V2/B5 S.E.</th>
<th>V3/B6 S.E.</th>
<th>M.S.</th>
<th>Treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total V</td>
<td>19.51 10.68</td>
<td>0.95</td>
<td>0.20</td>
<td>3.10</td>
<td>0.63 1.99</td>
</tr>
<tr>
<td>C V</td>
<td>1.80 0.86</td>
<td>1.16</td>
<td>0.27</td>
<td>1.17</td>
<td>0.32 0.09</td>
</tr>
<tr>
<td>C+1 V</td>
<td>11.81 8.28</td>
<td>1.36</td>
<td>0.31</td>
<td>3.02</td>
<td>0.66 0.41</td>
</tr>
<tr>
<td>C+2 V</td>
<td>49.69 39.00</td>
<td>1.31</td>
<td>0.26</td>
<td>6.74</td>
<td>1.23 0.55</td>
</tr>
<tr>
<td>Total H</td>
<td>2.85 0.20</td>
<td>1.06</td>
<td>0.04</td>
<td>1.36</td>
<td>0.05 0.06</td>
</tr>
<tr>
<td>C H</td>
<td>0.77 0.10</td>
<td>0.93</td>
<td>0.13</td>
<td>0.30</td>
<td>0.07 0.03</td>
</tr>
<tr>
<td>C+1 H</td>
<td>3.49 0.45</td>
<td>1.25</td>
<td>0.07</td>
<td>1.45</td>
<td>0.08 0.02</td>
</tr>
<tr>
<td>C+2 H</td>
<td>6.16 1.43</td>
<td>1.24</td>
<td>0.10</td>
<td>2.10</td>
<td>0.15 0.08</td>
</tr>
<tr>
<td>T V</td>
<td>3.11 0.70</td>
<td>0.25</td>
<td>0.11</td>
<td>1.18</td>
<td>0.26 0.15</td>
</tr>
<tr>
<td>C V</td>
<td>3.58 1.30</td>
<td>0.75</td>
<td>0.24</td>
<td>1.26</td>
<td>0.32 0.22</td>
</tr>
<tr>
<td>C+1 V</td>
<td>0.79 0.32</td>
<td>0.39</td>
<td>0.21</td>
<td>1.64</td>
<td>0.46 0.03</td>
</tr>
<tr>
<td>C+2 V</td>
<td>2.20 0.92</td>
<td>0.32</td>
<td>0.15</td>
<td>4.15</td>
<td>0.89 0.06</td>
</tr>
<tr>
<td>T H</td>
<td>3.65 0.21</td>
<td>1.17</td>
<td>0.06</td>
<td>1.54</td>
<td>0.07 0.07</td>
</tr>
<tr>
<td>C H</td>
<td>2.29 0.27</td>
<td>1.00</td>
<td>0.07</td>
<td>1.17</td>
<td>0.08 0.05</td>
</tr>
<tr>
<td>C+1 H</td>
<td>2.40 0.64</td>
<td>0.76</td>
<td>0.15</td>
<td>1.39</td>
<td>0.21 0.02</td>
</tr>
<tr>
<td>C+2 H</td>
<td>15.88 4.50</td>
<td>1.77</td>
<td>0.16</td>
<td>2.78</td>
<td>0.23 0.05</td>
</tr>
</tbody>
</table>

Table 1.5.2.2 Test of homogeneity of positions and regressions

<table>
<thead>
<tr>
<th>Vertical</th>
<th>Horizontal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total C</td>
<td>C+1 C+2</td>
</tr>
<tr>
<td>positions N S S S N S S S</td>
<td></td>
</tr>
<tr>
<td>regression N S S N N S S S</td>
<td></td>
</tr>
</tbody>
</table>

Note: N represents no significant difference, S represents a significant difference at the 5% level.

Table 1.5.2.3 The average proportions of needles in the different age classes

<table>
<thead>
<tr>
<th>Treatment</th>
<th>S.D.</th>
<th>C+1</th>
<th>S.D.</th>
<th>C+2</th>
<th>S.D.</th>
<th>No. of samples</th>
</tr>
</thead>
<tbody>
<tr>
<td>control</td>
<td>0.23</td>
<td>0.05</td>
<td>0.35</td>
<td>0.07</td>
<td>0.42</td>
<td>0.09 12</td>
</tr>
<tr>
<td>treated</td>
<td>0.62</td>
<td>0.07</td>
<td>0.16</td>
<td>0.09</td>
<td>0.22</td>
<td>0.12 7</td>
</tr>
</tbody>
</table>
fitted to the trees in the different treatments; if the difference of regression is not significant, but the difference in position is significant, the distribution functions are in parallel for the trees in the two treatments (see Williams 1959).

Results of analysis of variance in Table 1.5.2.2 show that there is no significant difference between the two treatments in the NAD distribution of all needles together: irrigation and fertilization did not significantly alter the NAD distribution of all needles together within the tree crown (see Figures 1.5.2.1 and 1.5.2.2).

The overall proportions of needles in different age classes are summarized in Table 1.5.2.3. Figures 1.5.2.3 to 1.5.2.5 show the vertical distributions of needles of different age classes from the two treatments, and Figures 1.5.2.6 to 1.5.2.8 show the corresponding horizontal distributions.

It can be seen from Table 1.5.2.3 that the proportion of current needles increased by 41% as a result of irrigation and fertilization, whereas the proportions of one-year-old and other older needles were halved.

In the vertical, the relative height of maximum NAD shifted towards the crown base of the treated trees for current and one-year-old needles (see Figures 1.5.2.3 and 1.5.2.4). Irrigation and fertilization can promote needle growth, the promotion of needle growth at different heights was also dependent on the the number of terminal shoots at a particular height: the shift of Vₙ of current needles may result from a larger number of terminal shoots lower in the tree crown, as the needle production depends on the number of shoot apices (Cannell 1987). For needles older than one year, irrigation and fertilization can increase longevity of younger needles (Linder 1984), but this may be compensated by increasing abscission of older needles in this age class. This may be the reason why the vertical NAD distribution of needles older than one year was not altered by irrigation and fertilization (see Figure 1.5.2.5), the difference in the amplitude of the distribution is because the relative proportion of needles older than one year is different between the untreated and treated trees.

In the horizontal, the relative radial distance of maximum NAD of current needles shifted towards the tree trunk, and the maximum NAD of current needles increased by irrigation and fertilization (see Figure 1.5.2.6). Irrigation and fertilization have the opposite effect on the horizontal NAD distribution of one-year-old needles (see Figure 1.5.2.7). The influence of irrigation and fertilization on the horizontal NAD distribution of needles older than one year was smallest but still significant (see Figure 1.5.2.8).
The total number of new shoots along a branch is, of course, maximal somewhere between the two ends of the branch. If irrigation and fertilization promoted shoot extension and needle growth on the new shoots, shift in the peak of the horizontal NAD distribution may result from a relatively large number of new shoots near the middle of the branch. The untreated trees suffered from stresses during the growing season, with the result that apical dominance was probably more prominent than in the treated trees (Wareing 1970), so the relative radial distance of maximum NAD was closer to the edge of the tree crown.

The needle age structure was significantly altered by drought and nutrient deficiency. This was also observed by Cromer et al (1984) for radiata pine trees. They concluded that the irrigation and fertilization can increase both litter fall of the older needles and needle length of current needles.

1.5.3. Conclusions

In summary, I conclude that:

1. Irrigation and fertilization do not have any significant influences on the NAD distribution of all needles together.

2. Irrigation and fertilization can alter the age structure within the tree crown by increasing the fraction of current needles within the tree crown. The height of maximum NAD in the vertical shifted towards the base of the tree crown, the relative radial distance of maximum NAD in the horizontal shifted towards the middle of the tree crown.

3. Irrigation and fertilization did not have a significant influence on the vertical NAD distribution of needles older than one year. This may be the result of compensation between increasing the longevity of younger needles and speeding up the abscission of older needles in this needle age class.

1.6. The needle age distribution within the tree crown

Since the photosynthetic properties change with the needle age, the needle age distribution is very important in determining the total photosynthetic rate of a tree crown (see 1.3.3). The age distribution of the needles within the tree crown is dependent on shoot extension, needle growth on the shoot, needle longevity and litter fall, all of which can be altered by irrigation and fertilization (see 1.5.3). The needle age distribution also varies from species to species, but there are some similarities among a number of conifers.
1.6.1. The needle age distribution in the vertical

Table 1.6.1.1 The parameters of the needle age distribution in the vertical

<table>
<thead>
<tr>
<th>species</th>
<th>B_1</th>
<th>B_2</th>
<th>B_3</th>
<th>C'_21</th>
<th>C'_22</th>
<th>C'_23</th>
<th>C'_31</th>
<th>C'_32</th>
<th>C'_33</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>SS</td>
<td>92.46</td>
<td>3.84</td>
<td>3.00</td>
<td>0.48</td>
<td>-1.21</td>
<td>0.20</td>
<td>1.34</td>
<td>-0.02</td>
<td>1.09</td>
<td>13</td>
</tr>
<tr>
<td>RP(O)</td>
<td>1.80</td>
<td>1.16</td>
<td>1.17</td>
<td>6.56</td>
<td>-0.20</td>
<td>1.85</td>
<td>4.21</td>
<td>-0.07</td>
<td>3.72</td>
<td>11</td>
</tr>
<tr>
<td>RP(*)</td>
<td>3.58</td>
<td>0.75</td>
<td>1.26</td>
<td>0.22</td>
<td>-0.36</td>
<td>0.38</td>
<td>2.78</td>
<td>-0.07</td>
<td>2.51</td>
<td>9</td>
</tr>
</tbody>
</table>

The needle age distribution in the vertical is more important than that in the horizontal (see 1.7). The needle age distribution can be described by the age transition function (see 1.2), this function describes the proportions of needles at different age classes at any height within the tree crown. The values of all parameters in the transition functions (see 1.2 for definitions) for Sitka spruce and radiata pine are presented in Table 1.6.1.1. The vertical NAD distributions of needles in the different age classes are also presented in Figures 1.5.2.3, 1.5.2.4 and 1.5.2.5. Figures 1.6.1.1 and 1.6.1.2 show that the needle age transition functions decrease monotonically with relative height within the tree crown, this indicates that the relative proportion of older needles increases from the top to the bottom of the tree crown.

For the needles in the different age classes, the relative heights of maximum NAD, h_{max}, are given by

\[ B_2/(B_2 + B_3), \]

\[ (B_2 + C'_{22})/(B_2 + B_3 + C'_{22} + C'_{23}), \]

and \[ (B_2 + C'_{22} + C'_{32})/(B_2 + B_3 + C'_{22} + C'_{23} + C'_{32} + C'_{33}) \]

for current, one-year-old and other older needles, respectively. As C'_{22} and C'_{32} are negative, and C'_{23} and C'_{33} are positive, the relative height of maximum NAD is lower for the older needles. This particular age structure may enable the tree crown to use incident PAR efficiently in photosynthesis (see 1.3.3).

1.6.2. The needle age distribution in the horizontal

The needle age distribution in the horizontal is determined by branch development and the growth of the shoots along the branch. Like the needle age distribution in the vertical, the current needles preponderate near the tips of the branches, but the needle age structure is
Figure 1.6.1.1 The vertical needle age transition function, \( f'_{10}(h) \). This function is used to describe the variation of the area proportions of the current needles relative to the area of one-year-old needles with the relative crown height within the crowns of Sitka spruce, control and treated radiata pine trees.

Figure 1.6.1.2 The vertical needle age transition function \( f'_{21}(h) \). This function is used to describe the variation of the area proportion of one-year-old needles relative to the area of other older needles with the relative crown height within the crowns of Sitka spruce, control and treated radiata pine trees.
more uniform than that in the vertical. All parameters in the needle age transition functions (see 1.2 for definitions) are presented in Table 1.6.2.1 for Sitka spruce and for untreated and treated radiata pine trees. A more uniform age structure in the horizontal may result from a more uniform distribution of light, nutrients and water along the branches compared to their distributions in the vertical. The relative radial distances of maximum NAD, \( r_{\text{max}} \), for one-year-old and other older needles lie near the mid-points of the branches.

| Table 1.6.2.1 The parameters of the needle age distribution in the horizontal |
|---------------------------------|------|------|------|------|------|------|------|------|------|------|------|
| \( R P(C) \) 0.77 | 0.93 | 0.30 | 4.53 | 0.32 | 1.15 | 1.77 | -0.01 | 0.65 | 11 |
| \( R P(IF) \) 2.29 | 1.00 | 1.17 | 1.05 | 0.24 | 0.22 | 6.62 | 1.01 | 1.39 | 9 |
| \( SS \) 92.45 | 3.80 | 3.00 | 0.48 | -1.21 | 0.20 | 1.34 | -0.02 | 1.09 | 3 |

To study variation of the horizontal needle age transition function with the radial distance, the first order differentials were calculated as follows:

\[
\frac{df}{dr} = C_{21}^{n} r^{(C_{21}^{n} - 1)/(1 - r)(C_{23}^{n} - 1)} \cdot \frac{-(C_{23}^{n} + C_{22}^{n})r + C_{22}^{n}}{C_{22}^{n}}
\]

\[
\frac{df}{dr} = C_{31}^{n} r^{(C_{31}^{n} - 1)/(1 - r)(C_{33}^{n} - 1)} \cdot \frac{-(C_{33}^{n} + C_{32}^{n})r + C_{32}^{n}}{C_{32}^{n}}
\]

therefore \( \frac{df}{dr} = 0 \) when \( r = C_{22}^{n} / (C_{22}^{n} + C_{23}^{n}) \),

and \( \frac{df}{dr} = 0 \) when \( r = C_{32}^{n} / (C_{32}^{n} + C_{33}^{n}) \).

The relative proportions of older needles decreases with the relative radial distance up to \( C_{22}^{n} / (C_{23}^{n} + C_{22}^{n}) \) and \( C_{32}^{n} / (C_{33}^{n} + C_{32}^{n}) \), and then increases. For radiata pine, \( C_{22}^{n} / (C_{23}^{n} + C_{22}^{n}) \) is 0.22 for \( f_{10} \) in the untreated tree crown, and \( C_{32}^{n} / (C_{32}^{n} + C_{33}^{n}) \) is 0.42 for \( f_{21} \) in the treated tree crown. The older needles are, therefore, more uniformly distributed within the treated tree crown.

Figure 1.6.2.1 shows that the proportion of current needles is high near the edge of the tree crown, but there is a high proportion of one-year-old needles near the middle of the branch within the crowns of the untreated trees.
Figure 1.6.2.1 The horizontal needle age transition function, $f_{10}(r)$. This function is used to describe the variation of the area proportion of current needles relative to the area of one-year-old needles with the crown radial distance within the crowns of Sitka spruce, control and treated radiata pine trees.

Figure 1.6.2.2 The horizontal needle age transition function $f_{21}(r)$. This function is used to describe the variation of the area proportion of one-year-old needles relative to the area of other older needles with the crown radial distance within the crowns of Sitka spruce, control and treated radiata pine trees.
The needle age structure differs between the treated and untreated tree crowns. As shown in Figures 1.6.2.1 and 1.6.2.2, the relative proportion of one-year-old needles with respect to current needles decreases with the radial distance within the treated tree crown, but within the untreated tree crown it increases with the relative radial distance up to 0.22, and then decreases. The relative proportion of other older needles with respect to one-year-old needles increases with the relative radial distance up to 0.42, and then decreases within the treated tree crown, but within the untreated tree crown it decreases with the relative radial distance monotonically.

1.6.3. Conclusions

From the previous analysis, I conclude that:

1. The needle age structure in the vertical is similar for Scots pine, Sitka spruce, treated and untreated radiata pine. The proportion of older needles increases monotonically from the top to the bottom of the tree crown. Younger needles preponderate in the upper part of the tree crown. This is consistent with the optimal needle age structure (see 3.4).

2. The needle age structure in the horizontal can be altered by irrigation and fertilization.

3. The needle age structure in the horizontal is more uniform than in the vertical.

4. For radiata pine trees, the relative height of maximum NAD of older needles is close to the bottom of the tree crown, but the relative radial distance of maximum NAD of older needles is near the middle of the branch.

1.7. The influence of two-dimensional NAD distribution on PAR transmission within the tree crown

Introduction

The flux density of beam PAR intercepted by an isolated tree crown can be obtained from the average transmittance within the shadow of the tree crown. As shown by Mann et al (1979), the flux density of beam PAR intercepted is

\[ I_0 \int \int_{R_g} (1 - \exp(-Ff(x,y))) \, dx \, dy, \]

where \( R_g \) is the projection of the tree crown on to the horizontal surface (see Diagram 1.7.1).
Diagram 1.7.1 the horizontal projection of an isolated tree crown.
\( f(x,y) \) is the distribution of the projected needle area within the region \( R_g \). \( F_1 \) is the total needle area.

As \( \exp(-F_1 f(x,y)) \) is a convex function, the following inequality relation holds

\[
\iint_{R_g} \exp(-F_1 f(x,y)) \, dx \, dy \geq \frac{S_c \exp(-F_1 / S_c)}{S_c}
\]

where \( S \) is the area of the projection \( R_g \).

This implies that the flux density of beam PAR absorbed is maximal for a tree crown if its projected needle area is uniformly distributed within the shadow of the tree crown in the horizontal.

It is obvious that the distribution of projected needle area within the shadow is more uniform for a tree crown with uniform NAD distribution, and therefore this crown will intercept more beam PAR. Therefore when the incident angle of the beam PAR is very close to the zenith, the flux density of beam PAR absorbed will be largely dependent on the horizontal distribution of NAD and rather insensitive to the vertical distribution. When the incident angle of the beam PAR is very close to the horizon, the amount of absorbed beam PAR is closely related to the vertical NAD distribution.

To demonstrate the influence of the NAD distribution on PAR transmission within the tree crown, by using MAESTRO (see Chapter 2), I calculate the beam and diffuse transmittances at different heights within the crown of a tree in the stand.

**Assumptions**

The following assumptions are made in this study:

1. The tree stocking number of the stand is 750 trees per ha. The dimensions of an individual tree are \( R \) 2.0 m; \( H \) 10.0 m; and \( Z_b \), the height from the ground to the crown base, 2.0 m. The total needle area within the tree crown is 55.0 m². These are the average properties of the radiata pine trees in plot 6 at the BFG site (see Chapter 2).

2. All trees in the plot are identical.

3. The shape of the tree crown is a half ellipsoid.

4. The radiance distribution of diffuse PAR in the sky is that of the standard overcast sky (S.O.S).
5. The NAD properties of the crown tested are as follows:

crown I: uniform NAD distribution in both the vertical and the horizontal within the tree crown;

crown II: one-dimensional vertical NAD distribution within the tree crown;

crown III: two-dimensional NAD distribution within the tree crown.

The distribution functions used were those described in 1.3.1 (see Table 1.3.1.1) and 1.4.5 (see Table 1.4.5.1) for radiata pine at the BFG site.

Results

At each of five heights, 0.0, 2.0 m, 4.0 m, 6.0 m and 8.0 m from the base of the tree crown, the average transmittances of beam and diffuse PAR were calculated as the average of the transmittance at 48 horizontal grid points located uniformly at each height, and presented in Figs. 1.7.1 and 1.7.2.

Figures 1.7.1 and 1.7.2 demonstrate that:

1. The NAD distribution has a similar influence on the transmission of beam and diffuse PAR within the tree crown.

2. Near the top of the crown, the transmittance of beam and diffuse PAR within crown I is much lower than within crowns II and III: the difference can be up to 40% of the transmittance. The transmittances of beam and diffuse PAR within crowns II and III are very close at any solar zenith angle. This is because the shading within the crown is more important than the shading between the crowns near the crown top. The NAD at the top of the crown is much smaller than the average NAD for the crown and therefore the transmittances within crowns II and III are much higher than within crown I. The average transmittances within crowns II and III are very close, even though variation in the transmittance within crown III is expected to be larger than within crown II.

3. Near the crown base, transmittances of diffuse PAR within crowns I and II are very close, and quite different from those within crown III. This is because shading between crowns is dominant near the crown base. Most diffuse PAR transmitted is from that part of the sky near the zenith, and therefore the transmittance is largely independent of the vertical NAD distribution. The diffuse transmittance within crown III is therefore higher than the transmittances within crowns I and II because a uniform NAD in the horizontal reduces the transmittance at the base of the tree crown.
Figure 1.7.1 Variations of the average transmittances of diffuse PAR at different heights within Crown I (.), Crown II (x) and Crown III (O). The average transmittance was calculated as the mean of transmittances at 48 grid points distributed uniformly at that height of the tree crown.

Figure 1.7.2 Variations of the average transmittance of beam PAR with the zenith angle of the sun at different heights within Crown I (.), Crown II (x) and Crown III (O). The average transmittance was calculated as the mean of the transmittances at 48 grid points distributed uniformly at that height of the tree crown.

H: height

Zenith angle of the sun (degree)
4. The transmittance of beam PAR generally decreases with the solar zenith angle. When the sun is near the horizon, the transmittance is determined by the vertical NAD distribution and the transmittances of beam PAR within crowns II and III are very close but higher than those within crown I. When the sun approaches the zenith, the transmittance of beam PAR is rather insensitive to the vertical NAD distribution and the transmittances within crowns I and II are very close but much smaller than those within tree crown III.

5. All of these differences are smallest at heights that are close to the middle of the tree crown.

6. At the relative crown height of 0.2 (4.0 m), the transmittances of beam and diffuse PAR within crown I are higher than those within crown II, but lower than those within crown III. When the beam is incident near the horizon, the beam transmittance within crown I is higher than the transmittances within crowns II and III. This is because the average NAD above the relative crown height of 0.2 (1.0 m) is larger than the average NAD for the whole crown. The beam transmittance is primarily determined by the vertical distribution of NAD.

7. The differences between average beam and diffuse transmittances at the base of the conical tree crown are larger than at the base of the half ellipsoidal crown, in the order crown II, I, III. This is because the horizontal NAD distribution is less uniform within a conical tree crown.

Conclusions

The NAD distribution within a tree crown plays an important role in PAR transmission within the crown. Near the top of the crown, the vertical NAD distribution is more important than the horizontal NAD distribution, closer to the base of the crown, the horizontal NAD distribution is more important. As the needles in the upper part of the tree crown contribute most of the crown photosynthesis, the vertical NAD distribution is of greater importance in determining the total crown photosynthesis than the horizontal NAD distribution.
2. A SIMULATION MODEL: MAESTRO

2.1. Introduction

Since the early work of de Wit (1965), many canopy simulation models have been developed to study canopy processes (Duncan et al 1967, Mohren et al 1983, McMurtrie et al 1986, Doyle et al 1986). They can be classified into dynamic models and steady-state models. A dynamic model is usually designed to study canopy development and tree growth (Jarvis et al 1985, McMurtrie et al 1986), whereas only a particular phase of canopy development is considered in a steady-state model. Canopy models can also be classified as uniform or random, and as one-dimensional, two-dimensional or three-dimensional models depending on the number of dimensions of the canopy considered in the model. As the elements of the canopy (leaves, stems, twigs, fruits and flowers etc.) are hardly ever evenly distributed along any dimension of the canopy, a three-dimensional model is ideal for taking them into account. MAESTRO is one of the few three-dimensional models that have been developed for studying the spatial variations of radiation, photosynthesis and transpiration within a tree crown (Whitfield & Connor 1980, Norman & Welles 1983, Myneni et al 1986).

An array model developed by Norman and Welles (1983) was modified and improved by Grace, Jarvis and Norman (1988) so that it can be applied to agroforestry stands of Pinus radiata. Crown structure, leaf boundary layer, stomatal and mesophyll conductances, photosynthesis and transpiration submodels were added to the original model in this study, and it has been named MAESTRO. The objectives of developing MAESTRO for forest stands are as follows:

1. To synthesize our knowledge about all the different processes studied. An explanatory and deterministic model, such as MAESTRO, can integrate our understanding about the individual processes, and enable us to study the system behaviour and interactions between the different processes.

2. To explore some aspects of the system that are not clear to us from our state-of-the-art knowledge, and that will stimulate some further research. In MAESTRO, some submodels (see 2.2) are very general and can be applied to a location where no relevant studies have been made. If the predictions do not agree reasonably well with observations, some assumptions in the model have to be re-evaluated, and therefore some further research is warranted.

3. To extrapolate results from laboratory experiments to the field, and to explain field observations. A model can be a useful tool to help us to understand field observations from measurements made in the laboratory where variables can be individually controlled. The model can synthesize our "reductionist" research so as to enable us to investigate the systematic response of a process to the simultaneous variation of environmental variables in the field.
4. To evaluate the importance of different variables (structural properties of the tree crown, physical and physiological properties of the leaves, environmental variables and so on) for the simulated processes, and to rank them in order of priority for future studies. Analysis of the sensitivity of the system outputs to the different inputs can clarify the important variables on which some further research may be concentrated, and may lead to the simplification or disposal of some inputs.

5. To use this model to study canopy processes in a widely spaced stand. A number of models have been developed to take account of the horizontal discontinuity of the canopy (Mohren et al. 1983, Norman & Welles 1983, Myneni et al. 1985, Doyle et al. 1986), but MAESTRO is the only model of this kind to have considered the heterogeneous distribution of leaf area density within the tree crown (see Chapter 1). This is very important in the study of canopy processes (see Chapter 3).

2.2. Description of MAESTRO

MAESTRO, an array model, can predict radiation absorption, photosynthesis and transpiration in the crown of an individual tree in a stand. The fluxes of radiation are treated in three wavebands: photosynthetic, near-infra red (NIR) and thermal. Beam and diffuse radiation are treated separately. Multiple scattering of radiation within the tree crowns is also considered. The model can predict the radiation flux at a particular location within the stand. This makes straightforward validation possible.

The essential inputs are as follows:

Site: hemisphere (northern or southern), latitude, longitude, day of the year, slopes and bearing, plot dimensions and total number of trees in the plot.

Soil: soil surface temperature, reflectances of PAR, NIR and thermal radiation of the soil surface.

Leaf: transmittances and reflectances of PAR, NIR and thermal radiation, inclination angle distribution, density distribution and physiological parameters.

Trees: positions, crown dimensions, the heights from the ground surface to the crown base, total area of leaves within the tree crown.

Weather: solar radiation, air temperature, the relative humidity of ambient air, wind speed and carbon dioxide concentration at the reference height.

The time scale is in hours, and the spatial scale is a point within the tree crown for radiation, and a leaf for photosynthesis and transpiration.
The following general assumptions have been made in MAESTRO:

1. The inputs of radiation fluxes, temperature, relative humidity are hourly average values, and they are appropriate for calculating the hourly and daily radiation absorption, photosynthesis and transpiration of the crown of a tree in the stand.

2. The stand is a pure stand. The crowns of the trees in the stand are of the same geometrical shape (cone, half-ellipsoid or paraboloid), and symmetrical around the tree trunk.

3. Leaves are continuously distributed within the tree crown. The horizontal and vertical distributions of leaf area density are independent of each other.

4. Up to 52 grid points are located within the tree crown, each representing a subvolume of the tree crown. The radiation absorption, photosynthesis and transpiration of the tree crown can be calculated as the weighted sum of the radiation absorption, photosynthesis and transpiration of these grid points: the weighting factor is the total leaf area within the subvolume.

5. The air temperature, water vapour pressure deficit of the ambient air and $\text{CO}_2$ concentration profiles are neutral within the canopy.

6. There are three different age classes of leaves within the tree crown: current, one-year-old and other older leaves. The leaves within each age class are separated into three ecological types according to their positions within the tree crown (upper, middle and lower). Leaves within the same age class and ecological type have the same physical and physiological properties.

7. Woody parts within the tree crown (tree trunk, twigs and branches) can be ignored for the purpose of simulating radiation transmission, photosynthesis and transpiration of the tree crown.

8. PAR is the driving variable for photosynthesis. The supply of water and nutrients in the soil does not stress the trees.

There are seven submodels in MAESTRO, each of which can function independently. Some submodels have been used and described previously (Jarvis et al 1985). A full description of MAESTRO can be found in "Documentation of program MAESTRO" (Wang and Jarvis 1988b). Only a brief description will be given here.

Submodel 1: sun position

This submodel calculates the hourly position of the sun in the sky during the day and the daylength. The inputs are the dates, latitude and longitude of the site, the outputs are the hourly zenith and azimuthal angles of the sun during the day and the daylength (see Barkstrom 1981 for more details).
Submodel 2: radiation partitioning

This submodel partitions the incident radiation into beam and diffuse in the PAR and NIR wavebands. If the diffuse fraction of incident radiation is less than 30%, diffuse radiation is split into two components, background and circumsolar diffuse radiation (Steven and Unsworth 1979). For the sake of simplicity, the circumsolar diffuse radiation is included into the beam radiation. The inputs of this submodel are the zenith angle of the sun and the incident radiation flux densities above the canopy. The outputs are the beam fractions of PAR and of NIR, cloudiness of the sky and hourly fractions of sunshine duration.

1. The flux density of thermal radiation from the atmosphere is calculated as $1.06^4 \sigma_s (T_a + 273.13)^4 - 119.0$ (Unsworth and Monteith 1975), where $T_a$ is the air temperature in °C, $\sigma_s$ is the Stefan-Boltzmann constant with a value of $5.67 \times 10^{-8}$ W m$^{-2}$ K$^{-4}$, and the unit for the thermal radiation flux density is W/m$^2$.

2. The cloudiness of the sky is calculated as $1.0 - I_a^{0.45}/I_a'$, where $I_a$ is the incident global radiation, $I_a'$ is the incident global radiation expected under a cloudless sky, and $I_a$ is calculated as $623.9 - 118.2m_a + 17.7m_a^2 - 1.88m_a^3 + 2.12m_a^4$ (Steven and Unsworth 1979), where $m_a$ is airmass and is calculated as $1/\cos \theta$, and $\theta$ is the zenith angle of the sun.

3. The hourly fraction of sunshine duration is calculated as $1.06F_b - 0.01$ (Steven 1977), where $F_b$ is the beam fraction.

4. The beam fractions of PAR and NIR are calculated using a partitioning model presented by Weiss and Norman (1985).

5. The radiance distribution of diffuse radiation in the sky can be simulated as $(1.0 + b \cos \theta)/(\pi + 2b/3)$, where $\theta$ is the zenith angle of incident diffuse radiation, and parameter $b$ is negative for the background diffuse radiation of a clear sky, 0.0 for the uniform overcast sky and 2.0 for the standard overcast sky.

Some parts of this submodel are optional. They will not be used if all of their outputs are provided as inputs, such as beam fractions, cloudiness and sunshine duration.

Submodel 3: crown structure

This submodel calculates the leaf area density at a location within the tree crown and the area fraction of leaves within an inclination angle class. The leaf area density can be either uniform or variable within the tree crown. Variations of leaf area density are taken into account using the complete beta function with three parameters in both the vertical and the horizontal dimensions.
If the actual leaf inclination angle frequencies are not provided as inputs, an ellipsoidal leaf inclination angle distribution with a single parameter is used to calculate the area fraction of leaves within an inclination angle class. The inputs of this submodel are parameters to define the leaf area density distribution within the tree crown and the parameter of the ellipsoidal leaf inclination angle distribution. The following assumptions are made:

1. It is appropriate to use the complete beta function to describe variations of leaf area density in the vertical and in the horizontal dimensions within a non-uniform tree crown.

2. It is appropriate to use the ellipsoidal leaf inclination angle distribution to describe the leaf inclination angle distribution.

3. The leaf orientation angle distribution is random.

If leaf area density is uniform within the tree crown, the proportions of leaves in different age classes have to be provided as inputs. The average leaf inclination angle can also be calculated (Wang and Jarvis 1988a) if required.

Submodel 4: radiation absorption

This submodel calculates the flux densities of PAR, NIR and thermal radiation absorbed by the leaves within the tree crown. This submodel is based on the theory of Norman (1979), and has previously been used by Jarvis et al (1985) with some simplifications. Clumping of leaves is approximately considered either using the heterogeneous distribution of leaf area density or an average clumping factor of foliage (Acock et al 1969) within the tree crown. The inputs are beam fractions of both PAR and NIR, incident flux densities of PAR, NIR and thermal radiation, identity of target tree and crown structural properties of all trees in the stand. The outputs are the hourly and daily amounts of PAR, NIR and thermal radiation absorbed by the target tree.

The following assumptions are made:

1. The radiance distribution of the scattered radiation within the tree crown is isotropic.

2. Leaf and air temperature are everywhere equal to the air temperature at a reference height (Jarvis et al 1976).

3. Penumbra effect can be ignored.

Penumbra has little influence on radiation absorption, but a considerable effect on photosynthesis in a clear day (Oker-blom 1985b). Where penumbra is considered in a
radiation model it is usually at the expense of a large amount of computation: this has prevented the consideration of penumbra effect in MAESTRO. The actual effect of penumbra on photosynthesis of a tree in the stand may be less than that estimated by Oker-blom because there are few clear days during the growing season in Scotland.

Submodel 5: leaf boundary layer, stomatal and mesophyll conductances

This submodel calculates the conductances of water vapour and CO₂ from the ambient air to the intercellular spaces and the mesophyll conductance for CO₂ diffusion. The inputs are the reference height and wind speed at that height, crown dimensions of all trees within the plot, leaf temperature, water vapour pressure deficit of the air and quantum flux density on the leaf surface. The outputs are the boundary layer, stomatal and mesophyll conductances of the leaf under the given conditions.

The following assumptions are made:

1. Stomatal conductance depends on the quantum flux density on the leaf surface, leaf temperature and water vapour pressure deficit of the air (Jarvis 1976). The response to each variable is independent of the response to the other variables.

2. The boundary layer conductance (gₑ) depends on the leaf area density and the local wind speed within the tree crown (Landsberg and Thom 1971).

3. Mesophyll conductance is a function of air temperature and quantum flux density on the leaf surface, and there are no interactions between these two variables.

4. Leaf temperature and water vapour pressure saturation deficits of the ambient air are everywhere equal to the values at the reference height above the canopy (Jarvis et al 1976).

The spatial variation of wind speed within the tree crown is only taken into account using a very simple approach (Jarvis et al 1976). Turbulent transfer processes should be included in the further development of MAESTRO. The feedback of stomatal response is not considered. The calculated mesophyll conductance under the given conditions is used only when the empirical photosynthesis model is used in Submodel 7.

Submodel 6: transpiration

This submodel is essentially the Penman-Monteith equation in the form expressed by Jarvis and McNaughton (1985). The inputs are the net radiation flux density on the leaf surface, water vapour pressure deficit of the ambient air, atmospheric pressure, leaf boundary layer
and stomatal conductances. The output is the transpiration rate of the leaf.

The following assumptions are made:

1. Identical pathways for heat and water vapour from the air spaces within the tree crown to the leaf surface.

2. Air temperature and saturation deficits are uniform within the canopy and equal to the values at the reference height (Jarvis et al 1976).

3. Influences of storage water of the trees on the diurnal variation of its transpiration can be ignored

This submodel is not directly applicable in the situation of the wet canopy. Nevertheless the Penman-Monteith equation has been validated many times in different situations. Good agreements were obtained with the measurements of transpiration of the whole canopy (Milne et al 1985).

Submodel 7: photosynthesis

This submodel calculates the photosynthetic rates of the leaves within the tree crown. It requires inputs of leaf temperature and quantum flux density on the leaf surface and all the outputs from submodel 5. The output is the net photosynthetic rate of the leaf.

The leaf photosynthetic rate is calculated using either an empirical model or a mechanistic model presented by Farquhar and Von Caemmerer (1983). The following assumptions are made in this submodel with the last three specific to the empirical model of photosynthesis. Assumptions in the mechanistic model are presented in Chapter 4.

1. The CO$_2$ compensation concentration of the leaf ($I^*$) is a linear function of the leaf temperature ($T_l$), that is $I^* = 1.4681 T_l + 11.6$, where $T_l$ is in $^\circ$C and $I^*$ in umol mol$^{-1}$ (Neilson et al 1972).

2. The dark respiratory rate of the leaf ($R_d$) is a function of the leaf temperature ($T_l$), i.e. $R_d = R_0 \exp (-C_R \cdot T_l)$, where $R_0$ is the dark respiratory rate of the leaf at a leaf temperature of $0^\circ$C, $C_R$ is an empirical coefficient with a value of 0.084 (Jarvis and Leverenz 1983).

3. Leaf temperature and ambient carbon dioxide concentration are uniform within the tree crown and equal to the values at the reference height (Jarvis et al 1976).

4. The net photosynthetic rate of the leaf ($P_n$) is related to the quantum flux density on the leaf surface ($I_0$) by a non-rectangular hyperbolic function (Thornley 1976), i.e.
\[ \theta_n(p_n+r_n)^2-(a_nI_0+p_{nmx}+r_n)(p_n+r_n)+a_nI_0(p_{nmx}+r_n)=0.0 \]

where \( a_n, \theta_n \) and \( r_{nmx} \) are the quantum efficiency, convexity factor and the maximum photosynthetic rate of the leaf, respectively.

5. The net photosynthetic rate of the leaf is linearly related to the mean intercellular space CO\(_2\) mole fraction \( C_i \) over the range of interest (Ludlow and Jarvis 1971). i.e. \( P_n=(C_i+1)g_m \).

6. \( C_i \) is determined by the photosynthetic rate and the stomatal conductance (Jarvis 1971). That is \( C_i=C_s-P_n/g_s \).

MAESTRO is very flexible. More assumptions can be made if the appropriate data are not available. Refinement of existing submodels can easily be incorporated. Seven submodels are assembled in MAESTRO in order.

2.3. Validation of MAESTRO

Two different kinds of canopy processes have been dealt with in MAESTRO: the physical process of the radiation transfer within the canopy and the physiological processes of photosynthesis and transpiration. The process of radiation transfer has been validated in this study. Validation of the photosynthesis and transpiration submodels requires measurements of the carbon dioxide and water vapour fluxes above and below the canopy (Jarvis et al 1976), and have not been included in this study.

2.3.1. Experimental sites

MAESTRO was independently validated against data collected in both a Sitka spruce stand in Scotland and a radiata pine stand in Australia.

The Sitka spruce experimental site is located near Tummel Bridge about 80 miles north of Edinburgh. Within the stand planted in 1968, six plots of 0.04 ha were chosen. The stocking density of all plots was 2500 trees ha\(^{-1}\) before thinning; about half the trees were removed from three thinned plots in March, 1985. Fertilizers (nitrogen or phosphorous) were applied to two thinned and two unthinned plots before the growing season every year during the study. The yield class of the site is 20, the monthly mean temperature of the ambient air was 2.7 °C in January and 13.0 °C in June. The maximum flux density of incident PAR in the summer can exceed 2000 umol m\(^{-2}\) s\(^{-1}\). The BFG site was described in Chapter 1. Data for validating MAESTRO were collected in plot 15 of the Sitka spruce experimental site and plot 6 of the radiata pine experimental site. Frequency distributions
Figure 2.3.1.1 The frequency distribution of the crown basal area of trees in Plot 15 at Tummel Forest. The basal area of a tree is calculated as $\pi R^2$, where $R$ is the average crown radius at the crown base.

Figure 2.3.1.4 The frequency distribution of the area of the crown base of all trees in Plot 6 at BFG.

Figure 2.3.1.2 The frequency distribution of the heights of all trees in Plot 15 at Tummel Forest.

Figure 2.3.1.5 The frequency distribution of the heights of all trees in Plot 6 at BFG.

Figure 2.3.1.3 The frequency distribution of the total area of leaves within the crowns of all trees ($F_l$) in Plot 15 at Tummel Forest.

Figure 2.3.1.6 The frequency distribution of the total area of leaves within the crowns of all trees ($F_l$) in Plot 6 at BFG.
of the area of the tree crown base, tree height and the total area of leaves within the tree crown are presented in Figures 2.3.1.1, 2.3.1.2, 2.3.1.3 for Sitka spruce trees in plot 15 at Tummel and in Figures 2.3.1.4, 2.3.1.5 and 2.3.1.6 for radiata pine trees in plot 6 at BFG.

2.3.2. Experimental methods

At the Tummel experimental site, the incident radiation flux density was measured by two Kipp solarimeters (Model CM5, Kipp & Zonen Ltd., Delft, The Netherlands), a Funk type net radiometer (Swissteco Pty, Ltd., East Hawthorn, Australia) and a quantum sensor (SD104Q, Macam Photometrics Ltd., Livingston, Scotland) at the top of a tower approximately 2.0 m above the canopy. One of the Kipp solarimeters was equipped with a dome which did not transmit PAR (R&G, Schott&Gen, Mainz, Eppley Corporation, Delft, The Netherlands) measured the incident NIR by the difference. An additional Macam quantum sensor at the top of the tower, facing downwards, measured the PAR density reflected by the canopy. Since August, 1987, when a second tower was erected, a Kipp solarimeter with a shade band (British Meteorological office Design) intermittently measured diffuse radiation from the sky. Within Plot 15, five Macam quantum sensors supported on the top of posts of 1.5 m high measured the quantum flux density transmitted through the canopy.

All the radiation sensors were scanned by a datalogger (CR7X, Campbell Scientific Ltd., Sutton Bonington, England) housed in a caravan, every two seconds. The external power supply for the datalogger consisted of two lead-acid batteries (Cyclon, DMS electronics, Southampton) charged continuously by a 18 Wp Solar array of 600*900 mm (Chronar Limited, Bridgend, Wales) mounted at the top of the third tower. A thin film humidity sensor (Humicap, Vaisala Ltd., Helsinki) and a thermistor (Model UUT51J1, Fenwall Ltd.) were housed inside a Stevenson Screen on the third tower at a height of 7.5 m. The humidity sensor was calibrated using a precisely controlled water bath (Model CC-20, Grant Instr. Ltd., Cambridge). External circuitry powered by the CR7X converted the capacitance output from the humidity sensor and the resistance from the thermistor to voltage outputs for logging. Hourly and daily radiation fluxes, hourly average relative humidity and temperature during the day, and daily maximum and minimum temperatures were stored in the datalogger.

The data were transferred to tape from the datalogger; then the data on the tape were read into the mainframe computer through a tape reader (C-20, Campbell Scientific Ltd., Sutton Bonington). They were subsequently analysed by a Fortran program.

There were seven quantum sensors at BFG: one Li-Cor quantum sensor (Li-Cor Corp. Ltd.,
Lincoln, Nebraska) above the canopy on the top of a tower in the forest measured the incident quantum flux density, and five Macam and one Li-Cor quantum sensors were distributed within the plot to measure the quantum flux density transmitted through the canopy. A datalogger (CR21X, Campbell Scientific Inc., Nebraska) was used to scan all the sensors every two seconds and to integrate all readings every hour. The data were stored in the datalogger and then transferred to the mainframe computer for detailed analysis in the same way as the data collected at Tummel.

2.3.3. Measurements of tree positions and crown dimensions

To use MAESTRO to predict the transmitted flux density of the incident PAR at any location within a canopy, information about the position and dimensions of each tree within the plot is required.

At Tummel Forest all the trees in the stand were planted in rows about 2.0 m apart, and all the trees in a row were about 2.0 m apart. Measurements to define the tree positions were straightforward. The measurement procedure was as follows:

1. Two reference lines running across the rows just outside the two opposite edges of the plot were arbitrarily chosen as reference line 1 and 2, and were marked by two tensed strings. All trees within the plot were located between these two reference lines. The azimuthal angles of the reference lines were measured with a compass with a precision of 0.5 degree.

2. A row closest to one edge of the plot was chosen as the first row of the plot. The azimuthal angle of the first row was measured with respect to the reference line 1 and 2.

3. The intersect of reference line 1 and the first row was taken as the origin. The co-ordinates of all trees (x, y) within the plot were determined relative to that origin.

4. The distance between adjacent rows of trees was measured between two points on each reference line with a precision of 0.01 m.

5. The distance from each tree in a row to reference line 1 was measured along the rows with a 30 m tape with a precision of 0.01 m.

6. The positions of all trees (x', y') within the plot relative to true north were determined from their co-ordinates by using the following transformation formulae:

\[x' = x \cos(\beta_i + \Delta \beta_i) + y \sin(\beta_i + \Delta \beta_i)\]

\[y' = -x \sin(\beta_i + \Delta \beta_i) + y \cos(\beta_i + \Delta \beta_i)\]
where $\theta_i$ is the angle between the reference line $i$ and the magnetic north, and $\Delta \theta_i$ is the angle difference between the magnetic north and the true north.

Crown dimensions of each tree were determined as the average crown radius ($R$) at the crown base and the live crown length ($l_c$). The height of the crown base ($Z_b$) was defined as the height of the lowest live whorl. Crown length was calculated as the difference between the tree height ($H$) and $Z_b$. The average crown radius of a tree was calculated as the mean of the two crown radii in the direction of the row and the two across the row. Crown radius was measured by one vertical and one horizontal pole, each was marked every 5 cm. The crown radius was read from the horizontal pole when the vertical pole was at the same distance from the centre of the tree trunk as the second longest branch in that direction. Tree height was measured directly using a combination of aluminium poles. The measurement errors were less than 0.5 m.

The positions of all the trees at the DFG site were obtained by digitizing the tree positions on a map which was based on an accurate survey. The errors of the distances between two trees obtained from the digitized data were less than 0.5 m (Benson, personal communication). The crown dimensions and the heights from the ground to the base of the crowns were measured in the same way as for the Sitka spruce trees at Tummel Forest. The tree height was estimated from the diameter of the tree at breast height (1.3 m) ($D_b$) using the following regression relation which was obtained from the dimensions of the twenty-six trees felled for the leaf area measurements (see Chapter 1):

$$H = 0.408D_b + 4.631 \quad r^2 = 0.6 \quad (\text{see Fig. 2.3.3.1})$$

where $H$ is in m, and $D_b$ in cm.

2.3.4. Estimation of the leaf area within an individual tree crown

The total leaf area within an individual tree crown ($F_l$) can be estimated by different methods. One of the best is the relation between the basal sapwood area and the total leaf area within the tree crown. The trees in the two stands studied here were quite young and the amount of heartwood is very small, hence the allometric relation between $D_b$ and $F_l$ was used to estimate $F_l$ of each tree from its $D_b$. I adopted the following relation between $D_b$ and $F_l$ which was obtained by Macintosh (1984) for 12 trees in a 23-year-old Sitka spruce stand in Wauchope Forest:

$$F_l = -3.963D_b - 26.92 \quad (r^2 = 0.8),$$
Figure 2.3.3.1 The relationship between the diameter at breast height ($D_b$) and the height ($H$) of twenty-six radiata pine trees sampled at BFG. The straight line was fitted.

Figure 2.3.4.1 The relationship between the diameter at breast height ($D_b$) and the total area of leaves within the crown ($F_t$) of twenty-six trees at BFG. The straight line was fitted.
where \( F_i \) is in \( m^2 \), and \( D_b \) in cm.

Macintosh found that this relationship was not affected by fertilization and thinning.

The following relation between \( D_b \) and \( F_i \) for radiata pine trees was obtained from the dimensions of the twenty-six sampled trees (see Chapter 1):

\[
F_i = 6.156D_b - 44.4 \quad (r^2 = 0.62) \quad \text{(see Fig. 2.3.4.1)}
\]

2.3.5. Estimation of beam fraction

Beam fractions have been measured intermittently since August, 1987 at Tummel Forest. The flux density of the diffuse radiation obstructed by the shade band was assumed to be 13\% of the total (Robinson and Stock 1964). Simple regression equations were derived from the data:

\[
F_b = \begin{cases} 
0.00 & R_b < 0.15 \\
1.35R_b - 0.13 & R_b > 0.15 \\
0.75 & r = 0.75 
\end{cases}
\]

\( R_b = I_g / I_g' \)

where \( I_g \) is the global radiation measured by the Kipp solarimeter (W m\(^{-2}\)), and \( I_g' \) (W m\(^{-2}\)) is the global radiation to be expected on a cloudless day and is calculated as follows:

\[
I_g' = I_v' / 0.45
\]

where \( I_v' \) is the visible radiation (W m\(^{-2}\)) on a cloudless day, and 0.45 is the fraction of visible radiation in the global radiation in a cloudless day. \( I_v' \) is calculated using the following equation obtained by Steven and Unsworth (1979):

\[
I_v' = 623.9 - 118.2m_a + 17.7m_a^2 - 1.88m_a^3 + 2.12m_a^4
\]

where \( m_a \) is the airmass, and is calculated as (see Lqbal 1983)

\[
m_a = \left[ \cosθ0.15(93.85-θ)^{1.25} \right]^{-1}
\]

where \( θ \) is the zenith angle of the sun in degrees.

As no measurements of beam fraction were made at BFG, the following equation derived by Spencer (1965) was used to calculate the beam fraction:

\[
F_b = 1.4899 - 654.65 \cosθ \cdot I_g
\]
MAESTRO was used to predict the PAR transmittance at each of five sensors below the Sitka spruce canopy at Tummel Forest for five days during 1987. The average daily beam fractions of these five days varied from 0.04 to 0.74. Apart from day I for which the average hourly beam fractions were estimated using the expression given above, the measured hourly average beam fractions were used. The leaf area density was assumed to be either uniform or variable in its distribution within the tree crown, depending on which submodel of leaf area density distribution was used.

Submodel I: leaf area density is uniform throughout the tree crown.

Submodel II: leaf area density is variable in the vertical but uniform in the horizontal dimension. The leaf area density at a height within the tree crown is calculated as

\[ 77.37n^{2.46}(1.0-h)^{2.77}L_c/H_t \]

for Sitka spruce and

\[ 6.84h^{0.57}(1.0-h)^{1.90}L_c/H_c \]

for radiata pine (see Chapter 1).

Submodel III: leaf area density is variable in both the vertical and the horizontal dimensions. The leaf area density within the tree crown is calculated as

\[ 20.45n^{0.57}(1.0-h)^{1.90}r^{1.10}(1.0-r)^{1.38}F_t H_c^{-1}R(h)^{-2} \]

for radiata pine (see Chapter 1).

2.3.6. Results and discussion

The daily courses of incident PAR and its beam fraction are shown in Fig. 2.3.6.1. The predicted and measured transmittances of quantum flux density at an "exposed" and a "shady" sensor are shown in Figures 2.3.6.2 and 2.3.6.3 for five days within Plot 15 at Tummel Forest.

The mean residual of hourly transmittance \( O_t \) is calculated as

\[ O_t - \sqrt{\frac{\sum (t_{mi} - t_{pi})^2}{n}} \]

where \( t_{mi} \) and \( t_{pi} \) are the measured and predicted transmittances, respectively, and \( n \) is an integer number of hours of the daytime.

The mean residuals of hourly transmittance are presented in Table 2.3.6.1 for the five quantum sensors within Plot 15 at Tummel Forest, and the measured and predicted daily transmittances are in Table 2.3.6.2.
Table 2.3.6.1 The mean hourly residual of transmittances for five sensors below the Sitka spruce canopy at Tummel Forest

<table>
<thead>
<tr>
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Note: p0, pl and p2 represent the predicted transmittances using submodel I, II and III, respectively. m represents the measured transmittance.

Table 2.3.6.2 The predicted and measured daily transmittance for five sensors below the Sitka spruce canopy at Tummel Forest

<table>
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Table 2.3.6.3 The hourly mean residual of transmittance for six sensors below the radiata pine canopy at BFG

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Table 2.3.6.4 The predicted and measured daily transmittance for six sensors below the radiata pine canopy at BFG

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Figure 2.3.6.1 Daily courses of incident quantum flux density, $I_0$, (A) and its beam fraction, $F_b$, (B) above the canopy over five days at Tummel Forest.

Figure 2.3.6.4 Daily courses of incident quantum flux density, $I_0$, (A) and its beam fraction, $F_b$, (B) above the canopy over three days at BFG.

Day | Date   
---|--------
I  | 15/11/86  
II | 13/11/86  
III| 25/10/86
Figure 2.3.6.2 The measured (m) and predicted transmittances at an "exposed"(A) sensor below the Sitka spruce canopy at Tummel Forest using submodel I (p₁) and II (p₂).

X: Time of day (h)
Y: Transmittance (%)
Figure 2.3.6.3 The measured (m) and predicted transmittances at a "shady"(E) sensor below the Sitka spruce canopy at Tummel Forest using submodel I (p₁) and II (p₂).

X: Time of day (h)

Y: Transmittance (%)
Figure 2.3.6.5 The measured (without symbol) and predicted PAR transmittances at a "shady (A)" and an "exposed (E)" sensor below the radiata pine canopy at BFG using submodel I(x), II(□) and III(○).

X: Time of day (h)  Y: Transmittance (%)
As shown in Figures 2.3.6.2 and 2.3.6.3, the predictions are very good. The occurrence of sunflecks was reasonably predicted. In general, a larger diurnal fluctuation of quantum flux density at the "shady" sensor was predicted using submodel II, whereas a larger diurnal fluctuation of quantum flux density at the "exposed" sensor was predicted using submodel I. The mean residuals of hourly transmittance for all five sensors in Plot 15 are less than 5% of the transmittance for all days except day I, the day with the highest daily average beam fraction, and that was estimated rather than measured (see Table 2.3.6.1). The differences between the predicted and measured daily average transmittances generally are less than 5% of the transmittance (see Table 2.3.6.2).

The mean residual of hourly transmittance of predictions from submodel I is always slightly smaller than from submodel II, but the daily average transmittances predicted using submodel II may be better than using submodel I, because submodel II predicts the occurrence of sunflecks better (see Figure 2.3.6.3).

The diurnal variations of incident quantum flux density and simulated beam fraction are shown in Figure 2.3.6.4, respectively, for three days at the BFG site.

The hourly transmittances predicted using the three different submodels are shown in Figures 2.3.6.5 and 2.3.6.6 together with the measured transmittances for a "shady" and an "exposed" sensor beneath the radiata pine stand over three days. As shown in Figures 2.3.6.5 and 2.3.6.6, the predictions are generally good: in particular, the occurrence of all sunflecks was reasonably well predicted using submodel III. This is quite important, as sunflecks can contribute a substantial proportion of daily total quantum flux in the lower part of the canopy (Gross 1982). The mean residuals of hourly transmittances are presented in Table 2.3.6.3 for all the six sensors within the plot. The predicted and measured daily average transmittances at six sensors are presented in Table 2.3.6.4.

Even though the mean residuals of hourly transmittance are quite large for the clearest day on which the measured hourly average transmittances varied from 100% to 3.0%, the differences between the predicted and measured daily transmittances are less than 10% of the transmittance. The large errors in the predicted hourly average transmittances resulted mainly from the temporal mismatch between the predicted and measured occurrence of sunflecks, as shown in Figure 2.3.6.6. This implies that there were systematic errors in the determination of tree positions.

All three submodels generally provide satisfactory predictions of the daily transmittances, although the predicted daily transmittances using submodel III are always the largest. The predicted diurnal variations of hourly average transmittances at different sensors are similar
to the measured diurnal variations, even though there may be some time differences in the predicted and measured occurrence of sunflecks.

In conclusion, MAESTRO provides satisfactory predictions of PAR transmittances. Using submodel I, daily transmittances are predicted as well as with other submodels, but using submodel III, the occurrence of sunflecks below the canopy was predicted better than with the other submodel. As photosynthesis of leaves in the lower part of the canopy is light limited, submodel III will be most suitable for simulating the photosynthesis of a tree crown on an hourly basis. However, predictions using submodel III seem more sensitive to errors in the measurements of crown dimensions and tree positions. Consequently, better methods of making these measurements should be used in the future.
3. APPLICATION OF PROGRAM MAESTRO TO SITKA SPRUCE

3.1. Introduction

One important aim of developing MAESTRO is to enhance our understanding of the functional significance of crown structure, and to evaluate the relative importance of different crown structural properties for PAR absorption, photosynthesis and transpiration by a tree; another is to help us to define our future research objectives and strategy.

Crown structure is defined as the shape and the size of a tree crown, the total area of all elements (leaves, stem, twigs, fruits etc.), and their inclination angles, orientations, and positions within a tree crown. For many broad-leaved species, leaf shape and leaf size should also be included in the definition. The variation of crown shape is quantitatively described by the ratio of crown length \( L \) to the average crown radius at the crown base \( R \).

The radiation regime within a tree crown depends not only on its structural properties but also on the radiance distribution of the diffuse radiation from the sky and the beam fraction of the incident radiation.

Using MAESTRO, I will investigate

1. the influence of different structural properties on PAR absorption, photosynthesis and transpiration by a tree crown;

2. the influence of the radiance distribution of the diffuse PAR, and the beam fraction of the incident PAR, on PAR absorption, photosynthesis and transpiration by a tree crown.

3.2. General assumptions

A number of assumptions are made for these applications, in addition to those made in Chapter 2. These assumptions are common to all sections in this chapter but some further assumptions may also be made for a specific study. All of them are based on studies made in plantations of Sitka spruce (\textit{Picea sitchensis} (Bong.) Carr.) in Scotland. The general assumptions are as follows:

1. All trees are identical and planted in a large, uniform stand with a stocking density of 1500 trees ha\(^{-1}\), and a spacing of 2.58 m.
Figure 3.2.1 The daily courses of incident diffuse PAR (D) and beam PAR (B) above the canopy.

Figure 3.2.2 The diurnal variation of air temperature ($T_a$) at the reference height.

Figure 3.2.3 The diurnal variation of relative humidity of the ambient air at the reference height.
Table 3.2.1 The physiological parameters
of the Sitka spruce needles

Definitions of all parameters are given
in "Symbols and definitions".

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Table 3.2.2 The physiological parameters
of the Sitka spruce needles

C, C+1 and C+2 designate current, one-year-old
and other older needles, respectively. $g_{smax}$
and $g_{smax}$ are the maximum values of stomatal
mesophyll conductances.

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<td>C+1</td>
<td>0.82</td>
<td>0.27</td>
</tr>
<tr>
<td></td>
<td>C+2</td>
<td>0.78</td>
<td>0.18</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>0.88</td>
<td>0.31</td>
</tr>
<tr>
<td>middle</td>
<td>C+1</td>
<td>0.84</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>C+2</td>
<td>0.79</td>
<td>0.14</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>0.91</td>
<td>0.16</td>
</tr>
<tr>
<td>lower</td>
<td>C+1</td>
<td>0.85</td>
<td>0.11</td>
</tr>
<tr>
<td></td>
<td>C+2</td>
<td>0.81</td>
<td>0.07</td>
</tr>
</tbody>
</table>
2. Crown shape is approximated by a half-ellipsoid with a radius of 1.5 m at the base and a length of 8.5 m. The total area of leaves within the crown is 40.0 m². The leaf inclination angle distribution is spherical; the LAD distribution is uniform unless specified; and the average leaf area density is calculated as the ratio of the total plan area of all needles within the crown to the volume of the crown.

3. Within a tree crown, the proportions of leaf area are 37%, 37%, 26% for current, one-year-old, and other older leaves, respectively. Leaves within each age class are separated into three types according to their relative positions in the crown (upper, middle and lower) (see Chapter 2). Leaves in different age classes and of different types may have different physiological parameters (see Tables 3.2.1 and 3.2.2). The average transmittance and reflectance of the Sitka spruce needles for PAR are 0.03 and 0.09, respectively (see Norman and Jarvis 1975).

4. The daily course of incident PAR and its beam fraction, and the diurnal variation of air temperature and ambient relative humidity are shown in Figures 3.2.1, 3.2.2 and 3.2.3, respectively. They are the basic meteorological inputs to MAESTRO in this study.

3.3. The influence of crown structural properties on PAR absorption, photosynthesis and transpiration

Four important structural properties of a tree crown are identified in this study (see 3.1): they are shape \((l_c/R)\), total area of leaves within a crown \((F_l)\), leaf area density distribution and leaf inclination angle distribution. Variations of those four structural properties are presented in Table 3.3.1 for all Sitka spruce trees in Plot 15 at Tummel Forest (see Chapter 2)

<table>
<thead>
<tr>
<th>Structural property</th>
<th>range</th>
<th>value¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>crown shape</td>
<td>2.0 - 10.0</td>
<td>5.60 (0.56)</td>
</tr>
<tr>
<td>(dimensionless)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>total leaf area within the tree crown (m²)</td>
<td>1.0 - 150.0</td>
<td>37.86 (12.64)</td>
</tr>
<tr>
<td>average leaf area density (m⁻¹)</td>
<td>0.5 - 3.0</td>
<td>1.0 (0.22)</td>
</tr>
<tr>
<td>²-average leaf inclination angle</td>
<td>30.0 - 75.0</td>
<td>57.0 (10.0)</td>
</tr>
</tbody>
</table>

¹: these values were obtained from measurements of fifty six trees in Plot 15 at Tummel Forest.
the standard deviation of average leaf inclination angle was not measured and was assumed to 0°.

3.3.1. Crown shape

A number of studies have been made on the influence of crown shape on PAR absorption (Jahnke and Lawrence 1965, Terjung and Louie 1972, Oker-blom and Kellomaki 1982, Kuuluvainen & Pukkula 1987) but only one on photosynthesis and transpiration (Rook et al. 1985). The photosynthetic rate of a tree crown depends not only on the flux density of incident PAR but also on the PAR regime which may be affected by the crown shape. Previous studies (Oker-blom and Kellomaki 1982) showed that there were small differences in PAR absorption by the crowns of a reasonably wide range of shapes, but influences of the crown shape on both photosynthesis and transpiration were not made clear. Since the influence of crown shape on PAR absorption, photosynthesis and transpiration may be affected by tree spacing (Kuuluvainen & Pukkula 1987), this will be studied for stands of Sitka spruce with different tree spacings.

Assumptions

The following additional assumptions have been made in this study:

1. Crown volume is constant but crown shape is a variable.

2. Leaf area density distribution within a tree crown is uniform and does not vary with crown shape and tree spacing.

The assumptions 1 and 2 together constrain the total area of leaves within a tree crown and therefore interactions between the crown shape and the total area of leaves are eliminated.

Results and discussion

Different crown shapes are simulated by varying \( l_c/R \) from 2.0 to 10.0, while tree spacing is varied from 10.0*10.0 m to 1.58*1.58 m, giving a stocking density of 100 to 4000 trees ha\(^{-1}\). This covers the full range of tree spacings and crown shapes in Sitka spruce plantations in the UK.
Figure 3.3.1.1 Variations of daily amounts of PAR absorption (A), photosynthesis (B) and transpiration (C) by a tree with crown shape ($I_c/R$) at different stocking densities as indicated beside each curve (trees ha$^{-1}$).
Figure 3.3.1.1 shows that the influence of the crown shape on daily amounts of both PAR absorption and photosynthesis depends on the tree spacing. When the tree spacing is 10.0*10.0 m, the narrowest crown \((l_c/R=10.0)\) has the largest daily amounts of both PAR absorption and photosynthesis. This is because the crown surface area of the narrowest crown is the largest. However, a crown with \(l_c/R\) of 4.0 has the smallest daily amounts of both PAR absorption and photosynthesis. This is consistent with Oker-blohm and Kellomaki’s conclusion that a vertically or a horizontally extended crown absorbs the maximum amount of PAR (Oker-blohm and Kellomaki 1982).

When the tree spacing is very close, the flattest tree crown \((l_r/R=2.0)\) has the largest daily amounts of both PAR absorption and photosynthesis. The relative differences are less than 10% for the daily amount of PAR absorption and less than 15% for the daily amount of photosynthesis among tree crowns of different shapes, over the range of tree spacings studied. This is because a canopy made up of flat crowns is more uniform in the horizontal and therefore more PAR will be absorbed (see Chapter 1) with the result that the daily amount of photosynthesis is also the largest.

Crown shape has only a small influence (less than 5%) on the daily amounts of both PAR absorption and photosynthesis over the range of stocking density 700 to 2500 trees ha\(^{-1}\), which includes the stocking densities of most Sitka spruce plantations in the U.K. This is in general agreement with other simulation studies (Oker-blohm and Kellomaki 1982, Kuuluvainen & Pukkula 1987).

As shown in Figure 3.3.1.1, differences in the daily amounts of transpiration are less than 5% among crowns of different shapes at any tree spacing. This is because transpiration rate is predominantly determined by the VPD of the air for an aerodynamically rough tree canopy (Jarvis and McNaughton 1985).

Because photosynthesis depends not only on the amount of PAR absorbed but also on the distribution of PAR within a tree crown, tree crown shape has the largest influence on the daily amount of photosynthesis but the smallest influence on the daily amount of transpiration by a tree crown in a stand.

**Conclusions**

The following conclusions can be drawn from this study:

1. Crown shape has little influence on daily amounts of PAR absorption, photosynthesis and transpiration over the range of
stocking density from 750 to 2500 trees ha\(^{-1}\).

2. When the stocking density is 100 trees ha\(^{-1}\), the differences between the narrowest crown (\(l_c/R=10.0\)) and a crown of any of the other four shapes studied can be up to 8% and 14% for the daily amounts of PAR absorption and photosynthesis, respectively. When the stocking density is 4000 trees ha\(^{-1}\), the relative differences among the different crown shapes can be up to 7% and 13% in favour of the flattest tree crown (\(l_c/R=2.0\)) for the daily amounts of PAR absorption and photosynthesis, respectively.

3. Crown shape hardly affects the daily amount of transpiration of a tree in a stand.

3.3.2. The total area of leaves within a tree crown

The total area of leaves, \(F_l\), is one of the most variable structural properties of a tree crown in a stand (see Table 3.3.1). A LAI of 15 can usually be considered as an upper limit for most coniferous stands and therefore a total area of leaves of 150 m\(^2\) within a crown will be the upper limit for the range of tree spacings considered here. For the Sitka spruce stand studied, LAI was about 6.0, and the average total area of leaves within the crown is 37.9 m\(^2\) (see Table 3.3.1). Hence I have varied \(F_l\) from 10.0 m\(^2\) to 80 m\(^2\) to study the influence of leaf area in the crown on PAR absorption, photosynthesis and transpiration by a tree in the stand.

Assumption

The area of leaves within a tree crown is assumed to vary between 10.0 m\(^2\) to 80.0 m\(^2\).

As crown size is kept constant, variation of \(F_l\) will result in variation of the average leaf area density (\(L_d\)) within a crown so that there are actually two variables in this study.

Results and discussion

Table 3.3.2.1 Daily amounts of PAR absorption (\(Q_g\)), photosynthesis (\(P_c\)) and transpiration (\(E_C\)) by a tree crown with the different area of leaves

<table>
<thead>
<tr>
<th>(F_l) m(^2)</th>
<th>(Q_g) mol/(tree*day)</th>
<th>(P_c)</th>
<th>(E_C)</th>
<th>LAI</th>
</tr>
</thead>
<tbody>
<tr>
<td>10.0</td>
<td>116.5</td>
<td>2.89</td>
<td>1200.4</td>
<td>1.5</td>
</tr>
<tr>
<td>20.0</td>
<td>156.3</td>
<td>4.31</td>
<td>2300.4</td>
<td>3.0</td>
</tr>
<tr>
<td>40.0</td>
<td>175.9</td>
<td>5.13</td>
<td>4463.7</td>
<td>6.0</td>
</tr>
<tr>
<td>60.0</td>
<td>178.0</td>
<td>4.84</td>
<td>6408.1</td>
<td>9.0</td>
</tr>
<tr>
<td>80.0</td>
<td>177.0</td>
<td>4.29</td>
<td>8228.8</td>
<td>12.0</td>
</tr>
</tbody>
</table>

The daily amounts of PAR absorption, photosynthesis and transpiration are presented in
Table 3.3.2.1 for tree crowns with different leaf area.

The results presented in Table 3.3.2.1 show that:

1. The daily amount of PAR absorption increases with $F_l$ up to a $F_l$ of 40.0 m$^2$ (LAI=6.0), and then becomes saturated with respect to $F_l$. For a horizontally uniform canopy with a LAI of 6.0 and with the spheric leaf inclination angle distribution, more than 90% of incident PAR will be absorbed. This is also true for a canopy made up of uniform tree crowns with some gaps among them.

2. The daily amount of photosynthesis increases with $F_l$ up to a $F_l$ of 40.0 m$^2$, and then decreases. This is because net photosynthesis of some leaves is negative if $F_l$ is larger than 40.0 m$^2$.

3. The daily amount of transpiration increases with $F_l$ over the range of $F_l$ studied. This is because the transpiring surface increases with $F_l$ and the transpiration rate of a tree crown is strongly dependent on the VPD that is more or less constant within a rough canopy, and the area of leaves within the tree crown (Jarvis & McNaughton 1985).

Conclusions

The following conclusions can be drawn from this study:

1. The daily amounts of both PAR absorption and photosynthesis increase with $F_l$ up to a $F_l$ of 40.0 m$^2$ (LAI=6.0). When $F_l$ is larger than 40.0 m$^2$, the daily amount of PAR absorption hardly increases with $F_l$, but the daily amount of photosynthesis decreases with $F_l$.

2. The daily amount of transpiration increases with $F_l$ over the range studied.

3.3.3. Leaf area density distribution

Leaf area density is highly variable within a tree crown (see Chapter 1). This non-uniform structure results in a more uniform PAR regime within the crown, and hence a higher photosynthetic rate of a non-uniform than of a uniform crown (see Chapter 1). In this study I will investigate the influence of LAD distribution within a tree crown on the daily amount of PAR absorption, photosynthesis and transpiration. The influence of a non-uniform LAD distribution on both PAR absorption and photosynthesis also depends on the area of leaves within a crown and therefore results of this section have to be interpreted by making use of the conclusions drawn in the previous section.
Assumptions

The following additional assumptions have been made in this study:

1. The average leaf area density \( L_d \) within a tree crown is 1.0 \( \text{m}^2/\text{m}^3 \).

2. The distribution of LAD within a tree crown is either uniform or variable in both the vertical and the horizontal dimensions.

3. \( F_l \) varies from 10.0 to 80.0 \( \text{m}^2 \) (see Table 3.3.3.1). If \( F_l \) is not larger than 20.0 \( \text{m}^2 \), the physiological parameters of all needles are the same (see Tables 3.2.1 and 3.2.2).

To keep \( L_d \) constant, the crown size is expanded with a constant \( L_c/R \) while \( F_l \) increases and therefore the gaps in the canopy become smaller as \( F_l \) becomes larger.

If LAD varies in both the vertical and the horizontal dimensions, LAD within the crown is calculated as

\[
L_d = F_l L_c^{-1} R (h)^{-2} 133.08 h^{2.46} (1.0-h)^{2.77} r^{0.23} (1.0-r)^{1.50}
\]

The coefficients in the equation are based on the study in Chapter 1.

<table>
<thead>
<tr>
<th>( F_l )</th>
<th>10.0</th>
<th>20.0</th>
<th>40.0</th>
<th>60.0</th>
<th>80.0</th>
<th>unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>( R )</td>
<td>0.94</td>
<td>1.19</td>
<td>1.50</td>
<td>1.72</td>
<td>1.89</td>
<td>( \text{m} )</td>
</tr>
<tr>
<td>( h )</td>
<td>5.35</td>
<td>6.75</td>
<td>8.50</td>
<td>9.73</td>
<td>10.73</td>
<td>( \text{m} )</td>
</tr>
<tr>
<td>( LAI )</td>
<td>1.5</td>
<td>3.0</td>
<td>6.0</td>
<td>9.0</td>
<td>12.0</td>
<td>( \text{m}^2 \text{ m}^{-2} )</td>
</tr>
</tbody>
</table>

Results and discussion

Figure 3.3.3.1 shows that the difference between the daily amount of PAR absorption by a uniform and by a non-uniform tree crown is very small up to a \( F_l \) of 10 \( \text{m}^2 \) (\( LAI\)=1.5) and then increases with \( F_l \) up to a \( F_l \) of 60.0 \( \text{m}^2 \) (\( LAI\)=9.0). The daily amount of PAR absorption is then saturated with respect to \( F_l \) for both a uniform and a non uniform tree crown. As a result, the non-uniform tree crown absorbs 30% more PAR within a day than the uniform tree crown. This is because the leaves within a non-uniform tree crown receive a higher flux density than the leaves within a uniform tree crown so that a non-uniform tree crown is advantageous in a dense stand. But when the crown size is small and gaps between the crowns are large, most leaves are well illuminated and non-uniform crowns are
Figure 3.3.3.1 Variations of daily amounts of PAR absorption (A), photosynthesis (B) and transpiration (C) with area of leaves within a tree crown with uniform (constant LAD) and non-uniform (2-D LAD) LAD distributions.

X: total area of leaves within the tree crown (m²).
of no advantage.

Figure 3.3.3.1 shows the variations of the daily amounts of photosynthesis with $F_i$ for both a uniform and a non-uniform tree crown. When $F_i$ is less than 10.0 m$^2$, the daily amount of photosynthesis of a uniform tree crown is larger than that of a non-uniform crown, but the relative difference is less than 10%; when $F_i$ is more than 10.0 m$^2$, the non-uniform crown has a larger amount of daily photosynthesis than the uniform crown; and the relative difference increases with $F_i$ up to 67% at a $F_i$ of 80.0 m$^2$.

The daily amount of photosynthesis increases with $F_i$ up to a $F_i$ of 60.0 m$^2$ (LAI=9.0) for a non-uniform crown and only up to a $F_i$ of 40.0 m$^2$ (LAI=6.0) for a uniform crown. This implies that PAR conditions within a non-uniform tree crown are better for photosynthesis and therefore that more leaves can survive, as leaves usually absciss after their net carbon gain has been negative for a period (Esau 1965). A non-uniform crown structure may be the reason why many coniferous tree stands can have a LAI of 6 to 15.

Figure 3.3.3.1 shows the variations of the daily amount of transpiration with $F_i$ for a uniform and a non-uniform tree crown. The relative difference between these two is less than 1% up to a $F_i$ of 20.0 m$^2$ (LAI=3.0), and then increases to 12% at a $F_i$ of 80.0 m$^2$ (LAI=12.0). This is because the transpiration rate is predominantly limited by the VPD of the air and the stomatal conductance, and net radiation only imposes a very small limitation. However, when $F_i$ is large, the PAR flux density on the leaf surface is small, with the result that the stomatal conductance is small and imposes a limitation to transpiration. As the radiation regime is more uniform within the non-uniform tree crown, limitation by stomatal conductance is less than in the uniform tree crown.

Conclusions

The following conclusions can be drawn from this study:

1. A non-uniform LAD distribution within a tree crown enables it to have larger amounts of PAR absorption, photosynthesis and transpiration than with a uniform LAD distribution when the total area of leaves within the crown is larger than 10.0 m$^2$.

2. The daily amount of net photosynthesis of a tree crown increases with the total area of leaves within the crown up to a $F_i$ of 60.0 m$^2$ (LAI=9.0) for a non-uniform crown, and up to a $F_i$ of 40.0 m$^2$ (LAI=6.0) for a uniform crown.

3. The effect of a non-uniform LAD distribution on the daily amount of transpiration is small.
3.3.4. Leaf inclination angle distribution

Measurements of leaf angle in the field can be very tedious and inaccurate, and extremely
difficult for forest trees. Whether it is worthwhile studying the leaf inclination angle
distribution precisely is not as yet clear. One proposal is to ignore the variances of leaf
inclination angles and to use a single average value (Campbell and Norman 1987); another
is to use the spherical leaf inclination angle distribution to approximate most canopies even
though we may know little about its suitability (Wit de 1965). I will analyse the errors in
these arbitrary approximations in this study.

According to Monsi and Saeki (1953), the PAR transmittance within a tree canopy can be
calculated approximately as \( \exp(-k_b L_d s) \), where \( s \) is the pathlength of the incident PAR.
The extinction coefficient, \( k_b \), is determined by the incident angle of the incoming PAR and
the inclination and azimuthal angles of the leaves within the canopy. As diffuse PAR is
multi-directional and beam PAR is approximately unidirectional, the PAR will be affected
differently by the leaf inclination angle distribution.

The ellipsoidal leaf inclination angle distribution and the average leaf inclination
angle

The ellipsoidal leaf inclination angle distribution function is one of the simplest functions
with reasonable flexibility. It has only one parameter and can be used to fit a wide range
of different leaf inclination angle distributions (Campbell 1986). The average leaf
inclination angle can also be determined from the single parameter (\( u \)). Although this is not
given by Campbell, I have established simple empirical relationships between \( u \) and the
average leaf inclination angle \( \alpha_f \) by solving the equation numerically, (Wang and Jarvis
1988a). The relations are:

\[
\begin{align*}
\alpha_f &= 1.0 \quad (u \leq 1, \quad r = 0.9986) \\
&= \frac{1.0}{0.3782u + 0.6131} \quad (u > 1, \quad r = 0.9991) \\
\end{align*}
\]

This relation is also shown in Figure 3.3.4.1.
For the spherical leaf inclination angle distribution, \( u \) equals 1.0, and the average leaf inclination angle is \( 57.4^0 \). In this simulation study, I also consider two other leaf inclination angle distributions with \( u = 5.0 \) and \( u = 0.5 \) and average leaf inclination angles of \( 18^0 \) and \( 72^0 \), respectively.

**Assumptions**

1. Three leaf inclination angle distributions are considered (\( u = 0.5, 1.0, 5.0 \))
2. The tree is isolated.

The case of an isolated tree is considered because this extreme case may maximize differences in the simulation results between average leaf inclination angles and the leaf inclination angle distributions. The approximation errors will be smaller for trees in a stand than for an isolated tree. This will be explained later (see 3.3.5).

**Influences of leaf inclination angle distribution on the absorption of diffuse PAR, photosynthesis and transpiration of a tree crown under an overcast sky**

In this test, the extinction coefficients of diffuse PAR are investigated in a tree crown with different leaf inclination angle distributions. Diffuse PAR absorption, photosynthesis and transpiration are calculated to test the hypothesis that they have only a small dependence on the leaf inclination angle distribution under an overcast sky in an isolated tree crown.

The sky was divided into five annuli. The amount of diffuse PAR from each annulus was calculated from the radiance distribution function \((1+2\cos(\theta))/3.0\). The extinction coefficient for each annulus \((k_d)\) was calculated using the middle zenith angle of this annulus: the middle angles \((\theta_i)\) for the five annuli were \(9^0, 27^0, 45^0, 63^0\), and \(81^0\).
respectively.

To compare the transmission of diffuse PAR within a tree crown with different leaf inclination angle distributions, an average extinction coefficient for diffuse radiation, $k_d$, has been calculated.

$$k_d = \frac{\sum k_{di}(1+2\cos(\theta_i))\sin\theta_i\cos(\theta_i)/3.0}{\sum(1+2\cos(\theta_i)\sin\theta_i)\cos(\theta_i)/3.0}$$

Assumption

The beam fraction is zero.

Results and discussion

It is shown in Table 3.3.4.1 that extinction coefficients calculated from the leaf inclination angle distributions and the average leaf inclination angle are very close. For $u=1$, the extinction coefficients are constant ($0.5$); for $u=0.5$, the extinction coefficient increases with the zenith angle of the sun, but for $u=5.0$, the extinction coefficient decreases with the zenith angle of the sun. At a large or small zenith angle, the extinction coefficients for $u=0.5$ and $5.0$ can differ by a factor of two, but the average extinction coefficients are very close.

Table 3.3.4.1 The calculated extinction coefficients of diffuse PAR ($k_d$)

I: calculated using the average leaf angle.
II: calculated using the ellipsoidal leaf inclination angle distribution.

<table>
<thead>
<tr>
<th>$\theta_i$</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>$k_d$</th>
</tr>
</thead>
<tbody>
<tr>
<td>900</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.53</td>
</tr>
<tr>
<td>270</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.47</td>
</tr>
<tr>
<td>450</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.46</td>
</tr>
<tr>
<td>600</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.50</td>
</tr>
<tr>
<td>810</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.53</td>
</tr>
<tr>
<td>0.50</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.5</td>
</tr>
<tr>
<td>0.5</td>
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<td></td>
<td></td>
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</tr>
<tr>
<td>5.0</td>
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<td></td>
<td></td>
<td>0.85</td>
</tr>
<tr>
<td>0.34</td>
<td></td>
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<td>0.67</td>
</tr>
<tr>
<td>0.45</td>
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<td>0.43</td>
</tr>
<tr>
<td>0.55</td>
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<td></td>
<td></td>
<td></td>
<td>0.21</td>
</tr>
<tr>
<td>0.60</td>
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<td></td>
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<td>0.60</td>
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<tr>
<td>0.44</td>
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<td></td>
<td>0.23</td>
</tr>
<tr>
<td>0.67</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.67</td>
</tr>
</tbody>
</table>

As the errors in the average leaf angle approximation are less than 2%, the results obtained by using that approximation are not presented.

As shown in Figure 3.3.4.2, the daily amount of PAR absorption by a tree crown increases
Figure 3.3.4.2 The diurnal variations of PAR absorption (A), photosynthesis (B) and transpiration (C) by an isolated tree crown with three different leaf inclination angle distributions (\(u=0.5, 1.0\) and 5.0) under an overcast sky.

- \(u\) curve type
- 0.5 broken curve with longer interval
- 1.0 broken curve with shorter interval
- 5.0 solid curve
with u. A tree crown with more horizontal leaves (u=5.0) has a larger average extinction coefficient and absorbs more PAR, but differences in the hourly amounts of PAR absorption are less than 5% compared with the spherical leaf inclination angle distribution (u=1.0).

Figure 3.3.4.2 shows that the differences in the hourly amount of photosynthesis by a tree crown with the different leaf inclination angle distributions are less than 5% compared with a tree crown with the spherical leaf inclination angle distribution. As the diffuse radiation regime within the tree crown is rather uniform, a tree crown with more horizontal leaves absorbs more PAR, and also has a higher photosynthetic rate than a tree crown with more vertical leaves.

Figure 3.3.4.2 shows that the leaf inclination angle distribution hardly affects the daily course of transpiration because the transpiration rate is predominantly determined by the VPD of the air for a rough canopy (Jarvis and McNaughton 1985).

**Conclusions**

The following conclusions can be drawn from this study:

1. There are very small errors in the approximation of an average leaf inclination angle for PAR absorption, photosynthesis and transpiration.

2. The errors are also very small (less than 5% for hourly and daily values) in the approximation of a spherical leaf angle distribution for PAR absorption, photosynthesis and transpiration.

These two conclusions indicate that the leaf angle distribution does not significantly affect the hourly amount of PAR absorption, photosynthesis and transpiration by a tree crown so that knowledge of the leaf inclination angle distribution within a tree crown is of little importance under an overcast sky.

**Influences of leaf angle distribution on PAR absorption, photosynthesis and transpiration under a unidirectional radiation flux field**

The aim of this test was to determine the importance of leaf inclination angle distribution to the absorption of beam PAR, photosynthesis and transpiration by an isolated tree crown. At the single leaf scale, the density of PAR flux on the leaf surface and the photosynthetic rate of a leaf are very sensitive to the leaf inclination angle, as shown by Kriedemann et al (1964), but some compensations may occur at the tree crown scale.
Assumption

The beam fraction is 1.0.

Results

Table 3.3.4.2 The extinction coefficients of the incident beam PAR for leaves with three different leaf inclination angle distributions

<table>
<thead>
<tr>
<th>u</th>
<th>33</th>
<th>38</th>
<th>45</th>
<th>53</th>
<th>66</th>
<th>74</th>
<th>83</th>
<th>93</th>
<th>99</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.5</td>
<td>0.41</td>
<td>0.43</td>
<td>0.46</td>
<td>0.50</td>
<td>0.55</td>
<td>0.57</td>
<td>0.58</td>
<td>0.58</td>
<td>0.58</td>
</tr>
<tr>
<td>1.0</td>
<td>0.50</td>
<td>0.50</td>
<td>0.50</td>
<td>0.50</td>
<td>0.50</td>
<td>0.50</td>
<td>0.50</td>
<td>0.50</td>
<td>0.50</td>
</tr>
<tr>
<td>5.0</td>
<td>0.77</td>
<td>0.72</td>
<td>0.66</td>
<td>0.57</td>
<td>0.41</td>
<td>0.30</td>
<td>0.21</td>
<td>0.19</td>
<td></td>
</tr>
</tbody>
</table>

As the errors resulting from the average leaf inclination angle approximation were less than 5% in the hourly amounts of PAR absorption, photosynthesis and transpiration, results calculated using the first approximation are not presented.

Figure 3.3.4.3 shows the daily course of PAR absorption by a tree crown with three different leaf inclination distributions. In the early morning and late afternoon, when the zenith angle of the sun ($\Theta$) is larger than 55°, a tree crown with more horizontal leaves ($u=5.0$) absorbs less PAR. The differences can be up to 100% in favour of a tree crown with more vertical leaves ($u=0.5$). When the zenith angle of the sun is small, a tree crown with more horizontal leaves absorbs more PAR, because its beam extinction coefficient increases with the zenith angle of the sun (see Table 3.3.4.2).

As shown in Figure 3.3.4.3, there is a distinct depression in the daily course of photosynthesis by a tree crown with more horizontal leaves around noon when PAR absorption is largest. This is because the PAR regime within a tree crown with more horizontal leaves ($u=5.0$) is less uniform and the PAR absorbed is not so efficiently used as by the leaves within the other tree crowns ($u=0.5$, 1.0). The leaf inclination angle distribution has different influences on hourly and daily photosynthesis when the beam fraction is 1.0. The difference between daily photosynthesis with $u=0.5$ and 5.0 may be 10% in favour of the tree crown with more vertical leaves ($u=0.5$), but differences in the hourly rate of photosynthesis may be up to 20% in favour of the tree crown with more horizontal leaves ($u=5.0$).

Figure 3.3.4.3 shows that the differences of the hourly rates of transpiration are less than 10% among the three different leaf inclination angle distributions when the sun is close to
Figure 3.3.4.3 The diurnal variations of beam PAR absorption (A), photosynthesis (B) and transpiration (C) by an isolated tree crown with three different leaf inclination angle distributions ($u=0.5$, 1.0 and 5.0) and a beam fraction of 1.0.

$u$ curve type
5.0 broken curve with longer interval
1.0 broken curve with shorter interval
0.5 solid curve
the horizon, but the differences for the daily amounts of transpiration are less than 2%.

Conclusions

1. The average leaf inclination angle approximation is sufficiently accurate for studies of PAR absorption, photosynthesis and transpiration.

2. The approximation of spherical leaf inclination angle distribution does not give accurate estimates of the hourly rates of photosynthesis, or even the daily amounts of PAR absorption, but this approximation does provide a reasonable estimate of the hourly rates of transpiration by a tree crown.

3. The influence of the leaf inclination angle distribution on PAR absorption of a tree crown is different from the influence on photosynthetic rate.

Influences of leaf angle distribution on the absorption of global PAR, photosynthesis and transpiration by an isolated tree crown

The previous studies showed that the leaf angle distribution has different effects on PAR absorption and on photosynthesis by a tree crown, but the approximation of the average leaf inclination angle is adequate for simulating both PAR absorption and photosynthesis. This conclusion has important implication for studies of tree crown structure because the average leaf angle can be obtained using the beam transmittance sensor (Lang et al 1985).

As shown previously, the influences of the leaf inclination angle distribution on PAR absorption and on photosynthesis depend on both the beam fraction and the solar zenith angle (i.e. the time of day and day of the year) but those effects were small. Similarly Oker-blom and Kellomaki (1982b) showed that the influence of the leaf angle distribution was small on PAR absorption and photosynthesis for a dense Scots pine canopy (LAI = 6) in Finland during the growing period. In this test, I will study the influences of leaf inclination angle distribution on PAR absorption, photosynthesis and transpiration of an isolated Sitka spruce crown in relation to the beam fractions during a sunny day.

Results and discussion

MAESTRO was used to calculate the hourly and daily amounts of diffuse and beam PAR absorbed and the photosynthesis and transpiration by an isolated tree crown. The hourly beam fractions during the day were calculated using an equation derived from the data (see Chapter 2).
Figure 3.3.4.4 The diurnal variations of PAR absorption (A), photosynthesis (B) and transpiration (C) by an isolated tree crown with three different leaf inclination angle distributions ($u$=0.5, 1.0 and 5.0) under a clear sky.

- **$u$** curve type:
  - 5.0 broken curve with longer interval
  - 1.0 broken curve with shorter interval
  - 0.5 solid curve
Figure 3.3.4.4 shows that a tree crown with more horizontal leaves ($u=5.0$) absorbs a larger amount of PAR but has a lower rate of photosynthesis when the beam fraction is large, and the zenith angle of the sun is small, than a tree crown with more vertical leaves ($u=0.5$). Difference between the tree crowns with the three leaf inclination angle distributions can be up to 19% in the hourly amount of photosynthesis, but as small as 5% in the daily amount of photosynthesis. The differences in the hourly amounts of both PAR absorption and photosynthesis increase with the beam fraction. The maximum difference in the daily amount of PAR absorption is 15% in favour of a tree crown with a $u$ of 5.0.

Figure 3.3.4.4 shows that differences between the hourly rates of transpiration by a tree crown with three different leaf inclination distributions are very small ($\leq 5\%$), and are not affected to any significant extent by beam fraction.

Conclusion

1. The approximation of an average leaf inclination angle is sufficiently accurate for studies of PAR absorption and photosynthesis by a tree crown.

2. The approximation of a spherical leaf inclination angle distribution is satisfactory for simulating the hourly rates of transpiration and daily amount of photosynthesis, but is not very accurate for simulating the hourly rates of photosynthesis or the daily amount of PAR absorption by an isolated tree crown on a sunny day.

Analysis of the insensitivity of PAR absorption to the leaf inclination angle distribution

Introduction

As shown previously, the definition of the leaf inclination angle distribution of leaves within a tree crown can be reduced to finding the average leaf inclination angle. A theoretical analysis of this result may give us some insight into the role of structure in the functioning of a tree crown or stand canopy. An isolated tree crown and a horizontally uniform canopy are two extremes of structure. The isolated tree crown is free of interference from other trees; a horizontally uniform canopy is assumed to be a perfect synthesis of all the tree crowns in the stand. Since the diffuse PAR can be approximated by a number of unidirectional fluxes, the study of beam PAR is fundamental to our understanding of the influences of leaf angle distribution on PAR absorption and photosynthesis.
Theoretical analysis of influence of leaf inclination angle distribution on PAR absorption

This theoretical analysis will be concerned with two aspects: self compensation and saturation.

Self compensation

Incident PAR ($I_0$) is made up of beam and diffuse PAR as follows:

$$I_0 = I_b F_b + I_d (1.0 - F_b)$$

Ignoring the scattered PAR, the absorbed global PAR ($Q_g$) consists of absorbed beam PAR ($Q_b$) and absorbed diffuse PAR ($Q_d$), i.e.

$$Q_g = Q_b + Q_d$$

$$= I_0 [k_b \exp(-k_b L_d s) + k_d T_d (1 - F_b)] \sigma$$

$$= [k_b C_b + k_d C_d] \sigma$$

and \( \sigma = (1 - \tau - \rho)/(1 - \tau) \)

$$C_b = I_b F_b \exp(-k_b L_d s) \quad C_d = I_d (1 - F_b) T_d$$

where \( k_b C_b \), \( k_d C_d \) are the intercepted flux densities of the beam PAR in the direction of \( \theta \) and of diffuse PAR by the leaves within the tree crown, respectively.

The flux density of PAR absorbed by the leaves within the tree crown increases with the extinction coefficient and PAR transmittance, both of which are in turn affected by leaf inclination angle distribution. For PAR incident from the zenith, the extinction coefficient increases with the average leaf inclination angle but the PAR transmittance within the tree crown decreases. Therefore the influence of leaf inclination angle distribution on PAR absorption is self-compensated.

For diffuse PAR, \( k_d \) is quite insensitive to the leaf inclination angle distribution (see Table 3.3.4.1). As \( k_b \) is more sensitive to the leaf inclination angle distribution (see Tables 3.3.4.1 and 3.3.4.2), in agreement with the simulation results presented in 3.3.4, this implies that the flux density of diffuse PAR absorbed is less sensitive to the leaf inclination angle distribution than the flux density of beam PAR absorbed by a tree crown.

For beam PAR, if the leaves are vertical and the solar zenith angle is small, \( k_b \) is small, but \( C_b \) will be larger. It is apparent that decrease and increase in \( k_b \) and \( C_b \) will not be of the same amplitude, or even of the same order. On the other hand, at a tree crown scale,
if the leaves in front of a point in the direction of a beam of PAR absorb a large flux density of PAR (i.e. $k_b$ is large), there is only a small flux density of PAR available for the leaves behind this point to absorb (i.e. $C_b$ is small). This compensation is the reason why the hourly amount of PAR absorption is rather insensitive to the leaf inclination angle distribution when the total area of leaves within the tree crown is large. Obviously the PAR regime will be different within the crown of a tree with different leaf inclination angle distributions. This may explain why photosynthesis is more sensitive to the leaf inclination angle distribution than PAR absorption because the photosynthetic PAR response is non-linear. On a daily basis, there are hourly variations in the degree of this compensation. For example, the value of $k_b$ for vertical leaves is larger in the morning and the late afternoon, but smaller for the horizontal leaves. This has also been shown by Oker-blom and Kellomaki (1982b).

Compared with beam PAR, diffuse PAR has a range of extinction coefficients for each leaf inclination angle distribution. This may be the main reason why the absorption of diffuse PAR is much less sensitive to the leaf inclination angle distribution; in other words, self compensation is more evident.

Saturation

When the transmittance of PAR through the canopy is very small, the flux density of PAR intercepted by the tree crown approaches the flux density of incident PAR, and is very insensitive to the leaf inclination angle distribution; this is saturation.

When incident PAR passes through the crown of an isolated tree, the flux density of PAR absorbed by the leaves along the pathlength is approximately given by (see Kuroiwa 1969):

$$F_b\sigma(1-\exp(-k_bL_d\theta/\cos\theta))+(1-F_b)\sigma(1.0-\exp(-k_dL_d\theta))$$

and its sensitivity to leaf inclination angle is given by

$$\sigma F_b\left(\sum k_b^n(L_d)^{n-1}/n!\right)\left(\sum k_d^n(L_d)^{n-1}/n!\right)^{-1}(dk_b/d\theta) + \sigma(1-F_b)\left(\sum k_d^n(L_d)^{n-1}/n!\right)^{-1}(dk_d/d\theta)$$

The sensitivity of PAR absorption to leaf inclination angle is inversely proportional to $k_bL_d\theta$ and $k_dL_d\theta$, i.e. the projected leaf area density along the pathlength of beam and diffuse PAR. The deeper into the canopy, the less sensitive is PAR absorption to the leaf inclination angle. This is because the fractional amount of PAR absorbed approaches 1.00. This saturation is dependent on the structural characteristics of the crowns of all trees and the distances between them in a stand. Compared with an isolated tree, PAR absorption by a tree crown in a stand may reach saturation nearer to the crown top, as the
pathlength through the foliage may be longer.

Calculation of PAR absorbed by a tree crown is usually done numerically, although an analytical solution would provide a more elegant explanation. However a general analytical solution may be difficult or even impossible to obtain and therefore I restrict this analysis to the absorption of PAR incident from the two zenith angles, 0.0° and 90.0°, for which solutions are much simpler. This analysis should account for the range of sensitivities of PAR absorption to the different leaf inclination angle distribution.

When the zenith angle of incident PAR is 0°, the flux density of PAR absorbed is

$$I_0' = A_s (1 - T_b) \sigma$$

where $T_b = 2.0 l_c^{-2} \int_y \exp(-k_b \gamma d) \frac{2\gamma R\sqrt{(1-x^2)}}{l_c} dx dy$,

and $I_0'$ is the PAR flux density normal to the direction of incident PAR, and $A_s$ denotes the area of the tree crown projected onto a plane perpendicular to the direction of the incident PAR. $x$ is relative radial distance from the tree trunk at a height of $y$ from the crown base, $x$ varies from 0.0 to 1.0.

![Figure 3.3.4.5](image)

When the zenith angle of incident PAR is 90°, the flux density of beam PAR absorbed is

$$\sigma 2l_c^2 \pi R^2 C^{-2}(C-1.0 + \exp(-C))$$

where $C = 3F_l k_b / (\pi R^2)$.

The average absorptance of beam PAR incident from the zenith angles of 0.0° and 90.0° within the area of the crown shadow on a plane normal to the direction of the incident PAR are plotted against the extinction coefficients in Figure 3.3.4.5, which shows that the
average PAR absorptance is nearly constant when the extinction coefficient is larger than 0.6. This can be accounted for by self-compensation, as the total flux density of PAR absorbed by a tree crown is an integration of the amount of PAR absorbed by each individual leaf within the tree crown.

Conclusions

1. Self-compensation at the single leaf scale can be built up at the tree crown scale, with the consequence that the total flux density of PAR absorbed saturates with the extinction coefficient.

2. Self-compensation is more evident in the absorption of diffuse PAR than beam PAR.

3.3.5. Evaluation of the importance of crown structural properties for PAR absorption, photosynthesis and transpiration by a tree crown in a Sitka spruce stand

Previous studies have shown that different crown structural properties are of quite different importance in assessing PAR absorption, photosynthesis and transpiration of a tree crown. The influence of different crown structural properties also depends on their variations in the stand. Evaluation of the importance of these properties for PAR absorption, photosynthesis and transpiration is of great use in determining what to measure and the necessary accuracy of the measurements.

Measurements of different crown structural properties were made for all trees in plot 15 within a Sitka spruce stand (see Chapter 2), and have been presented in Table 3.3.1.

Table 3.3.5.1 Evaluation of different crown structural properties

<table>
<thead>
<tr>
<th>Property</th>
<th>(Y_{max} - Y_{min})/Y_{mean} PAR absorption</th>
<th>photosynthesis</th>
<th>transpiration</th>
</tr>
</thead>
<tbody>
<tr>
<td>crown shape</td>
<td>2%</td>
<td>3%</td>
<td>1%</td>
</tr>
<tr>
<td>total leaf area within a crown</td>
<td>12%</td>
<td>21%</td>
<td>92%</td>
</tr>
<tr>
<td>LAD distribution</td>
<td>21%</td>
<td>30%</td>
<td>11%</td>
</tr>
<tr>
<td>average leaf inclination angle</td>
<td>2%</td>
<td>15%</td>
<td>2%</td>
</tr>
</tbody>
</table>

Here MAESTRO is used to evaluate the importance of four crown structural properties of the trees in the stand for PAR absorption, photosynthesis and transpiration. The value of (Y_{max} - Y_{min})/Y_{mean} is used to evaluate the influences of a structural property. Y_{max} and
$Y_{\text{min}}$ are the maximum and minimum values of a output (daily amount of PAR absorption, photosynthesis or transpiration of a tree crown) obtained by varying an input (one of four structural properties) over the range of $[m_c - 1.96s_c, m_c + 1.96s_c]$, where $m_c$ is the mean value of the input and $s_c$ is the standard deviation of the input. $Y_{\text{mean}}$ is the value of the output obtained by using the mean value of the input. The results are presented in Table 3.3.5.1.

They show that

1. The influence of crown shape on the daily amounts of PAR absorption, photosynthesis and transpiration by the crown of a tree in the stand is very small.

2. The total area of leaves within a tree crown has a significant influence on PAR absorption, photosynthesis and transpiration by the crown of a tree in the stand, and the influence on transpiration is far larger than on PAR absorption and photosynthesis.

3. The LAD distribution within a tree crown has a large influence on the daily amounts of PAR absorption and photosynthesis and a smaller influence on transpiration by the crown of a tree in the stand.

4. Average leaf inclination angle has only a small influence on the daily amounts of PAR absorption and transpiration, but a large influence on the daily amount of photosynthesis by the crown of a tree in the stand.

3.4. The influence of the radiance distribution of diffuse PAR in the sky on PAR absorption, photosynthesis and transpiration of a tree crown

The actual radiance distribution is, without any doubt, far more complicated than that used in the simulation, but the range of radiance variations in the sky can be taken into account by a simple model, which can be used to investigate the possible influence of radiance distribution on PAR absorption, photosynthesis and transpiration by the tree crown.

Grant (1985) showed that the radiance distribution of diffuse radiation is very important for radiation absorption by the crown of an isolated tree, but he did not study a tree in a stand or the influence of radiance distribution on photosynthesis. Usually either a uniform overcast sky (UOC) or a standard overcast sky (SOS) is used to simulate the radiance distribution, without any consideration of the variations of the actual diffuse radiance distribution. Whether these are good approximations with respect to radiation absorption and photosynthesis has not been well studied.
Assumptions

1. The radiance distribution in the sky is given by \((1+b\cos \theta)/(\pi+2b/3)\). The parameter \(b\) varies from -1.0 to 2.0 (see Fig. 3.4.1).

2. The beam fraction is 0.0

Results and discussion

MAESTRO was used to calculate the diffuse transmittance at thirteen grid points which are located at six different heights (see Chapter 2) within the crown of an isolated tree and a tree in the stand. The results are presented in Tables 3.4.1 and 3.4.2. The hourly amounts of PAR absorption, and rates of photosynthesis and transpiration by an isolated tree and a tree in the stand were also calculated and are shown in Figure 3.4.2 and 3.4.3, respectively.

It is shown in Tables 3.4.1 and 3.4.2 that the value of the diffuse transmittance at any grid point within the crown of an isolated tree or of a tree in the stand is rather insensitive to the radiance distribution of the incident diffuse PAR when parameter \(b\) is not less than 0.0. This is because a large proportion of diffuse PAR is incident near the zenith and the pathlength of the incident PAR through a half-ellipsoidal tree crown is short. Hence the transmittance of diffuse PAR is much more sensitive to the pathlength and to the leaf area density along the pathlength (see 3.3.4). However when parameter \(b\) is less than 0.0, a large proportion of the diffuse PAR is incident near the horizon, and is attenuated to a greater degree than is the PAR incident from a small zenith angle for the grid points within the crown of a tree in the stand, and to a less degree for the grid points within an isolated tree crown. Therefore diffuse transmittance decreases with parameter \(b\) at a grid point within an isolated tree crown, but increases with parameter \(b\) at a grid point within the crown of a tree in the stand. If the sky radiance of diffuse PAR does not decrease with the zenith angle, the SOS is a reasonable approximation: the maximum difference of the diffuse transmittance is 3% of the transmittance under an isotropic diffuse sky \((b=0.0)\) and an overcast sky \((b=2.0)\) at a point both within an isolated tree crown and within the crown of a tree in the stand.

It is shown in Figure 3.4.2 that the hourly amounts of PAR absorption, photosynthesis and transpiration of an isolated tree crown decrease with increase in the parameter \(b\). An isolated tree crown absorbs nearly 10% more PAR during a day with a clear sky \((b=-0.9)\) than with an overcast sky \((b=2.0)\). The influence of the radiance distribution of diffuse
Figure 3.4.1 The diffuse radiance distribution in the sky. The curves are drawn from a distribution function, $(1+b \cos \theta)/(\pi+2b/3)$ with parameter $b$ of $-0.9$, $-0.5$, $0.0$, $0.5$, $1.0$, $1.5$ and $2.0$.

Table 3.4.1 The values of diffuse transmittance at thirteen grid points within the crown of an isolated tree

<table>
<thead>
<tr>
<th>$b$</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.0</td>
<td>0.35</td>
<td>0.50</td>
<td>0.37</td>
<td>0.52</td>
<td>0.40</td>
<td>0.65</td>
<td>0.44</td>
<td>0.59</td>
<td>0.50</td>
<td>0.64</td>
<td>0.61</td>
<td>0.73</td>
<td>0.83</td>
</tr>
<tr>
<td>0.0</td>
<td>0.37</td>
<td>0.52</td>
<td>0.39</td>
<td>0.53</td>
<td>0.42</td>
<td>0.56</td>
<td>0.46</td>
<td>0.60</td>
<td>0.52</td>
<td>0.65</td>
<td>0.62</td>
<td>0.73</td>
<td>0.83</td>
</tr>
<tr>
<td>-0.9</td>
<td>0.43</td>
<td>0.56</td>
<td>0.45</td>
<td>0.57</td>
<td>0.47</td>
<td>0.59</td>
<td>0.50</td>
<td>0.62</td>
<td>0.56</td>
<td>0.67</td>
<td>0.64</td>
<td>0.73</td>
<td>0.82</td>
</tr>
</tbody>
</table>

Table 3.4.2 The values of diffuse transmittances at thirteen grid points within the crown of a tree in the stand

<table>
<thead>
<tr>
<th>$b$</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.0</td>
<td>0.04</td>
<td>0.02</td>
<td>0.08</td>
<td>0.06</td>
<td>0.14</td>
<td>0.13</td>
<td>0.24</td>
<td>0.31</td>
<td>0.40</td>
<td>0.48</td>
<td>0.57</td>
<td>0.68</td>
<td>0.83</td>
</tr>
<tr>
<td>0.0</td>
<td>0.04</td>
<td>0.02</td>
<td>0.07</td>
<td>0.05</td>
<td>0.13</td>
<td>0.11</td>
<td>0.23</td>
<td>0.28</td>
<td>0.38</td>
<td>0.45</td>
<td>0.56</td>
<td>0.65</td>
<td>0.83</td>
</tr>
<tr>
<td>-0.9</td>
<td>0.03</td>
<td>0.01</td>
<td>0.05</td>
<td>0.03</td>
<td>0.09</td>
<td>0.08</td>
<td>0.18</td>
<td>0.21</td>
<td>0.32</td>
<td>0.37</td>
<td>0.53</td>
<td>0.59</td>
<td>0.81</td>
</tr>
</tbody>
</table>
Figure 3.4.2 The diurnal variations of PAR absorption (A), photosynthesis (B) and transpiration (C) by an isolated tree crown under a diffuse sky with three different diffuse radiance distributions (b=-0.9, 0.0 and 2.0).

b  curve type
-0.9  broken curve with longer interval
0.0  broken curve with shorter interval
2.0  solid curve
Figure 3.4.3 The diurnal variations of PAR absorption (A), photosynthesis (B) and transpiration (C) by the crown of a tree in the stand under a diffuse sky with three different diffuse radiance distributions ($b=-0.9, 0.0$ and $2.0$).

- 0.9 broken curve with longer interval
- 0.0 broken curve with shorter interval
- 2.0 solid curve
PAR on the transpiration of an isolated tree crown is very small ($\leq 5\%$).

It is shown in Figure 3.4.3 that the hourly amounts of PAR absorption, photosynthesis and transpiration by the crown of a tree in the stand increase with $b$. The maximum differences between the three radiance distribution are 30%, 35% and 6% for the hourly amounts of PAR absorption, and for hourly rates of photosynthesis and transpiration, respectively. The corresponding differences for the daily amounts of PAR absorption, photosynthesis and transpiration by the crown of a tree in the stand are 27%, 32% and 5%.

Radiance distribution of sky diffuse radiation has a stronger influence on photosynthesis than on PAR absorption. Compared with the SOS, photosynthetic rates of a tree crown under a sky of different radiance distribution can differ by up to 35% for a tree in a stand, and up to 32% for an isolated tree. The comparable differences for the hourly amount of PAR absorption are 30% and 10% for a tree in the stand and an isolated tree, respectively. This is because a large PAR flux is not used as efficiently as a small flux by the leaves. These results generally agree with previous studies by Cowan (1968) and Thornley (1976).

Grant (1985) showed that the radiance distribution of diffuse PAR for a clear sky has a significant influence on the transmittance of PAR in the shadow area of a tree crown. His radiance distribution for a clear sky is equivalent to a distribution with $b$ larger than the 2.0 used in this study. However, I have separated the diffuse PAR for a clear sky into two components: the circumsolar and the background components. For the distribution function of the background component, parameter $b$ has a value of -0.87 (Steven and Unsworth 1981). The results on PAR absorption agree with Grant's studies for an isolated tree. However the effect of radiance distribution on photosynthesis of an isolated tree crown is different from that of a crown in the stand. The calculated amount of photosynthesis decreases with $b$ for the former, but increases with $b$ for the latter.

3.4.1. Conclusions

1. The standard overcast sky is a good approximation of the radiance distribution of the sky for cloudy days ($b > 0.0$) but not for clear days ($b < 0.0$).

2. For an isolated tree or a tree in a sparse stand, the SOS radiance distribution underestimates the amount of PAR absorption of a tree crown and hence the photosynthesis, but overestimates PAR absorption and photosynthesis for a tree crown in a dense stand.
3.5. Influence of beam fraction on PAR absorption, photosynthesis and transpiration

As the beam and diffuse radiation are attenuated quite differently within a tree crown, the radiation regime is dependent on the beam fraction of the incident radiation. The influence of crown structure on PAR absorption, photosynthesis and transpiration depends on the beam fraction of incident PAR, as has been shown in 3.3.4 for the leaf inclination angle distribution. This has been studied for a dense Sitka spruce canopy assuming horizontal homogeneity (Jarvis et al 1985).

It is known that diffuse radiation can be more efficiently used by the plants in the field (Zelwaski et al 1973). In this study I investigate the influences of the beam fraction of incident PAR on PAR absorption, photosynthesis and transpiration by a tree crown in the stand.

Assumption

The hourly fractions of incident beam PAR are constant with values of 0.0, 0.3, 0.5, 0.7 and 1.0 during the day.

Results and discussion

MAESTRO was used to calculate the hourly and daily amounts of PAR absorption, photosynthesis and transpiration by a tree crown in the stand for each of five days with different hourly beam fractions. The results are presented in Fig. 3.5.1 which shows that the hourly amount of PAR absorption increases with beam fraction at any sun zenith angle. Over the range of the angles studied, beam PAR is absorbed 40% more than diffuse PAR by the tree crown, and this difference is larger at large solar zenith angle. This result agrees with previous study (see 3.3.1).

Figure 3.5.1 shows that beam fraction has a strong influence on rate of photosynthesis, which decreases with increase in beam fraction in opposition to the increase on PAR absorption. This is also shown in Table 3.5.1, where the daily light use efficiency of the tree crown is shown to decrease with increase in beam fraction. The daily light use efficiency of diffuse PAR is twice that of beam PAR. This agrees with other simulation studies (Allen et al 1974, Oker-blom 1985, Jarvis et al 1985).

Figure 3.5.1 shows that the hourly rate of transpiration also decreases with beam fraction. When the beam fraction lies between 0.0 and 0.50 and the zenith angle of the sun is not greater than 80.0°, the
Figure 3.5.1 The diurnal courses of PAR absorption (A), photosynthesis (B) and transpiration (C) by the crown of a tree in the stand when the hourly beam fraction of incident PAR varies from 0.0 to 1.0.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Beam Fraction</th>
</tr>
</thead>
<tbody>
<tr>
<td>x</td>
<td>0.0</td>
</tr>
<tr>
<td>+</td>
<td>0.3</td>
</tr>
<tr>
<td>□</td>
<td>0.5</td>
</tr>
<tr>
<td>◆</td>
<td>0.7</td>
</tr>
<tr>
<td>○</td>
<td>1.0</td>
</tr>
</tbody>
</table>
differences are less than 10\%, but the difference can be as large as 40\% when the beam fraction changes from 0.50 to 1.0. The influence of the beam PAR on transpiration does not vary much with the zenith angle of the sun.

Table 3.5.1 The light use efficiency of a tree crown during a day with different beam fractions

<table>
<thead>
<tr>
<th>Fb</th>
<th>0.0</th>
<th>0.3</th>
<th>0.5</th>
<th>0.7</th>
<th>1.0</th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>0.039</td>
<td>0.036</td>
<td>0.030</td>
<td>0.025</td>
<td>0.020</td>
</tr>
</tbody>
</table>

Note: light use efficiency, a, was calculated as the molar ratio of the amount of photosynthesis to the amount of PAR absorbed during the daytime.

Conclusions

The following conclusions can be drawn from this study:

1. The amount of PAR absorbed by a tree crown increases with beam fraction.

2. The hourly rates of photosynthesis by a tree crown decrease with beam fraction, and this effect becomes stronger when beam fraction is larger.

3. The hourly amount of transpiration by a tree crown decreases with beam fraction, and this effect is much stronger when beam fraction is larger than 50\%.