5. PAR ABSORPTION AND ITS RELATION TO DRY MATTER PRODUCTION OF THE SITKA SPRUCE

5.1. Introduction

Since Monteith (1972) put forwards his hypothesis that the dry matter production of above-ground biomass is proportional to its interception of radiation, this hypothetic linear relationship has been demostrated for a number of agricultural crops (e.g. Gallagher and Biscoe 1974, Coulson 1985), and for a few tree species (Linder 1984, Cannell et al 1986). However, some studies have shown that this linear relationship can be modified by environment and stresses, such as water stress and nutrient deficiencies (Gallagher & Biscoe 1974, Byrne et al 1986). Our understanding of this linear relationship is of great importance in forest management, as one major objective of forest management is to increase the productivity of the above-ground biomass. In this study, PAR absorption by the stand is derived from measurements and is related to estimated increments of the above-ground biomass for six plots of Sitka spruce with different fertilizers and thinning treatments.

5.2. Description of the experimental site

This study was carried out in a Sitka spruce stand. The forest belongs to the Forestry Commission who laid out a replicated (*4) thinning and fertilizer trial in 1984 when the stand was 16 years old. The site is near Tummel Bridge, about eighty miles to the North of Edinburgh. A description of the local climate has been presented in Chapter 2. Six plots of 0.04 ha were chosen, and three of them were thinned at the beginning of 1985. Fertilizers (phosphorus or nitrogen) have been applied to two thinned and two unthinned plots before the growing season every year. The average slope of the ground surface within a plot is less than 5°. The average tree height of a plot varied from 8 to 10 m in October of 1987. The average NAI of the unthinned plots was ca 3.6 at the beginning of 1985 and increased to ca 5.4 in October of 1987, the average NAI of the unthinned plot was ca 5.8 at the beginning of 1985 and increased to ca 8.0 in October of 1987 (see Table 5.2.1 for more details), as estimated from the regression relation between total leaf area of a tree and its diameter at breast height (see Chapter 2).
Table 5.2.1 General information about six plots in a Sitka spruce stand near Tummel Bridge

<table>
<thead>
<tr>
<th>plot</th>
<th>treatment</th>
<th>NAI</th>
<th>basal area (m² ha⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>NT</td>
<td>3.44</td>
<td>3.96</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4.66</td>
<td>5.52</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8.35</td>
<td>8.97</td>
</tr>
<tr>
<td>10</td>
<td>PO</td>
<td>5.96</td>
<td>7.64</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8.29</td>
<td>9.09</td>
</tr>
<tr>
<td></td>
<td></td>
<td>9.79</td>
<td>11.28</td>
</tr>
<tr>
<td>11</td>
<td>OT</td>
<td>5.08</td>
<td>5.65</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6.25</td>
<td>7.04</td>
</tr>
<tr>
<td></td>
<td></td>
<td>7.85</td>
<td>9.35</td>
</tr>
<tr>
<td>12</td>
<td>NO</td>
<td>5.29</td>
<td>6.02</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6.90</td>
<td>7.91</td>
</tr>
<tr>
<td></td>
<td></td>
<td>9.71</td>
<td>11.55</td>
</tr>
<tr>
<td>14</td>
<td>PT</td>
<td>3.62</td>
<td>4.11</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4.72</td>
<td>5.44</td>
</tr>
<tr>
<td></td>
<td></td>
<td>7.01</td>
<td>8.12</td>
</tr>
<tr>
<td>15</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

N, P and Ψ represents nitrogen, phosphorus fertilization and thinning, respectively. The NAI was estimated from the relationship between the area of leaves within the tree crown and the diameter at breast height of that tree.

5.3. Data collection and analysis

PAR transmittances were measured at five locations in each plot by quantum sensors distributed uniformly below the canopy. The incident solar radiation, near-infra red radiation, PAR, net radiation and the canopy reflectance of PAR were measured by Kipp solarimeters, a quantum sensor, a Funk-type net radiometer and an inverted quantum sensor, respectively, all of which were installed on the top of a tower in the stand (see Chapter 2 for more details).

The overbark diameters at breast height of trunks (Dₜ) of all the trees in all six plots were measured before or after the growing season every year during this study. The frequency distributions of basal area at breast height of the trees within the six plots are shown in Fig. 5.3.1.

The total area indices of both needles and woody parts were measured before and after the growing season of 1987 for all six plots, and in 1986 for Plot 15 only using the beam transmittance sensor (Lang et al. 1985, Lang 1987). The NAI of the plot was also estimated by summing the leaf area of all the individual trees in a plot estimated from the relation with Dₜ (see Chapter 2). A comparison of the estimates of NAI from these two methods is shown in Fig. 5.3.2. It was assumed that the area index of the woody part was 10% of the total area index of needles and woody parts estimated using the beam transmittance sensor. Discrepancies between these two estimates mainly result from the limited range of zenith angle at which it was possible to measure beam transmittances. The agreement is extremely good (less than 6% difference) for Plot 15 where the beam transmittances were measured over a wide range of zenith angles of the sun.
Some data were lost as a result of sensor or logger failure. If the number of days' data that were lost was less than fourteen days, the lost data were substituted with the most recent data collected before or after the failure; otherwise the lost data were substituted with the data collected during the same period of another year. The amount of incident PAR during the growing season (from May to October) constituted of more than 70% of the annual amount of incident PAR. Complete sets of data were collected during the growing seasons in this study except for August, 1986 when one month's data were lost because of limitations of the CR7 data logger. The logger was upgraded to the CR7X specification after that failure.

5.4. Some relationship between different radiant fluxes

PAR is usually a conservative fraction of the total incident solar radiation (Szeicz 1974), but this fraction may vary with climate. Some of the incident solar radiation is transmitted, and some is reflected back to the atmosphere and some is absorbed by the canopy, depending on its structure. The amount of net radiation available to the canopy may vary with canopy structure (Gay 1971) with the incident radiation (Ross 1981) and with canopy and atmospheric temperature. The interrelationship between the different radiant fluxes are discussed here.

5.4.1. The relationship between PAR and solar radiation

The incident solar radiation mainly consists of PAR and NIR radiation. The relative fractions of these two components are affected by beam fraction, weather condition and the incident angle of the incoming solar radiation. In general, the fraction of PAR radiation is less than 45% in the beam solar radiation, but about 65% in the diffuse solar radiation. As the climate in central Scotland is rather wet and cloudy, the average fraction of PAR in the incident solar radiation would be expected to be high. As shown in Fig. 5.4.1.1, variations of the daily values of $I_o/I_g$ and $I_o/I_g'$ are larger at the beginning and the end of
the year than those during the remainder of the year. This is most obvious in the data collected in 1987. The seasonal variation of \( I_0/I_g \) generally agrees with the data presented by Szeicz (1974). The daily fraction of visible radiation is higher in the summer than in the winter or spring because the fraction of visible radiation decreases with the zenith angle of the sun (Ross 1976), and the average zenith angle of the sun is smaller in the summer. The larger variations of \( I_v/I_g \) and \( I_0/I_g \) in the winter and early spring may result from the more erratic changes of weather conditions then than during the summer.

Based on the daily data collected in this study, but excluding the data collected during snowy periods, the following relations were obtained.

<table>
<thead>
<tr>
<th>Year</th>
<th>Regression Coefficients</th>
<th>( r )</th>
<th>Ratio</th>
<th>S.D.</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>83</td>
<td>0.1437</td>
<td>0.52</td>
<td>0.99</td>
<td>0.55</td>
<td>0.004</td>
</tr>
<tr>
<td>84</td>
<td>-0.1097</td>
<td>0.60</td>
<td>0.99</td>
<td>0.58</td>
<td>0.003</td>
</tr>
<tr>
<td>87</td>
<td>-0.0939</td>
<td>0.60</td>
<td>0.99</td>
<td>0.59</td>
<td>0.002</td>
</tr>
<tr>
<td>All</td>
<td>-0.0740</td>
<td>0.59</td>
<td>0.99</td>
<td>0.59</td>
<td>0.002</td>
</tr>
<tr>
<td>85</td>
<td>0.2210</td>
<td>2.07</td>
<td>0.99</td>
<td>2.12</td>
<td>0.010</td>
</tr>
<tr>
<td>86</td>
<td>1.2325</td>
<td>1.94</td>
<td>0.99</td>
<td>2.11</td>
<td>0.022</td>
</tr>
<tr>
<td>87</td>
<td>0.3130</td>
<td>2.01</td>
<td>0.99</td>
<td>2.14</td>
<td>0.022</td>
</tr>
<tr>
<td>All</td>
<td>0.2971</td>
<td>2.02</td>
<td>0.99</td>
<td>2.08</td>
<td>0.005</td>
</tr>
</tbody>
</table>

\( a, b \) are two regression coefficients in the linear regression equation \( I_v(t) = a + bI_g(t) \) (the first four lines) or \( I_0(t) = a + bI_g(t) \) (the last four lines), where \( I_v, I_0 \) and \( I_g \) are PAR flux in J m\(^{-2}\) \( \text{day}^{-1} \), PAR flux density in mol m\(^{-2}\) \( \text{day}^{-1} \) and incoming solar radiation in J m\(^{-2}\) \( \text{day}^{-1} \), respectively. The ratios were calculated as \( I_v(t)/I_g(t) \) (the first four lines) or \( I_0(t)/I_g(t) \) (the last four lines). \( n \) is the number of days.

The coefficients in the linear regression relation and the ratios in 1986 and 1987 are very close, but slightly different from in 1985. That may result from the yearly variation of the climate.
Figure 5.4.2.1 Variation of ratio of daily total amount of net radiation ($I_{net}$) to the incident solar radiation ($I_o$) above the canopy at the different time of the year.

Figure 5.4.1.1 Variations of the daily (solid curves) and monthly (broken curves) fraction of PAR ($I_o$) in incident solar radiation ($I_o$) and variation of the ratio daily (solid curves) and monthly (broken curves) amount of PAR ($I_o$) to the incident solar radiation above the canopy measured during this study.
5.4.2. The relationship between net radiation and solar radiation

Net radiation measured above the canopy is the difference between all the downwards and upwards fluxes of solar and long-wave radiation. It depends on the weather conditions above the canopy, canopy architecture, and both the optical properties and temperature of the canopy and of the soil surface.

Measurements of net radiation ceased after June, 1986. Based on the daily data collected in this study, but excluding the data collected during snowy periods, the following relations were obtained.

\[ I_{\text{net}}(t) = 0.16 + 0.66I_g(t) \quad r = 0.99 \quad n = 207 \]

\[ I_{\text{net}}(t)/I_g(t) = 0.68 (\pm 0.0041) \quad n = 207 \]

The value of intercept parameter of 0.16 can be taken as the average effective thermal (or long wave) radiation at sunrise and sunset (Ross 1981). The daily average ratio of \( I_{\text{net}}/I_g \) is less than that obtained for other Sitka spruce and coniferous canopies (Jarvis et al 1976). Some of this discrepancy can be attributed to the bias arising from the use of daily data as a relatively large ratio would be expected at a large zenith angle of the sun when the flux density of incident radiation is only a small fraction of the daily total.

The linear regression relation between \( I_{\text{net}}(t) \) and \( I_g(t) \) based on the daily data practically is not as useful as the ratio of \( I_{\text{net}}(t)/I_g(t) \), as the linear regression relationship includes the variation of daylength during the year in the intercept parameter.

The daily average values of \( I_{\text{net}}/I_g \) are strongly influenced by the snow in the winter season as shown in Fig. 5.4.2.1. The value of \( I_{\text{net}}/I_g \) can decrease down to 0.1 because of the high reflectance of the canopy surface covered with snow. Snow on the sensors may also make some of these values unreliable.

5.4.3. Conclusions

From this study, the following conclusions can be drawn:

1. The daily fraction of visible radiation in the solar radiation varies from 40% to 60% with an average daily value of 50%, and this fraction is more variable during the winter than during the summer. The ratio of incident quantum flux to incident solar radiation varies from 1.8 to 2.4 with an mean of 2.08. The yearly variations of both ratios are similar.

2. The net radiation is closely related to the incident short-wave
radiation with a daily mean ratio \( \frac{I_{\text{net}}}{I_g} \) of 0.68.

5.5. Estimation of PAR absorption

The average amount of PAR absorbed by the canopy, \( \sum_{t=1}^{n} Q_g(t) \), can be estimated as

\[
\sum_{t=1}^{n} Q_g(t) = \sum_{t=1}^{n} I_g(t)(1.0-T_g(t)-\rho_c+T_d(t)\rho_s)
\]

where \( T_g(t) \) is the daily transmittance of incident PAR through the canopy of day \( t \), \( T_d(t) \) the daily transmittance of diffuse PAR through the canopy of day \( t \), \( \rho_c \) the canopy reflectance for PAR, \( \rho_s \) the reflectance of the soil surface for PAR.

\( T_g \) was measured. The mean transmittance over a period was calculated as the ratio of the amount of PAR transmitted to the amount of incident PAR. The monthly mean transmittance during a year was maximal during April and minimal during the September in 1987 (see Fig. 5.5.1). This may result from interactions between seasonal variations of weather conditions and canopy structure.

The hourly mean transmittance usually decreases with the zenith angle of the sun (see Chapter 2). Even though the zenith angle of the sun is smallest during June, the monthly mean transmittance was less than in April. The explanation for this may be that the average beam fraction in June was higher. The transmittance of beam radiation is smaller than that of diffuse radiation and therefore when the beam fraction is large, the mean transmittance may not be as large as expected. Another possible explanation is that trees started shooting during May, and therefore the NAI of the canopy was larger in June than in April. Growth of current needles has usually stopped by August for Sitka spruce in Scotland. Thus in September the NAI of the canopy is maximal and in September the mean beam fraction of incident solar radiation was still large compared with that in the winter and the spring; this may be the reason for the lowest monthly mean transmittance in September, 1987.

The yearly mean values of daily transmittance of PAR decreased as the canopy became denser, as shown in Fig. 5.5.2. Even though the canopy structure is quite different among the six plots, the annual variation of monthly mean transmittances of the six canopies is very similar as shown in Fig. 5.5.2. All six plots had smaller transmittances in June, 1986 than in May or July, for the reason discussed above.
During this study, $\rho_C$ was constant with a value of 0.04, and did not show any daily or seasonal variation. The canopy albedo of PAR can be approximately calculated as (Ross 1981):

$$\rho_C = 0.5\rho (1.0 - \exp(-2L_c)) + \rho_C \exp(-2L_c)$$

In this study, $L_c$ was larger than 3.5 and therefore $\rho_C$ is approximately equal to $0.5\rho$. The average value of $\rho$ for Sitka spruce needle is 0.08 (Norman and Jarvis 1974), so that $\rho_C$ would be expected to be 0.04. That figure closely agrees with the measured value.

The annual totals of PAR absorbed in the six plots during 1985, 1986 and 1987 are presented in Table 5.5.1.

<table>
<thead>
<tr>
<th>plot</th>
<th>1985</th>
<th>1986</th>
<th>1987</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>39.767</td>
<td>54.862</td>
<td>60.744</td>
</tr>
<tr>
<td>10</td>
<td>42.745</td>
<td>57.434</td>
<td>62.108</td>
</tr>
<tr>
<td>11</td>
<td>42.237</td>
<td>57.281</td>
<td>61.950</td>
</tr>
<tr>
<td>12</td>
<td>38.146</td>
<td>52.444</td>
<td>58.324</td>
</tr>
<tr>
<td>14</td>
<td>42.249</td>
<td>57.251</td>
<td>61.874</td>
</tr>
<tr>
<td>15</td>
<td>34.640</td>
<td>51.113</td>
<td>58.034</td>
</tr>
</tbody>
</table>

The amount of PAR absorbed by a plot in 1985 was calculated from 24th, April, 1985, when the thinning and fertilization had been carried out. As the radiation measurements did not commence until 21st, May, 1985, the amount of incident radiation from 24th, April, 1985 to 21st, May, 1985 was estimated as the average of incident radiation over the same period in 1986 and 1987. The average transmittances ($T_a$) of a plot was assumed to be the same as the mean transmittance of that plot during 21st, May, 1985 to 21st, June, 1985. The dimension of the absorbed PAR is Mmol ha$^{-1}$ yr$^{-1}$. 
Table 5.6.1 The estimated above-ground biomass after the growing seasons of 1985, 1986 and 1987 and the annual increments for six plots in a Sitka spruce stand

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>66.32</td>
<td>79.81</td>
<td>99.20</td>
<td>8.83</td>
<td>13.49</td>
<td>19.40</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>144.14</td>
<td>161.14</td>
<td>184.08</td>
<td>15.99</td>
<td>17.00</td>
<td>22.94</td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>103.13</td>
<td>115.35</td>
<td>133.01</td>
<td>10.65</td>
<td>12.23</td>
<td>17.65</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>71.07</td>
<td>79.34</td>
<td>92.35</td>
<td>6.57</td>
<td>8.27</td>
<td>13.01</td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>111.86</td>
<td>131.34</td>
<td>156.93</td>
<td>14.44</td>
<td>19.48</td>
<td>25.59</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>69.93</td>
<td>82.39</td>
<td>99.04</td>
<td>8.81</td>
<td>12.47</td>
<td>16.64</td>
<td></td>
</tr>
</tbody>
</table>

Table 5.6.2 The estimates of regression coefficients, a, b and the 95% confidence limits of different treatments, and all six plots together

"S" represents a significant difference between two treatments, "N" represents no significant difference between two treatments.

<table>
<thead>
<tr>
<th>a</th>
<th>b</th>
<th>limit *</th>
<th>r</th>
<th>n</th>
<th>&quot;t&quot; test</th>
</tr>
</thead>
<tbody>
<tr>
<td>plot 9</td>
<td>-10.20</td>
<td>0.4654</td>
<td>0.1524</td>
<td>0.95</td>
<td>3</td>
</tr>
<tr>
<td>plot 10</td>
<td>3.00</td>
<td>0.2892</td>
<td>0.2332</td>
<td>0.78</td>
<td>3</td>
</tr>
<tr>
<td>plot 11</td>
<td>-2.30</td>
<td>0.2937</td>
<td>0.2017</td>
<td>0.82</td>
<td>3</td>
</tr>
<tr>
<td>plot 12</td>
<td>-4.70</td>
<td>0.2820</td>
<td>0.1549</td>
<td>0.88</td>
<td>3</td>
</tr>
<tr>
<td>plot 14</td>
<td>-7.65</td>
<td>0.5110</td>
<td>0.1876</td>
<td>0.94</td>
<td>3</td>
</tr>
<tr>
<td>plot 15</td>
<td>-2.42</td>
<td>0.3143</td>
<td>0.0876</td>
<td>0.96</td>
<td>3</td>
</tr>
<tr>
<td>plots with N</td>
<td>-10.58</td>
<td>0.5200</td>
<td>0.0956</td>
<td>0.84</td>
<td>6 S</td>
</tr>
<tr>
<td>plots without N</td>
<td>-4.15</td>
<td>0.3440</td>
<td>0.1653</td>
<td>0.70</td>
<td>12 S</td>
</tr>
<tr>
<td>thinned plots</td>
<td>-5.70</td>
<td>0.3540</td>
<td>0.1111</td>
<td>0.82</td>
<td>9 N</td>
</tr>
<tr>
<td>unthinned plots</td>
<td>-2.42</td>
<td>0.3660</td>
<td>0.0948</td>
<td>0.67</td>
<td>9 N</td>
</tr>
<tr>
<td>all six plots</td>
<td>-6.58</td>
<td>0.4092</td>
<td>0.1517</td>
<td>0.73</td>
<td>18</td>
</tr>
</tbody>
</table>

*: this is the 95% confidence limit of coefficient b.
5.6. The relationship between PAR absorption and above-ground biomass production

The maximum above-ground dry biomass production recorded for a pole-stage Sitka spruce stand is 25 tons ha\(^{-1}\) a\(^{-1}\) (Ford 1982). The production can be affected by the stocking density, stand age and environment. The above-ground biomass of a stand is closely related to its basal area. Mitchell et al (1981) found the following relationship from harvest data for young Sitka spruce stands at an age of 13 to 22 years, yield class of 10 to 28 and stocking density of 2520 to 4160 trees ha\(^{-1}\),

\[
G = 2.30985B_s + 0.0218B_s^2 + 5.90025
\]

where \(G\) is the above-ground biomass in tonnes ha\(^{-1}\), \(B_s\) is the basal area of the stand in m\(^2\) ha\(^{-1}\). This relation is shown in Figure 5.6.1.

The Sitka spruce stand studied here was 16 to 19 years old with yield class 22 (C. Taylor, Forestry Commission, Personal communication). Therefore it is justifiable to use the above equation to estimate the above-ground biomass production.

The frequency distributions of basal area of the trees in the six plots are shown in Fig. 5.3.1 for 1985 to 1987. The corresponding values of above-ground biomass and the annual increments of biomass during the study period are presented in Table 5.6.1.

The annual production of above-ground dry biomass is plotted against the annual PAR absorbed in Fig. 5.6.2 for the six plots. A linear regression, \(G(t) = a + bQ(t)\), was fitted to the data collected for each plot with the different treatments and to all the data of the six plots together (see Table 5.6.2). The "t" test was used to test whether there are significant differences between the different treatments and the results are presented in Table 5.6.2.

Only Plot 10 has a positive value of the intercept parameter \(a\) and that is associated with the lowest correlation coefficient. The negative values of coefficient \(a\) can be ascribed to the dry-matter production of below-ground biomass (Linder 1984). The slope, coefficient \(b\) varies from 0.28 to 0.51 g mol\(^{-1}\), giving a solar radiation conversion efficiency of 1.2% to 2.0% (see Jarvis & Leverenz 1982). The average conversion efficiency for all six plots is about 1.6%. This is only half of that obtained for agricultural crops (e.g. Gallagher and Biscoe 1978).

The slope of the dry matter:PAR absorption quotient is not significantly affected by thinning, but is strongly influenced by nitrogen fertilization. The plots with nitrogen fertilizer have a significantly higher above-ground biomass production for the same amount.
Figure 5.6.1 The relation between the above-ground biomass in dry weight (G) and the basal area of the Sitka spruce stand (B_5). The curve is drawn from a relation obtained by Mitchell et al (1981): 
G=2.30985B_5+0.0218B_5^2+5.90025, where G in tons ha^{-1}, and B_5 in m^2 ha^{-1}, the vertical bars at each point on the curve are 95% confidence limits of G at a B_5.

Figure 5.6.2 Variation of the annual production of above-ground biomass (ΔG) with PAR absorption (Q_5) for six plots with different treatments in a Sitka spruce stand.
of PAR absorbed, as also found in wheat (Gallagher & Biscoe 1978). Nitrogen stress can reduce needle photosynthesis and the production of needle area, and may possibly also change the needle age structure (see Chapter 1). Thus reducing both PAR absorption and photosynthetic efficiency. Therefore, a higher canopy photosynthesis, for the same amount of PAR absorbed, may account for the larger value of the dry matter: radiation absorption quotient for the fertilized plot than that for the plot without fertilization.

5.7. Conclusion and discussion

This study has shown that the dry matter: PAR absorbed quotient of a Sitka spruce stand is significantly affected by nitrogen fertilization, but not by thinning. The average solar energy conversion efficiencies are 2.0% and 1.2% for a Sitka spruce plot with and without nitrogen fertilization, respectively. As the data were only collected for three years, more data would be necessary to warrant of this conclusion.

As expected by Jarvis and Leverenz (1982), the energy conversion efficiency of the Sitka spruce stand was found not to change with the amount of PAR absorbed, but to be altered by stresses. The difference between the potential and the actual solar energy conversion efficiency results from non-optimal conditions of environment and from the trees themselves. Madgwick et al (1977) found that the solar energy conversion efficiency of a radiata pine stand increased after thinning, possibly as a result of the improved water conditions in the soil of the thinned stand. But water supply may not be stressful for the Sitka spruce stand studied so that thinning has had little effect on the energy conversion efficiency of the stand. Nitrogen has often been found to be an important determinant of leaf photosynthesis and hence of tree growth. Even though both thinning and nitrogen fertilization increase the area of leaves on a tree, and hence the PAR interception, nitrogen fertilization can enhance the photosynthetic activities of the leaves much more than does thinning. Thinning can only improve the PAR regime within the canopy and enable the leaves in the lower part of the canopy to intercept more PAR, with the result that the dry matter production of the above-ground biomass will also increase so that the solar energy conversion efficiency is not significantly changed.

This study has shown the growth of Sitka spruce trees studied without nitrogen fertilization suffered from nitrogen deficiency that diminishes the solar energy conversion efficiency of the stand by 40%. It seems likely that substantial economic benefits would result from the controlled application of nitrogen to Sitka spruce stands in the U.K.. Further experimentation is justified to see whether the actual productivity would be increased to that of agricultural crops.
6. GENERAL DISCUSSION

Conceptual models have become useful tools for studying the contribution to tree growth of a number of partial processes. Following Jarvis & Leverenz (1982), the energy conversion efficiency of a stand, $\varepsilon$, is defined as the amount of above-ground dry matter produced per unit amount of PAR absorbed, and can be split into a number of factors, each representing a specific partial process, i.e.

$$\Delta G / \Delta Q_g = \varepsilon = f a v Y_m Y_g d$$

where $\Delta G$ and $\Delta Q_g$ are the production of above-ground dry matter and the absorption of incident PAR by the stand canopy over the same period, respectively; $f$ is the fraction of incident PAR absorbed by the canopy; $a$ is the canopy photosynthetic efficiency, defined as the ratio of the sum of day time net photosynthesis plus night time respiration over a period longer than one day to the amount of PAR absorbed by the canopy over the same period; $v$ is the proportion of assimilate allocated to the above-ground biomass; $Y_m$ is the proportion of the assimilate not used in maintenance respiration by the above-ground biomass; $Y_g$ is the proportion of the assimilate not used in growth respiration by the above-ground biomass; and $d$ is the proportion of the assimilate not lost in litter fall, insect attack and so on. Canopy structure can strongly affect radiation regime and radiation-dependent partial processes of tree growth within the canopy, this is direct influence, some partial processes of tree growth are little affected by the canopy structure directly, but are affected by a partial process that is strongly dependent on the canopy structure, that is indirect influence. Canopy structure has direct effects on $f$ and $a'$ (see Chapters 1, 3 and 4) and possibly indirect effects on all the other four factors.

For a dense canopy with leaf area index larger than 6.0, $f$ approaches its limit for PAR (0.9 for a Sitka spruce canopy) and is rather insensitive to the structural properties of the canopy. Factor $a$ is determined by the quantum yield of the leaves and the degree of co-limitation of canopy photosynthesis by RuBP carboxylase activity and potential electron transport rate. The degree of co-limitation is, in turn, dependent on both canopy structure and photosynthetic activities of the leaves within the canopy. Compared with canopies of agricultural crops, a coniferous forest canopy has two important structural characteristics: the heterogeneous distribution of leaves within the canopy space and the complex age structure of the leaf population.

Direct influences of canopy structure on factors $f$ and $a$ have been discussed in previous chapters. In conclusion, $f$ is strongly dependent on the $L_c$ of the canopy, and $a$ is strongly affected by the leaf area density distribution within the canopy. The particular structure
of the Sitka spruce canopy results in an efficient use of incident PAR. However, direct influences become quite small after canopy closure (see Chapter 1).

Data about indirect influences of canopy structure on any of the other four factors are very sparse. Because dry matter production of above-ground biomass of a stand is proportional to PAR interception by the canopy, the indirect influences of canopy structure before the onset of between-tree competition, are, at least, not as important as the direct influences if incident PAR is the primary factor limiting canopy photosynthesis and hence stand productivity. After canopy closure, indirect influences become much more important. If the actual solar energy conversion efficiency of the canopy does not change significantly after canopy closure, the annual dry matter production of above-ground biomass is determined by the annual amount of incident PAR not affected directly or indirectly by canopy structure. Partitioning of the assimilate among different organs of above-ground and below-ground biomass is very important, as the stem-wood is the valuable, harvestable product. The indirect influences of canopy structure on stem-wood production therefore warrant attention. It has been suggested in Finland (Karki & Tigerstedt 1985) that genotypes with narrow crowns would be ideal for stem-wood production, as a stand of such trees would have a uniform PAR regime, leaf shedding would be minimized and more assimilate could be invested in stem-wood production. This suggestion, however, remains to be tested in practice, since stands of narrow-crowned genotypes have only recently been planted. Simulation results of MAESTRO do, however, suggest that such a stand has a high photosynthetic rate.

Both direct and indirect influences of canopy structure can be moderated by the atmospheric environment and by the availability of water and nutrients in the soil. The Scots pine trees in an irrigated and fertilized experimental plot in Sweden allocated only 31% of their assimilate to roots compared with 59% in the untreated trees (Linder and Axelsson 1982). Thus stress modifies canopy structure so that the trees make use of the limiting resources more efficiently. Canopy structure is, therefore, subject to acclimation to environment as well as to genetic adaptation. However, no studies have yet been made on the adaptive structure of a coniferous canopy.

The dynamics of the Sitka spruce canopy also deserve more attention. Seasonal variation of canopy structure will affect all the six partial processes of tree growth, and this should be included in MAESTRO so that it can be used to study the canopy processes over one or two years period. Because foliage is grouped on to shoots, and shoots on to branches, an appropriate approach would be to link the branching dynamics with foliage dynamics in studying canopy dynamics: a large amount of data would be needed to build this linkag
quantitatively. Unfortunately there are few data so that many field measurements will need to be made to allow this approach.
Appendix 4.A: Parameterization of a photosynthesis model for predicting canopy photosynthesis

In predicting the photosynthesis of a canopy, $C_i$ for the leaf is unknown, therefore $C_i$ has to be eliminated from equations in 4.2.

$C_i = C_a - P_n / g_t$ \hspace{1cm} 4.A.1

When the leaf photosynthetic rate is limited by Rubisco, the photosynthetic rate, $P_{nc}$, can be calculated as:

$P_{nc} = C_i V_{cmax} (1.0 - \Gamma^a / C_i) / (C_i + k_m) - R_d$ \hspace{1cm} 4.A.2

By substituting 4.A.1 into 4.A.2, we have a quadratic equation with only one variable, $P_{nc}$, that is:

$p_{nc}^2 + B_1 p_{nc} + C_1 = 0.00$ \hspace{1cm} 4.A.3

with

$B_1 = g_t (C_a + k_m) + R_d V_{cmax}$, and

$C_1 = g_t (C_a V_{cmax} \Gamma^a V_{cmax} - C_a R_d k_m R_d)$

$P_{nc}$ is the smaller solution of equation 4.A.3.

When the leaf photosynthetic rate is limited by the potential electron transport rate, Equation 4.2.6 is combined with 4.A.1 to obtain $P_{ne}$, and $P_{ne}$ is then the smaller solution of

$A_2 p_{ne}^2 + B_2 p_{ne} + C_2 = 0.0$

where $A_2 = -4.5 / g_t$,

$B_2 = -4.5 / g_t + J / g_t + 4.5 C_a - 10.5 \Gamma^a$

$C_2 = R_d (4.5 C_a - 10.5 \Gamma^a) - J (C_a - \Gamma^a)$

and $J$ is calculated from equation 4.2.2.
The actual photosynthetic rate of the leaf, $P_n$, is the smaller value of $P_{nc}$ and $P_{ne}$, i.e.

$$P_n = \min\{P_{nc}, P_{ne}\}$$
Appendix 4.B: The silhouette area of a shoot

I have presented a method for calculating the silhouette area of a shoot (SAS) inside the leaf chamber in 4.7.2, where the angle between the illumination direction and shoot axis is 90°. A shoot in the forest canopy is exposed to both beam and diffuse radiation, and may be inclined at any angle from the horizontal, so that determination of SAS for a shoot in the forest canopy is significantly more difficult than for a shoot in the leaf chamber.

Consider a shoot located above the x, y-plane, and illuminated by a parallel beam from the z direction. The shoot axis lies within the x, z-plane, and the end of shoot axis is attached to the z axis (see Figure 4.B.1). The angle between the shoot axis and the positive z axis is $\gamma$, $\alpha_f$, $\beta_f$ denote the angle between the needle surface and the shoot axis, and the needle orientation angle relative to the direction of illumination, respectively. $\alpha_f$, $\beta_f$ denote the inclination angle of the needle to the x, y-plane and the angle between the positive x axis and the projection of that needle on the x, y-plane. The relations among those angles are:

$$\sin\alpha_f = \cos\alpha_f \cos\gamma + \sin\alpha_f \sin\beta_f \sin\gamma$$

$$\cos\beta_f = (\cos\alpha_f - \cos\gamma \sin\alpha_f) / (\sin\gamma \cos\alpha_f)$$

Because of the symmetry, I only consider the projection of needles with orientation of 0.0 to $\pi$.

The projection of the needle tip on to the x, y-plane is a point $P(t, l_n \cos\alpha_f \cos\beta_f, l_n \cos\alpha_f \sin\alpha_f)$, where $t$ is distance from the origin to the projection of the needle end on the...
x, y-plane. Therefore the projection of all needles on the x, y-plane is inside the region of a square ABCD (see Fig. 4.B.1), the length of AB is \( L_s \sin \gamma + 2.0 l_n \), and the width AC is \( l_n \).

To calculate SAS, square ABCD is then divided into 2000 small squares with length of 0.01AB and width of 0.05AC, and a point \( P(x, y) \) is located in the middle of each small square.

Needles on the shoot are divided into 18 orientation angle classes. The projection of all needles within an orientation angle class \( i \) is assumed to be uniformly distributed within a parallelogram ABC'D'. If a point \( P(x, y) \) is inside ABC'D', the projected needle area density from needles in the orientation angle class \( i \) at point \( P \) is \( N_s d_n/(36 \cos \gamma \sin \beta_f) \).

The conditions under which point \( P(x, y) \) is inside ABC'D' are:

\[ a. \quad y < l_n \cos \alpha_f \sin \beta_f \]
\[ b. \quad 0.0 < x < (L_s \sin \gamma + l_n \cos \alpha_f \cos \beta_f) \quad \text{if} \quad \beta_f < \pi/2 \]
\[ l_n \cos \alpha_f \cos \beta_f < x < l_n \sin \alpha_s \quad \text{otherwise} \]
\[ c. \quad y/x < \tan \beta_f \quad \text{if} \quad x < L_s \sin \gamma, \quad \beta_f < \pi/2 \]
\[ y/(x-L_s \sin \gamma) > \tan \beta_f \quad \text{if} \quad x > L_s \sin \gamma, \quad \beta_f < \pi/2 \]
\[ y/(x-L_s \sin \gamma) > \tan \beta_f \quad \text{if} \quad x > 0.0 \quad \text{and} \quad \beta_f > \pi/2 \]
\[ y/x < \tan \beta_f \quad \text{if} \quad x < 0.0 \quad \text{and} \quad \beta_f > \pi/2 \]

The gap fraction within each small square, \( g(x, y) \), is given by

\[ g(x, y) = \exp(-\sum_{i} d_i \delta_i) \]

where \( d_i \) is equal to \( N_s d_n/(36 \cos \gamma \sin \beta_i) \), and

\[ \delta_i = 1.0 \quad \text{if point } P(x, y) \text{ is inside ABC'D'} \]
\[ \delta_i = 0.0 \quad \text{otherwise} \]

The silhouette area of a shoot \( S_s(\gamma) \) is given by

\[ 2.0 \int_{S} (1.0 - g(x, y)) dx dy \]

where \( S \) is the region of ABCD.
Symbols and their definitions

Capital letters

\( A_c \): the tree crown silhouette area on a plane normal to the wind direction per unit ground area in the stand.

\( A_s \): the area of a tree crown projection on a plane normal to the direction of incident radiation (\( m^2 \)).

\( B_i \): parameters in the NAD distributions within the tree crown or canopy (\( i=1, 2 \) and 3 for the vertical NAD distribution and 4, 5 and 6 for the horizontal NAD distribution)

\( B_s \): the total basal area of a stand (\( m^2 \ ha^{-1} \)).

\( C_c \): the \( CO_2 \) concentration in the leaf chloroplasts (\( \mu mol \ mol^{-1} \)).

\( C_i \): the intercellular \( CO_2 \) concentration (\( \mu mol \ mol^{-1} \)).

\( C_{ij} \): parameters in the needle age transition functions in the vertical (\( j=0, 1 \) and \( i=j+1 \)).

\( C_{ij}'' \): parameters in the needle age transition functions in the horizontal (\( j=0, 1 \) and \( i=j+1 \)).

\( C_R \): the temperature coefficient of dark respiration (\( ^oC^{-1} \)).

\( C_Q \): the quantum flux coefficient of dark respiration (\( m^2 \ s \ umol^{-1} \)).

\( D_b \): the diameter of the tree trunk at breast height (cm).

\( D_i \): the water vapour pressure difference across the leaf surface (kPa).

\( F_b \): the beam fraction of the incident radiation

\( F_i \): the total area of leaves within a tree crown (\( m^2 \)).

\( G \): the above-ground biomass in dry weight of a stand (tonnes \( ha^{-1} \)).

\( H \): the tree height (m).

\( H_c \): the canopy height (m).

\( H_s \): the skewness factor of the horizontal NAD distribution.

\( H_x \): the relative radial distance of maximum NAD in the horizontal.

\( F(I) \): the photosynthetic light response function or the cumulative relative quantum flux density frequency function of the needles on a shoot.
I: the radiation flux density within the shoot or a canopy, it has a dimension of umol m$^{-2}$ s$^{-1}$ for PAR flux density, and W m$^{-2}$ for near-infra red and thermal radiation.

$I_0$: the incident radiation flux density, it has the same dimension as I.

$I'_0$: the flux density of the incident PAR on a plane normal to the direction of incident PAR (umol m$^{-2}$ s$^{-1}$).

$I_d$: the flux density on the surface of the shaded needles on a shoot within the canopy (umol m$^{-2}$ s$^{-1}$).

$I_g$: the flux density of incident global radiation (W m$^{-2}$).

$I'_g$: the flux density of global radiation under a cloudless day (W m$^{-2}$).

$I_n$: the flux density on the surface of the sunlit needles on a shoot within the canopy (umol m$^{-2}$ s$^{-1}$).

$I_{net}$: the flux density of net radiation above the canopy (W m$^{-2}$).

$I_v$: the flux density of incident PAR (W m$^{-2}$).

$I'_v$: the flux density of incident PAR under a cloudless day (W m$^{-2}$).

$J$: the potential electron transport rate of the leaf (ue m$^{-2}$ s$^{-1}$).

$J_{max}$: the maximum rate of the potential electron transport of the leaf (ue m$^{-2}$ s$^{-1}$).

$L_c$: the leaf area index of the canopy (m$^2$ m$^{-2}$).

$L_d$: the leaf area density within the tree crown or canopy (m$^1$).

$L_s$: the length of the shoot twig (cm).

$N_d$: the needle number density along the shoot twig (needles cm$^{-1}$).

$N_s$: shoot density within the canopy (shoot m$^{-3}$).

$O_c$: the oxygen concentration in the leaf chloroplasts (mmol mol$^{-1}$).

$O_t$: the hourly mean residual of transmittance.

$P_c$: the canopy photosynthetic rate (umol m$^{-2}$ s$^{-1}$).
$P_{ci}$: the total photosynthesis of all needles at age class $i$ within the canopy \((i=0, 1 \text{ and } 2)\) (umol s$^{-1}$).

$P_n$: the needle photosynthetic rate (umol m$^{-2}$ s$^{-1}$).

$P_{nc}$: the Rubisco-limited rate of needle photosynthesis (umol m$^{-2}$ s$^{-1}$).

$P_{ne}$: the electron transport rate-limited rate of needle photosynthesis (umol m$^{-2}$ s$^{-1}$).

$P_{nmi}$: the maximum photosynthetic rate of the needles at age class $i$ \((i=0, 1 \text{ and } 2)\) (umol m$^{-2}$ s$^{-1}$).

$P_{nmx}$: the maximum photosynthetic rate of the needles (umol m$^{-2}$ s$^{-1}$).

$P_s$: the shoot photosynthetic rate (umol m$^{-2}$ s$^{-1}$).

$P_{smx}$: the maximum photosynthetic rate of the shoot (umol m$^{-2}$ s$^{-1}$).

$Q_1$: the PAR flux density absorbed by a unidirectionally illuminated shoot in the leaf chamber (umol m$^{-2}$ s$^{-1}$).

$Q_2$: the PAR flux density absorbed by a bidirectionally illuminated shoot in the leaf chamber (umol m$^{-2}$ s$^{-1}$).

$Q_b$: the flux density of beam PAR absorbed by a tree crown or canopy.

$Q_d$: the flux density of diffuse PAR absorbed by a tree crown or canopy.

$Q_g$: the flux density of global PAR absorbed by a tree crown or canopy.

$Q'$: the scattered PAR flux density absorbed by a shoot illuminated unidirectionally in the leaf chamber (umol m$^{-2}$ s$^{-1}$).

$Q''$: the scattered PAR flux density absorbed by a shoot illuminated bidirectionally in the leaf chamber (umol m$^{-2}$ s$^{-1}$).

$R$: the average crown radius at the tree crown base (m).

$R'(h)$: the crown radius at the relative crown height of $h$ (m).

$R_d$: the day respiratory rate (umol m$^{-2}$ s$^{-1}$).

$R_g$: the shadow region of a tree crown.
$R_n$: the dark respiratory rate ($\text{umol m}^{-2} \text{s}^{-1}$).

$S_e$: the area shaded by the tree crown within region $R_g$.

$S_n$: the total plan area of all needles on a shoot ($\text{cm}^2$).

$S_s$: the silhouette area of a shoot ($\text{cm}^2$).

$T_a$: the air temperature ($^\circ\text{C}$).

$T_b$: the transmittance of beam radiation.

$T_d$: the transmittance of diffuse radiation.

$T_l$: the leaf temperature ($^\circ\text{C}$).

$V_c$: the carboxylation rate ($\text{umol m}^{-2} \text{s}^{-1}$).

$V_{c_{\text{max}}}$: the maximum rate of carboxylation ($\text{umol m}^{-2} \text{s}^{-1}$).

$V_o$: the oxygenation rate ($\text{umol m}^{-2} \text{s}^{-1}$).

$V_{o_{\text{max}}}$: the maximum rate of oxygenation ($\text{umol m}^{-2} \text{s}^{-1}$).

$V_s$: the skewness factor of the vertical NAD distribution.

$V_x$: the relative crown height of the maximum NAD in the vertical.

$W_c$: the Rubisco-limited carboxylation rate ($\text{umol m}^{-2} \text{s}^{-1}$).

$W_{cj}$: the co-limiting factor of carboxylation rate ($\text{umol m}^{-2} \text{s}^{-1}$).

$W_j$: the electron transport rate limited carboxylation rate ($\text{umol m}^{-2} \text{s}^{-1}$).

$Z_b$: the height from the ground surface to the tree crown base ($\text{m}$).

\textbf{small letters}

a: the light use efficiency of the canopy.

a': the leaf absorptance for PAR.

b: a parameter in the radiance distribution function of sky diffuse radiation.
c: the clumping factor of leaves within the tree crown or canopy.

d_n: the needle diameter (cm).

d_s: the ratio of the total projected area of the individual needles and the twig on the shoot to the projected area of the complete shoot.

f: the fraction of PAR not absorbed by the chloroplast.

f_o: the area fraction of needles the photosynthetic rates of which are limited by the potential electron transport rate.

f': the vertical NAD distribution within the tree crown (m⁻¹).

f'': the horizontal NAD distribution within the tree crown (m⁻¹).

f_i: the vertical NAD distribution of needles within needle age class i (i=0, 1 and 2 for current, one-year-old and other older needles).

f''_i: the horizontal NAD distribution of needles within needle age class i.

f'_{ij}: the needle age transition function in the vertical (i=0, 1 and j=i+1).

f''_{ij}: the needle age transition function in the horizontal (i=0, 1 and j=i+1).

f(γ): the area fraction of the needles that have an angle γ between their surface and the beam direction for an isolated shoot with an inclination angle of α_s.

f_n(γ, h): the area fraction of the needles that have an angle γ between their surfaces and the beam direction at the relative canopy height h.

g(x,y): the gap fraction at a point (x, y).

g_a: the boundary layer conductance for water vapour (mol m⁻² s⁻¹).

g_a': the boundary layer conductance for CO₂ (mol m⁻² s⁻¹).

g_m: the mesophyll conductance of the leaf (mol m⁻² s⁻¹).

g_s: the stomatal conductance for water vapour (mol m⁻² s⁻¹).

s_s': the stomatal conductance for CO₂ of the leaf (mol m⁻² s⁻¹).
$g_a$: the total conductance for water vapour from the leaf boundary layer to the intercellular space of the leaf (mol m$^{-2}$ s$^{-1}$).

$g_a'$: the total conductance for CO$_2$ from the leaf boundary layer to the intercellular space of the leaf (mol m$^{-2}$ s$^{-1}$).

$h$: the relative height within the tree crown or the canopy.

$h_{\text{max}}$: the relative height of the maximum NAD within the tree crown.

$h'$: the height from the base of the tree crown (m).

$i_1$: the average PAR flux density on the sunlit leaf surface (umol m$^{-2}$ s$^{-1}$).

$i_2$: the average PAR flux density on the shaded leaf surface (umol m$^{-2}$ s$^{-1}$).

$k_b$: the extinction coefficient of beam radiation.

$k_c$: the Michaelis-Menten constant for CO$_2$ (umol mol$^{-1}$).

$k_d$: the extinction coefficient for diffuse radiation.

$k_d'$: the average extinction coefficient of diffuse radiation.

$k_m$: the effective Michaelis-Menten constant for CO$_2$ (umol mol$^{-1}$).

$k_o$: the Michaelis-Menten constant for O$_2$ (mmol mol$^{-1}$).

$l_c$: the crown length (m).

$l_n$: the needle length (cm).

$m_a$: airmass.

$n(\alpha_t)$: the needle inclination angle density distribution.

$n_1(t)$: the projected needle area density on a plane normal to the direction of illumination (cm$^2$).

$n_2(t)$: the projected needle area density on a plane normal to the direction of illumination (cm$^2$).

$p(t)$: the projected needle area density at a point at a distance $t$ from the projection of the
shoot twig on a plane normal to the direction of illumination.

\( r_{\text{max}} \): the relative radial distance of the maximum NAD within the tree crown.

\( r' \): the horizontal distance from the centre of the tree trunk (m).

\( s_0^* \): the fraction of sunlit needles on the isolated shoots with the spherical inclination angle distribution.

\( s_0^*(h) \): the fraction of sunlit needles on the shoots with the spherical inclination angle distribution at the relative canopy height \( h \).

\( t_m \): the measured radiation transmittance.

\( t_p \): the predicted radiation transmittance.

\( u \): the single parameter in the ellipsoidal leaf inclination angle distribution.

\( v_1 \): the variance of the PAR flux density on the surface of all needles on a unidirectionally illuminated shoot in the leaf chamber.

\( v_2 \): the variance of the PAR flux density on the surface of all needles on a bidirectionally illuminated shoot in the leaf chamber.

**Greek letter**

\( \alpha \): the inclination angle (in radian).

\( \alpha \): the average leaf inclination angle (in radian).

\( \alpha_0 \): the initial slope of the PAR response curve of the potential electron transport.

\( \alpha_i \): the angle between the needle upper surface and the shoot twig (in radian).

\( \alpha'_i \): the angle between the needle surface and the x, y-plane (in radian).

\( \alpha_g \): the initial slope of the quantum response of the stomatal conductance (mmol umol\(^{-1}\)).

\( \alpha_l \): the initial slope the photosynthetic quantum response of the shoot.

\( \alpha_n \): the quantum efficiency of the needles.

\( \alpha_s \): the inclination angle of the shoot axis (in radian).
$\beta$: the azimuthal angle (in radian).

$\beta_i$: the azimuthal angle of a needle on the shoot (radian).

$\beta_n$: the orientation angle of the needle relative to the direction of illumination (in radian).

$\beta'_n$: the angle between the needle projection on the $x, y$-plane and the positive $x$ axis (in radian).

$\beta_s$: the azimuthal angle of the shoot (in radian).

$\gamma$: the angle between the shoot axis and the direction of illumination (in radian).

$\theta$: the zenith angle of the sun (in radian).

$\theta_e$: the convexity of the quantum response of the potential electron transport of a shoot or a needle.

$\theta_n$: the convexity of the photosynthetic quantum response of the needle.

$\theta_i$: the convexity of the photosynthetic quantum response curve of the needles at age class i ($i=0, 1$ and $2$).

$\theta_s$: the convexity of the photosynthetic quantum response of the shoot.

$\Gamma$: the CO$_2$ compensation concentration (umol mol$^{-1}$).

$\Gamma^*$: the CO$_2$ compensation concentration attributable to photorespiration (umol mol$^{-1}$).

$\rho$: the needle reflectance for PAR.

$\rho_c$: the canopy albedo for PAR.

$\rho_s$: the reflectance of the soil surface for PAR.

$\gamma$: the angle between the shoot axis and the direction of incident radiation (in radian).

$\sigma$: the absorption coefficient of the leaf for PAR.

$\sigma_s$: Stefan-Boltzmann constant ($5.67 \times 10^{-8}$ W m$^{-2}$ K$^{-4}$).

$\tau$: the needle transmittance for PAR.
REFERENCE


capacity of conifers in diffuse light of high illuminance. Photosynthetica, 7(4):351-357