A MODEL OF CANOPY PHOTOSYNTHESIS AND TRANSPERSION
FOR SITKA SPRUCE (Picea sitchensis (BONG.) CARR.)

by

HELOISA SINATORA MIRANDA

A thesis submitted in fulfilment of the requirement
for the degree of Doctor of Philosophy to the University
of Edinburgh
1982
ABSTRACT

A model was developed to calculate the photosynthetic and transpiration rates for a closed canopy of Sitka spruce (*Picea sitchensis* (Bong.) Carr.), considering the following climatic variables as inputs: solar radiation, fraction of direct beam radiation, air temperature, vapour pressure deficit and wind speed; all measured above the canopy. The model consists of five sub-models which describe the spatial and temporal distribution of needles of different age classes, the interception of radiation by the canopy, the stomatal conductance, photosynthesis and transpiration of single needles. The canopy was divided into layers of leaf area index of 0.5. For each layer the photosynthetic and transpiration rates were calculated as the sum of the contribution of shaded and sunlit needles of different age classes. The total rates were then calculated by integrating the contribution of each layer. Each sub-model was implemented as a subroutine written in FORTRAN 77. A modular modelling approach was used for experimenting with individual sub-models or with the complete model.

Outputs from each sub-model were compared with experimental data and they accounted for 95% of variation in the data. Photosynthetic and transpiration rates for the whole canopy were compared with data published by James (1977). Daily total showed reasonable agreement, but the model did not follow very well the hourly values for the fluxes. The possible reasons for this are discussed: errors on the observed data, the absence of observed values for one climatic input, or weaknesses in the model.

The model predicts higher photosynthetic and transpiration rates when the radiation above the canopy is predominantly diffuse. This effect was greater for photosynthesis. From profiles of the fluxes
within the canopy, the relative importance of different age classes of needles, sunlit and shaded needles were evaluated. It was possible to predict the level at which loss by respiration of needles was greater than photosynthesis.
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 was executed by myself unless otherwise stated.
ACKNOWLEDGEMENTS

I would like to thank my supervisors, Professor P. G. Jarvis and Dr. R. I. Muetzelfeldt for their help and guidance throughout this work.

I also wish to extend my sincere appreciation to the following:

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To all my friends and members of the staff of the Department of Forestry and Natural Resources for all their help.

To my husband, "Tonico", for all the support and encouragement throughout this work.

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<th>Description of the variable</th>
<th>Unity</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A_j$</td>
<td>AN;AV</td>
<td>Albedo of layer $j$ ($N =$ near infrared radiation, $V =$ variable radiation)</td>
<td></td>
</tr>
<tr>
<td>$A_s$</td>
<td>-</td>
<td>Assymptote of the curve relating dark respiration to photon flux density</td>
<td>mg m$^{-2}$ s$^{-1}$</td>
</tr>
<tr>
<td>$a$</td>
<td>-</td>
<td>Leaf age class; $a = 0, 1, 2, \ldots 7$</td>
<td></td>
</tr>
<tr>
<td>$C_a$</td>
<td>CA</td>
<td>CO$_2$ concentration in the air</td>
<td>mg m$^{-3}$</td>
</tr>
<tr>
<td>$C_i$</td>
<td>-</td>
<td>CO$_2$ concentration at the intercellular spaces</td>
<td>mg m$^{-3}$</td>
</tr>
<tr>
<td>$c_p$</td>
<td>-</td>
<td>Specific heat of air</td>
<td>J g$^{-1}$ °C$^{-1}$</td>
</tr>
<tr>
<td>$D$</td>
<td>DN</td>
<td>Day of the year</td>
<td></td>
</tr>
<tr>
<td>$e_s(T)$</td>
<td>-</td>
<td>Saturation vapour pressure at temperature $T$</td>
<td>kPa</td>
</tr>
<tr>
<td>$F_j$</td>
<td>-</td>
<td>Downward diffuse radiation arising from scattering of intercepted beam radiation above layer $j$.</td>
<td>Wm$^{-2}$</td>
</tr>
<tr>
<td>$F_j'$</td>
<td>-</td>
<td>Upward diffuse radiation arising from scattering of intercepted beam radiation above layer $j$.</td>
<td>Wm$^{-2}$</td>
</tr>
<tr>
<td>$F_T$</td>
<td>LAI</td>
<td>Total leaf area index</td>
<td></td>
</tr>
<tr>
<td>$F_o$</td>
<td>TNEW</td>
<td>Leaf area index of current year leaves</td>
<td></td>
</tr>
<tr>
<td>$F_1$</td>
<td>TLAI1</td>
<td>Leaf area index of 1-year-old leaves</td>
<td></td>
</tr>
<tr>
<td>$F_2$</td>
<td>TLAI2</td>
<td>Leaf area index of 2-year-old leaves</td>
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</tr>
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<td>$F_3$</td>
<td>TLAI3</td>
<td>Leaf area index of 3-year-old leaves</td>
<td></td>
</tr>
<tr>
<td>$F_4$</td>
<td>TLAI4</td>
<td>Leaf area index of 4-year-old leaves</td>
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</tr>
<tr>
<td>$F_5$</td>
<td>TLAI5</td>
<td>Leaf area index of 5-year-old leaves</td>
<td></td>
</tr>
<tr>
<td>$F_6$</td>
<td>TLAI6</td>
<td>Leaf area index of 6-year-old leaves</td>
<td></td>
</tr>
<tr>
<td>$F_7$</td>
<td>TLAI7</td>
<td>Leaf area index of 7-year-old leaves</td>
<td></td>
</tr>
<tr>
<td>$f_b$</td>
<td>FRAC</td>
<td>Fraction of solar radiation above the canopy which is beam.</td>
<td></td>
</tr>
<tr>
<td>$f_{i1}$</td>
<td>FSA</td>
<td>Fraction of sunlit leaf area in leaf angle class $i$.</td>
<td></td>
</tr>
<tr>
<td>$G_1$</td>
<td>G1</td>
<td>Assymptotic value of stomatal conductance ($g_s$) at infinite light</td>
<td>cm s$^{-1}$</td>
</tr>
<tr>
<td>$G_2$</td>
<td>G2</td>
<td>$\Delta g_s/\Delta Q_s$ at the point where the hyperbola meets the abscissa</td>
<td>cm s$^{-1}$/(µE m$^{-2}$)</td>
</tr>
<tr>
<td>Symbol</td>
<td>FORTRAN</td>
<td>Description of the variable</td>
<td>Unity</td>
</tr>
<tr>
<td>--------</td>
<td>-----------</td>
<td>---------------------------------------------------------------------------------------------</td>
<td>---------</td>
</tr>
<tr>
<td>G3</td>
<td>G3</td>
<td>Value of $g_s$ in the dark</td>
<td>m s$^{-1}$</td>
</tr>
<tr>
<td>G4</td>
<td>G4</td>
<td>Low temperature for $g_s = 0$</td>
<td>°C</td>
</tr>
<tr>
<td>G5</td>
<td>G5</td>
<td>Temperature for maximum $g_s$</td>
<td>°C</td>
</tr>
<tr>
<td>G6</td>
<td>G6</td>
<td>High temperature for $g_s = 0$</td>
<td>°C</td>
</tr>
<tr>
<td>G7</td>
<td>G7</td>
<td>Slope of the curve relating $g_s$ to temperature and vapour pressure deficit.</td>
<td>kPa °C$^{-1}$</td>
</tr>
<tr>
<td>$g_a$</td>
<td>GA</td>
<td>Boundary layer conductance</td>
<td>m s$^{-1}$</td>
</tr>
<tr>
<td>$g_s$</td>
<td>GS</td>
<td>Stomatal conductance</td>
<td>m s$^{-1}$</td>
</tr>
<tr>
<td>$h_a$</td>
<td>HEIGHT</td>
<td>Height occupied by foliage of one specific age class</td>
<td>m</td>
</tr>
<tr>
<td>$\bar{h}_a$</td>
<td>-</td>
<td>Mean height of foliage of one specific age class</td>
<td>m</td>
</tr>
<tr>
<td>$I_{b}$</td>
<td>-</td>
<td>Irradiance of uninterrupted radiation averaged over a horizontal plane</td>
<td>W m$^{-2}$</td>
</tr>
<tr>
<td>$I_{b,j}$</td>
<td>-</td>
<td>Direct beam irradiance above layer j</td>
<td>W m$^{-2}$</td>
</tr>
<tr>
<td>$I_{b,i}$</td>
<td>IBA</td>
<td>Direct beam irradiance incident on sunlit leaves in leaf angle class i (same for all layers)</td>
<td>W m$^{-2}$</td>
</tr>
<tr>
<td>$I_{b,o}$</td>
<td>-</td>
<td>Direct beam irradiance incident above the canopy</td>
<td>W m$^{-2}$</td>
</tr>
<tr>
<td>$I_{bd,j}$</td>
<td>-</td>
<td>Total flux density incident on sunlit leaves at layer j</td>
<td>W m$^{-2}$</td>
</tr>
<tr>
<td>$I_{d,j}$</td>
<td>EDV;EDN</td>
<td>Downward diffuse flux above layer j</td>
<td>W m$^{-2}$</td>
</tr>
<tr>
<td>$I_{d,j}'$</td>
<td>EUV;EDN</td>
<td>Upward diffuse flux above layer j</td>
<td>W m$^{-2}$</td>
</tr>
<tr>
<td>$I_{d,o}$</td>
<td>-</td>
<td>Downward diffuse irradiance above the canopy</td>
<td>W m$^{-2}$</td>
</tr>
<tr>
<td>$\bar{I}_{j}$</td>
<td>LNIC</td>
<td>Fraction of diffuse irradiance penetrating unintercepted through a single layer.</td>
<td></td>
</tr>
<tr>
<td>$I_{j}(\theta,\phi)$</td>
<td>-</td>
<td>Fraction of downward incident radiation from a single direction above layer j which is not intercepted by that layer.</td>
<td></td>
</tr>
<tr>
<td>$I_{s,j,i}$</td>
<td>-</td>
<td>Solar direct flux appropriated for each leaf at layer j and angle class i</td>
<td>W m$^{-2}$</td>
</tr>
<tr>
<td>$I_{T,j}$</td>
<td>LD</td>
<td>Downward flux of thermal radiation above layer j</td>
<td>W m$^{-2}$</td>
</tr>
<tr>
<td>$I_{T,j}'$</td>
<td>LU</td>
<td>Upward flux of thermal radiation above layer j</td>
<td>W m$^{-2}$</td>
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<td>--------</td>
<td>--------------</td>
<td>-------------------------------</td>
<td>-------</td>
</tr>
<tr>
<td>i</td>
<td>I</td>
<td>Arbitrary leaf-angle class</td>
<td>Unity</td>
</tr>
<tr>
<td>j</td>
<td>J</td>
<td>Arbitrary layer</td>
<td></td>
</tr>
<tr>
<td>k</td>
<td></td>
<td>Extinction coefficient</td>
<td></td>
</tr>
<tr>
<td>(k_s(Q_p))</td>
<td>GQV</td>
<td>Dimensionless function describing the response of (g_s) to photon flux density.</td>
<td></td>
</tr>
<tr>
<td>(k_s(T))</td>
<td>GT</td>
<td>Dimensionless function describing the response of (g_s) to temperature</td>
<td></td>
</tr>
<tr>
<td>(k_s(\delta e))</td>
<td>GDL</td>
<td>Dimensionless function describing the response of (g_s) to vapour pressure deficit.</td>
<td></td>
</tr>
<tr>
<td>(L_a(h))</td>
<td>FH</td>
<td>Leaf area density within a 0.1 m interval at height (h); for each age class</td>
<td>(m^{-1})</td>
</tr>
<tr>
<td>(L_T(h))</td>
<td>STH</td>
<td>Leaf area density at height (h); for the total leaf area</td>
<td>(m^{-1})</td>
</tr>
<tr>
<td>(M')</td>
<td>CF</td>
<td>Convexity parameter of the curve relating photosynthesis to light.</td>
<td></td>
</tr>
<tr>
<td>(N)</td>
<td>N</td>
<td>Number of layers of equal leaf area increment.</td>
<td></td>
</tr>
<tr>
<td>(P)</td>
<td>P</td>
<td>Net photosynthesis</td>
<td>(mg \ m^{-2} s^{-1})</td>
</tr>
<tr>
<td>(P_G)</td>
<td></td>
<td>Gross photosynthesis</td>
<td>(mg \ m^{-2} s^{-1})</td>
</tr>
<tr>
<td>(P_j)</td>
<td>PC</td>
<td>Photosynthetic rate of layer (j)</td>
<td>(mg \ m^{-2} s^{-1})</td>
</tr>
<tr>
<td>(P_{j(I_d,j)})</td>
<td></td>
<td>Photosynthesis for shaded leaves at layer (j)</td>
<td>(mg \ m^{-2} s^{-1})</td>
</tr>
<tr>
<td>(P_{j,i(I_b,i)})</td>
<td></td>
<td>Photosynthesis for leaves at layer (j) and angle class (i)</td>
<td>(mg \ m^{-2} s^{-1})</td>
</tr>
<tr>
<td>(P_{max})</td>
<td></td>
<td>Asymptotic value of photosynthesis at infinit light</td>
<td>(mg \ m^{-2} s^{-1})</td>
</tr>
<tr>
<td>(P_a(h))</td>
<td>FR</td>
<td>Proportion of leaves belonging to a specific age class at height (h).</td>
<td></td>
</tr>
<tr>
<td>(Q_p)</td>
<td>QV</td>
<td>Photon flux density</td>
<td>(\mu E \ m^{-2} s^{-1})</td>
</tr>
<tr>
<td>(R_d)</td>
<td>RD</td>
<td>Dark respiration</td>
<td>(\mu E \ m^{-2} s^{-1})</td>
</tr>
<tr>
<td>(R_d(0,0))</td>
<td>RDO</td>
<td>Dark respiration at (T = 0) and (Q_p = 0)</td>
<td>(mg \ m^{-2} s^{-1})</td>
</tr>
<tr>
<td>(R_{f3})</td>
<td>RF3</td>
<td>Rate of fall of 3-year-old leaves</td>
<td>LAI/day</td>
</tr>
<tr>
<td>(R_{f4})</td>
<td>RF4</td>
<td>Rate of fall of 4-year-old leaves</td>
<td>LAI/day</td>
</tr>
<tr>
<td>(R_{f5})</td>
<td>RF5</td>
<td>Rate of fall of 5-year-old leaves</td>
<td>LAI/day</td>
</tr>
<tr>
<td>Symbol</td>
<td>FORTRAN Name</td>
<td>Description of the variable</td>
<td>Unit</td>
</tr>
<tr>
<td>--------</td>
<td>--------------</td>
<td>----------------------------</td>
<td>------</td>
</tr>
<tr>
<td>$R_{f6}$</td>
<td>RF6</td>
<td>Rate of fall of 6-year-old leaves</td>
<td>LAI/day</td>
</tr>
<tr>
<td>$R_{f7}$</td>
<td>RF7</td>
<td>Rate of fall of 7-year-old leaves</td>
<td>LAI/day</td>
</tr>
<tr>
<td>$R_l$</td>
<td>-</td>
<td>Photorespiration</td>
<td>mg m$^{-2}$ s$^{-1}$</td>
</tr>
<tr>
<td>$R_{N,j}$</td>
<td>DIFN</td>
<td>Load of radiation on shaded leaves at layer j</td>
<td>Wm$^{-2}$</td>
</tr>
<tr>
<td>$R_{N,j,i}$</td>
<td>DIRN</td>
<td>Load of radiation on leaves at layer j and angle class i</td>
<td>Wm$^{-2}$</td>
</tr>
<tr>
<td>$R_{nj}$</td>
<td>DNET</td>
<td>Net radiation at layer j</td>
<td>Wm$^{-2}$</td>
</tr>
<tr>
<td>$R_{s,j}$</td>
<td>-</td>
<td>Downward solar diffuse flux at layer j</td>
<td>Wm$^{-2}$</td>
</tr>
<tr>
<td>$R_{s,j}'$</td>
<td>-</td>
<td>Upward solar diffuse flux at layer j</td>
<td>Wm$^{-2}$</td>
</tr>
<tr>
<td>$r_a$</td>
<td>RA</td>
<td>Boundary layer resistance</td>
<td>s m$^{-1}$</td>
</tr>
<tr>
<td>$r_a'$</td>
<td>-</td>
<td>Diffusion resistance for CO$_2$ transfer through the boundary layer</td>
<td>s m$^{-1}$</td>
</tr>
<tr>
<td>$r_s'$</td>
<td>-</td>
<td>Diffusion resistance for CO$_2$ through the stomata</td>
<td>s m$^{-1}$</td>
</tr>
<tr>
<td>$r_m$</td>
<td>RM</td>
<td>Mesophyll resistance</td>
<td>s m$^{-1}$</td>
</tr>
<tr>
<td>$r_{min}$</td>
<td>-</td>
<td>Minimum mesophyll resistance</td>
<td>s m$^{-1}$</td>
</tr>
<tr>
<td>St</td>
<td>IT</td>
<td>Solar radiation above the canopy (0.4-3.0 $\mu$m)</td>
<td>Wm$^{-2}$</td>
</tr>
<tr>
<td>$S_a$</td>
<td>S</td>
<td>Standard deviation of the mean height</td>
<td></td>
</tr>
<tr>
<td>T</td>
<td>T</td>
<td>Air temperature</td>
<td>°C</td>
</tr>
<tr>
<td>$T_{b}$</td>
<td>-</td>
<td>Transmittance for direct radiation for one layer.</td>
<td></td>
</tr>
<tr>
<td>$T_{bj}$</td>
<td>-</td>
<td>Transmittance for direct beam for j layers</td>
<td></td>
</tr>
<tr>
<td>$T_{high}$</td>
<td>-</td>
<td>High temperature for maximum $r_m$</td>
<td>°C</td>
</tr>
<tr>
<td>$T_{l,j}$</td>
<td>T</td>
<td>Leaf temperature at layer j</td>
<td>°C</td>
</tr>
<tr>
<td>$T_{low}$</td>
<td>-</td>
<td>Low temperature for maximum $r_m$</td>
<td>°C</td>
</tr>
<tr>
<td>$T_m$</td>
<td>-</td>
<td>Temperature for minimum $r_m$</td>
<td>°C</td>
</tr>
<tr>
<td>$T_{sky}$</td>
<td>TSKY</td>
<td>Sky temperature</td>
<td>°K</td>
</tr>
<tr>
<td>$T_{soil}$</td>
<td>TSOIL</td>
<td>Soil temperature</td>
<td>°C</td>
</tr>
<tr>
<td>$U_h$</td>
<td>UH</td>
<td>Wind speed at the top of canopy</td>
<td>m s$^{-1}$</td>
</tr>
<tr>
<td>Symbol</td>
<td>Name</td>
<td>Description of the variable</td>
<td></td>
</tr>
<tr>
<td>--------</td>
<td>------</td>
<td>-----------------------------</td>
<td></td>
</tr>
<tr>
<td>U(z)</td>
<td>UZ</td>
<td>Wind speed at height z within the canopy</td>
<td></td>
</tr>
<tr>
<td>U(z₁)</td>
<td>UZ1</td>
<td>Wind speed at reference height above the canopy</td>
<td></td>
</tr>
<tr>
<td>α</td>
<td>A</td>
<td>Initial slope of the curve relating photosynthesis to light</td>
<td></td>
</tr>
<tr>
<td>αᵢ</td>
<td>AM</td>
<td>Angle between the plane normal to the leaf's plane and the direction of the sun.</td>
<td></td>
</tr>
<tr>
<td>Γ</td>
<td>CCP</td>
<td>CO₂ compensation point</td>
<td></td>
</tr>
<tr>
<td>Y</td>
<td>SC</td>
<td>Psychrometer constant</td>
<td></td>
</tr>
<tr>
<td>Δ</td>
<td>SLOPE</td>
<td>Slope of the curve relating the saturated vapour pressure of water to temperature</td>
<td></td>
</tr>
<tr>
<td>ΔF</td>
<td>-</td>
<td>Thickness of each layer</td>
<td></td>
</tr>
<tr>
<td>ΔFᵢⱼ</td>
<td>SLAI</td>
<td>Leaf area index of sunlit leaves at layer j.</td>
<td></td>
</tr>
<tr>
<td>ΔFⱼᵢ</td>
<td>SLAA</td>
<td>Sunlit leaf area index for leaves at layer j and angle class i</td>
<td></td>
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<tr>
<td>ΔFS</td>
<td>SHLAI</td>
<td>Leaf area index of shaded leaves at layer j.</td>
<td></td>
</tr>
<tr>
<td>δ</td>
<td>TC</td>
<td>Temperature coefficient for dark respiration</td>
<td></td>
</tr>
<tr>
<td>δₑ</td>
<td>DL</td>
<td>Vapour pressure deficit</td>
<td></td>
</tr>
<tr>
<td>ζ</td>
<td>QC</td>
<td>Radiation coefficient for dark respiration.</td>
<td></td>
</tr>
<tr>
<td>θ</td>
<td>THETA</td>
<td>Solar zenith angle</td>
<td></td>
</tr>
<tr>
<td>λ</td>
<td>-</td>
<td>Latent heat of vaporization of water</td>
<td></td>
</tr>
<tr>
<td>λₑ</td>
<td>EVP</td>
<td>Transpiration</td>
<td></td>
</tr>
<tr>
<td>ρ</td>
<td>-</td>
<td>Density of air</td>
<td></td>
</tr>
<tr>
<td>ρₒₗⱼ</td>
<td>-</td>
<td>Layer reflectivity (same for all layers)</td>
<td></td>
</tr>
<tr>
<td>ρₒᵢⱼ,ρ_leaf</td>
<td>-</td>
<td>Leaf reflectance</td>
<td></td>
</tr>
<tr>
<td>ρₒᵢN</td>
<td>RN</td>
<td>Leaf reflectance for near-infrared radiation</td>
<td></td>
</tr>
<tr>
<td>Symbol</td>
<td>Name</td>
<td>Description of the variable</td>
<td>Unity</td>
</tr>
<tr>
<td>----------</td>
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<td>------------------------------------------------------------------</td>
<td>---------</td>
</tr>
<tr>
<td>$\rho_{LV}$</td>
<td>RV</td>
<td>Leaf reflectance for visible radiation</td>
<td></td>
</tr>
<tr>
<td>$\rho_{soil,N}$</td>
<td>RNSOIL</td>
<td>Soil reflectance for near-infrared radiation</td>
<td></td>
</tr>
<tr>
<td>$\rho_{soil,V}$</td>
<td>RVSOIL</td>
<td>Soil reflectance for visible radiation</td>
<td></td>
</tr>
<tr>
<td>$\sigma$</td>
<td>-</td>
<td>Stefan-Boltzmann constant $(5.67 \times 10^{-8})$</td>
<td>$Wm^{-2}K^{-4}$</td>
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<tr>
<td>$\sigma_1$</td>
<td>-</td>
<td>Shoot/density</td>
<td>$m^2/m^3$</td>
</tr>
<tr>
<td>$\tau_{L,j}$</td>
<td>TLN;TLV</td>
<td>Layer transmittance</td>
<td></td>
</tr>
<tr>
<td>$\tau_{lj,\text{leaf}}$</td>
<td>-</td>
<td>Leaf transmittance</td>
<td></td>
</tr>
<tr>
<td>$\tau_{1,N}$</td>
<td>TN</td>
<td>Leaf transmittance for near-infrared radiation</td>
<td></td>
</tr>
<tr>
<td>$\tau_{LV}$</td>
<td>TV</td>
<td>Leaf transmittance for visible radiation</td>
<td></td>
</tr>
<tr>
<td>$\phi$</td>
<td>-</td>
<td>Azimuth angle</td>
<td>Degrees</td>
</tr>
<tr>
<td>$\theta(\theta,\phi)$</td>
<td>-</td>
<td>Normalized downward diffuse radiation above layer $j$ at incident angle $\theta$ and azimuth angle $\phi$.</td>
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CHAPTER 1

INTRODUCTION

The areas devoted to forest plantations in Britain have considerably increased in the last decade, mainly in Scotland which, because of its soil, climate and topography is less suitable for agriculture. The dominant species being planted throughout the U.K. is Sitka spruce (Picea sitchensis (Bong.) Carr.). Consequently, Sitka spruce has become a crop of major economic importance.

There has been a considerable research effort into the physiological responses of Sitka spruce to environmental factors. Studies in the field and laboratory have been made to provide a description of the characteristics of photosynthesis, transpiration, respiration, stomatal and mesophyll conductance to environmental factors such as solar radiation, air temperature, vapour pressure deficit and wind speed (see for example Ludlow and Jarvis, 1971; Neilson et al, 1972; Grace et al., 1975; Turner and Jarvis, 1975; Neilson and Jarvis 1975; Watts et al, 1976; Watts and Neilson, 1978; Beadle et al, 1978, 1979; Leverenz and Jarvis 1979, 1980).

There are also information about bud development (Owens and Molder 1976, 1976a); phenology (Lines and Mitchell, 1965); forest litter (Owen 1954; Adams 1974; Carey and Farrel 1978); fine roots (Ford and Dean 1977); radiation interception by the canopy (Landsberg et al 1973; Norman and Jarvis 1974).

Despite the considerable amount of information available, far less is known for Sitka spruce than for other conifers of less economic importance nowadays in the U.K.
Linder (1979, 1980) reviewed the published papers on photosynthesis, transpiration and respiration for conifers. From these reviews, it is clear that the number of published papers on these processes for Sitka spruce is less than 5% of the total for conifers as a whole. Of this 5%, only one third is concerned with field observations, and the majority refer to research done under controlled environment. This large discrepancy may result from the difficulties associated with field work when compared with controlled environments. Field work generally requires extensive and expensive instrumentation; it presents difficulties in sustaining observations throughout the year, and the need to meet site requirements. On the other hand, field measurements coupled with micrometeorological observations have the main advantage of investigating processes like photosynthesis and transpiration with minimum interference and disturbance to the canopy and its environment. By using this approach the photosynthetic and transpiration rates for a complete canopy are determined, while studies under controlled conditions generally determine the rates for single leaves or parts of the plant.

Observations of plant responses in controlled environments may be related and compared to responses gathered under field conditions using a computer model. For Sitka spruce, there are published models describing the radiation penetration (Norman and Jarvis 1975); the response of stomatal conductance to climatic variables (Jarvis 1976); development of branching structure (Cochrane and Ford 1978); water storage on a forest canopy (Hancock and Crowther 1979) and growth (Cochrane and Ford 1978; Kilpatrick 1978; Kilpatrick et al 1981). However it was not possible to find a published model for predicting photosynthetic and transpiration rates for a Sitka spruce stand.
Therefore, the aim of this project is to produce a model which simulates rates of photosynthesis and transpiration for a Sitka spruce stand. In order to calculate these fluxes, five sub-models are used: vertical and temporal distribution of foliage; radiation interception by the canopy; stomatal conductance; photosynthesis and transpiration.

Subsidiary objectives are to determine the relative importance of needles of different age classes, and sunlit or shaded needles to the total rates.

As the rates of CO₂, water and energy exchange of individual needles also depends on their position within the canopy (Woodman 1971; Watts et al 1976), the canopy is divided into N layers of equal leaf area index. The layers are considered thin enough to avoid the overlap of needles. Within each layer needles of different age classes are considered to be randomly distributed. In this case only the inclination angle of the needles define the structure of the foliage. For this a spherical leaf distribution with nine different leaf angle classes is chosen to describe the structure of the foliage (Norman and Jarvis 1975).

Each sub-model is implemented as a sub-routine written in FORTRAN 77 (ERCC, 1981). As well as writing a small program to allow each sub-routine to be analysed by itself, and a main program for linking them all together, a modular modelling approach available as a package program in the Department of Forestry and Natural Resources was also explored. This approach allows great flexibility for experimenting with each sub-model or with the complete model. At the same time, the modular modelling approach allows changes to be
made in any sub-model without major alterations in the structure of the computer program.

The outputs from each sub-model are compared with data available in the literature, and the simulated rates are compared with measurements taken by James (1977) for a Sitka spruce stand.
CHAPTER 2

THE DESCRIPTION OF THE MODEL

In this chapter a model to predict hourly rates of photosynthesis and transpiration for a closed canopy is presented. The model consists of a number of sub-models which describe the structure of the canopy, the microenvironment and rate processes at the level of a single leaf. From them, the contribution of different foliage layers to the photosynthetic and transpiration rates of the complete canopy is calculated. The equations used within sub-models are usually empirical in the sense that they are based on observations and measurements without reference to the underlying physiological processes.

The model has two boundaries: the top is a plane 2 to 4 meters above the canopy, and the bottom is the soil surface. At the top, the climate is defined by solar radiation, temperature, vapour pressure deficit, wind speed, and carbon dioxide concentration; and at the bottom, the only variable being considered is the soil temperature. These are the hourly inputs required by the different sub-models, but it should be clear that the sub-models are inter-dependent and outputs from one sub-model are used as inputs for another. Figure 2.1 illustrates the interdependence between the sub-models.

In the following sections the information required and the assumptions made in the development of each one of the sub-models are considered in detail. In the final section the sub-models are brought together to form the complete model.
Figure 2.1: Interrelationship between the various sub-models. The inputs are: air temperature (T), vapour pressure deficit (vpd), solar radiation (St), fraction of solar radiation which is beam (fb), solar zenith angle (θ), soil temperature (Tsoil), day of the year (day), height interval occupied by leaves of different age classes (height), and canopy height (h₀).
2.1 Modelling the leaf area index

The structure of plant canopies have a great influence upon the process of action and reaction between its individual elements (leaves, woody elements, flowers, etc.) and their environment through the modification and interception of fluxes of radiation, carbon dioxide and water vapour.

Woodman (1971) and Watts et al. (1976) have shown that the rate of CO₂, water vapour and energy exchange for individual leaves do not depend only upon the leaf position within the canopy, but it also depends upon the leaf age and physiological conditions. Therefore, the spatial and temporal distribution of leaves within the canopy is needed to estimate the contribution of individual
leaves to the rates of CO$_2$, water vapour and energy exchange by
the whole canopy.

A model was written to provide information about the
spatial and temporal distribution of needles within a spruce
canopy taking into account the distribution of needles of
different ages. It is written in a life table format, in a manner
similar to that described by Mitchell (1974) for Douglas-fir and

The model deals with overlapping generations and is therefore
keyed to specific time periods or anniversaries.

Assumptions

1. The same leaf area of needles is produced each year;
2. The life cycle of one generation of needles is eight
   years;
3. The needles remain on the tree for three years before
   starting to fall;
4. Rates of fall are different, but constant throughout the
   year, for each age class.

The temporal distribution of foliage

New shoots begin to form on 1st June (reference date) and grow
at a steady rate until 20 July, linearly increasing the canopy leaf
area index. The needles remain on the tree for 3 years suffering no
loss. Thereafter, over the next 5 years, they decline at a rate
which increases every 1st June (D.E.Ford, personal communication).

According to the previous assumptions, after a number of cycles
of 365 days from the 1st of June, the leaf area index for each
different age class encountered at this arbitrary reference date is given by:

\[ F_0 = 0 \quad (2.1) \]
\[ F_1 = F_2 \quad (2.2) \]
\[ F_a = (1 - 365 R_{fa}) F_{a-1} \quad a = 3, \ldots, 7 \quad (2.3) \]

where, \( F_0 \) is the leaf area of current year leaves; \( F_1 \) and \( F_2 \) are the leaf area of one and two-year-old leaves, respectively; \( F_a \) is the leaf area of older leaves remaining on the tree; and \( R_{fa} \) is the daily rate of fall for each age class (a) concerned.

For practical purpose the model uses the Julian Calendar, numbering days from 1 to 365 starting on January 1st.

The following steps describe how the temporal distribution of needles is obtained for any day from 1st January to 31st of December.

From 1st January to 31st of May (day 1 to day 151)

During the period from 1st January to 31st May the leaf area of current, 1-year-old and 2-year-old needles remains the same and the older needles are declining at their respective daily rate. Since the needles start to decline on 1st June, then on 1st January they have been falling for 214 days. The leaf area of needles of different age classes that remain on the tree at any day \( D \) between 1st January and 31st of May is given by:

\[ F_0 = F_1 = F_2 \quad (2.4) \]
\[ F_a = (1 - (214 + D) R_{fa}) F_{a-1} \quad a = 3, \ldots, 7 \quad (2.5) \]

where \( D \) is a Julian day number.
From 1st June to 31st December (day 152 to day 365)

A. Current year needles

New needles begin to form on 1st June and grow at a steady rate until 20 of July when all new growth stops. The leaf area of new needles added to the tree at any time from 1st June to 20 July (day 152 to day 172), is

\[ F_o = \left( \frac{D - 151}{50} \right) F_1 \]  

(2.6)

where \( F_1 \) is that given by equation (2.4).

From 20 July until 31st December the leaf area index of current year needles remains constant.

B. Old needles

At 1st June the needles are classified as one year older. The leaf area of 1-year-old and 2-year-old needles are constant, however, the 3-year-old needles start to decline and the older ones change their rate of fall. Then, the leaf area of old needles that remain on the tree at any day between 1st June and 31st December is given by:

\[ F_1 = F_2 \]

(2.7)

\[ F_a = (1 - (D - 151)R) F_{a-1} \quad a = 3, ..., 7 \]  

(2.8)

At any day the total leaf area is given by the sum of the leaf area index of each different age class, as given by

\[ F_T = \sum_{a=0}^{7} F_a \]  

(2.9)
The spatial distribution of foliage

Knowing the leaf area index for each age class of needles and their respective height distribution within the live crown, the vertical distribution of foliage can be estimated.

Previously the normal distribution has been used to approximate the vertical distribution of foliage in canopies (Kinerson et al 1974, Wats et al 1976, Whitehead 1978). This same approach is used here. The equation used to describe the normal curve for each age class of needles was:

\[
L_a(h) = \frac{0.1 F_a}{s_a^2 \pi} \exp \left( -\frac{(h - \bar{h}_a)^2}{2 s_a^2} \right) \quad a = 0, \ldots, 7
\]  

(2.10)

where \( L_a(h) \) is the leaf area density within a 0.1 m interval at height \( h \), \( F_a \) is the leaf area index of each age class, \( \bar{h}_a \) is the mean height of foliage of one specific age class and \( s_a \) is the standard deviation of the mean height. For each individual age class the mean height \( \bar{h}_a \) was taken as the mid-point of the height occupied in the live crown by this specific age class (Stephens, 1969), and the standard deviation was taken as 17% of the height. This value for the standard deviation is consistent with values estimated for \textit{Picea glehnii} (Schmidt) Mast (15%) and \textit{Aiptomerica japonica} (L.f.) Don (16% Tadaki, 1963, cited by Beadle et al 1981), \textit{Picea abies} (L.) Karst (20% Schöpfer, 1962, cited by Stephens, 1969), \textit{Pinus resinosa} (16 - 19% Stephens, 1969) and \textit{Pinus sylvestris} (L.) (17% Beadle et al 1981).

The vertical distribution for the total leaf area was calculated by adding up the distribution of each age class according to

\[
L_T(h) = \sum_{a=0}^{7} L_a(h)
\]

(2.11)
For each height interval the proportion of leaves belonging to each age class \( p_a(h) \) is calculated as the ratio \( L_a(h)/L_T(h) \). This ratio will be used later to calculate the fluxes of \( \text{CO}_2 \) and water vapour for the complete canopy as the integrated value of the contribution of each individual leaf.

2.2 Modelling radiation penetration

Radiation influences plant process through its effect on photosynthesis, photomorphogenesis, transpiration, leaf temperature and the general microclimate. Therefore, the importance of a quantitative understanding of the interactions between plants and their radiative environment is unquestionable. This interaction involves characteristics of the incident radiation, as well as the
spectral properties, structural arrangement and physiological response of individual foliage elements. A proper understanding of the interaction between plants and radiation thus hinges on the elucidation of the distribution of radiation within the canopy.

Since Monsi and Saeki (1953) introduced the idea of exponential extinction of radiation within the canopy much theoretical and experimental research has been done. A great part of the published literature is concerned with the development of elaborate models for light distribution in plant canopies. Excellent reviews are available from Monsi et al. (1973), Bunnink (1978) and Norman (1979). Some of these models have been developed in studies of photosynthesis and growth of crops, and relate the penetration of direct solar radiation and diffuse sky radiation into a plant canopy to the optical properties of the components, the soil and the canopy architecture (Monsi and Saeki, 1953; Monteith, 1965; de Wit, 1965; Duncan et al. 1967; Cowan, 1968; Goudriaan, 1977).

The model describing the extinction of radiation in the canopy was constructed with base in three models published: Norman (1979, 1980) and Norman and Jarvis (1975).

The model determines the direct and diffuse solar radiation flux densities in layers throughout the depth of the canopy (visible and near-infrared independently); it calculates the incident solar radiation for classes of leaves that are shaded or exposed at various angles to direct beam; the thermal radiation and the total radiation load for shaded and sunlit leaves.
Assumptions

1. Random distribution of foliage;
2. Spherical leaf distribution with nine angle classes;
3. Canopy is divided in N layers of equal leaf area index $(\Delta F)$, each layer being thin enough to avoid the overlap of leaves.

The physical structure of the canopy (inclination, orientation and location of individual leaves and woody elements) forms the base of a detailed radiation model.

Information about the location of individual elements is needed. The simplest solution, and widely adopted, is to assume that individual foliage elements are randomly positioned. As stated by Norman (1979), "this has proved to be a good assumption in most canopies of full cover even when the foliage actually is not randomly distributed, such as in Sitka spruce".

If the individual elements are assumed to be randomly distributed, then the foliage inclination and orientation angle distribution define the structure. Canopies with significant asymmetry about the azimuth are very rarely found (Monsi et al. 1973; Norman, 1979), thus only the foliage inclination angle needs to be determined.

The spherical leaf angle distribution is often used for canopies that do not have a predominant leaf angle distribution. This distribution is obtained by supposing that the relative frequency of leaf inclinations is the same as the relative frequency of the inclinations of the surface elements of a sphere (de Wit, 1965).
Interception of direct radiation

When a beam of radiation is incident on the top of the canopy, making an angle $\theta$ with the vertical, part of the radiation penetrates through the canopy without being intercepted by the leaves.

If the canopy is divided into $N$ layers of equal leaf area index ($\Delta F$), the intensity of uninterrupted radiation averaged over a horizontal plane at a level corresponding to a single layer is given by Norman (1979):

$$I_b = I_{b,0} T_b$$

(2.12)

where $I_{b,0}$ is the direct beam incident above the canopy and,

$$T_b = \exp \left( -k \frac{\Delta F}{\cos \theta} \right)$$

(2.13)

is the transmittance for direct beam radiation to below the layer, and $k$ is the fraction of the leaf area projected into the direction of the incident beam, this area fraction is called the extinction coefficient. For spherical leaf angle distribution $k$ is equal to $\frac{1}{3}$ (Cowan, 1968; Norman, 1979).

For $j$ of these layers

$$I_{b,j} = I_{b,0} T_{b,j}$$

(2.14)

where

$$T_{b,j} = \exp \left( -k \frac{j \Delta F}{2 \cos \theta} \right) = T_b^j$$

(2.15)

Penetration of diffuse radiation

The model used here to calculate the flux of diffuse radiation at any level within the canopy was first presented by Norman et al. (1971)
for canopies with horizontal leaves, and was later developed by Norman and Jarvis (1975) to include any leaf angle distribution.

For a canopy with random leaf distribution and spherical leaf angle distribution the model is described as follows:

Diffuse radiation incident on a leaf in a canopy arises from the sky, other foliage and the soil. An estimate of the fraction of diffuse radiation penetrating unintercepted through a single layer of thickness ΔF of a random canopy can be approximated by:

\[ I_j = \frac{\int_0^{\pi/2} \int_0^{2\pi} \theta_j(\theta,\phi) I_j(\theta,\phi) \sin\theta \cos\theta \, d\theta d\phi}{\int_0^{\pi/2} \int_0^{2\pi} \theta_j(\theta,\phi) \sin\theta \cos\theta \, d\theta d\phi} \]  

(2.16)

where \( \theta_j(\theta,\phi) \) is the normalized downward diffuse radiation above layer j at incident angle \( \theta \) and azimuth angle \( \phi \), and \( I_j(\theta,\phi) \) is the fraction of downward incident radiation from a single direction above layer j which is not intercepted by that layer. When the leaves are symmetrically distributed and an isotropic sky is considered, then equation (2.16) becomes

\[ I_j = \frac{\int_0^{\pi/2} I_j(\theta) \sin\theta \cos\theta \, d\theta}{\int_0^{\pi/2} \sin\theta \cos\theta \, d\theta} \]  

(2.17)

where

\[ I_j(\theta) = \exp \left( -\frac{\Delta F}{2 \cos\theta} \right) \]  

(2.18)

is the layer non-interception factor for upward or downward fluxes.

If the abaxial and adaxial leaf reflectivities are identical, there are no stems and branches, and the layers are so thin that the probability of a beam intercepting more than one leaf on passage through the layer is negligible, then the layer reflectance and transmittance are given by:
\[
\begin{align*}
\rho_j &= \rho_{lj} (1 - \bar{\tau}_j) \\
\tau_j &= \tau_{lj} (1 - \bar{\tau}_j) + \bar{\tau}_j
\end{align*}
\]

where \( \tau_{lj} \) and \( \rho_{lj} \) are the leaf transmittance and reflectance in layer \( j \), respectively.

The diffuse flux above layer \( j \) originating from the sky and other foliage can be defined as in Figure 2.2.

Figure 2.2 A diagram of diffuse fluxes of radiation in two layers of a canopy composed of \( n \) layers. At the top of the canopy \( j = 0 \) and at the soil surface \( j = N \) (from Norman and Jarvis 1975).

where, \( I'_{d,j} \) and \( I'_{d,j+1} \) are the downward and upward diffuse fluxes above layer \( j \), respectively, \( F_j \) and \( F'_j \) are the downward and upward
diffuse fluxes arising from the scattering of intercepted beam.

The downward diffuse flux above layer \( j \) in terms of the upward diffuse flux and the scattered direct beam is

\[
I_{d,j} = I_{d,j-1}^\tau j + I_{d,j}^\beta + I_{b,j-1}(1-T_b)^\tau_{lj-1} \tag{2.20}
\]

and the upward diffuse flux above layer \( j-1 \) is

\[
I_{d,j-1}' = I_{d,j}^\tau j + I_{d,j}^\beta + I_{b,j-1}(1-T_b)^\rho_{lj-1} \tag{2.21}
\]

Solving equation (2.20) for \( I_{d,j-1}' \), and assuming the same transmittance and reflectance for all layers \( (\tau_L \text{ and } \rho_L) \) the following equation results.

\[
I_{d,j-1} = \frac{(I_{d,j} - I_{d,j}^\rho_L - I_{b,j-1}(1-T_b)^\tau_{lj})/\tau_L}{I_{d,j-1}'} \tag{2.22}
\]

Dividing both sides of equation (2.21) by \( I_{d,j-1}' \) and assuming \( \rho_{lj} = \rho_{\text{leaf}} \text{ and } \tau_{lj} = \tau_{\text{leaf}} \), gives

\[
\frac{I_{d,j-1}}{I_{d,j-1}'} = \frac{I_{d,j}^\tau_L}{I_{d,j}^\tau j - I_{d,j}^\rho_L - I_{b,j-1}(1-T_b)^\tau_{\text{leaf}}} + \rho_L
\]

Re-arranging equation (2.23) yields

\[
\frac{I_{d,j-1}}{I_{d,j-1}'} = \frac{I_{d,j}^\tau_L}{I_{d,j} - (I_{d,j} - I_{d,j}^\rho_L - I_{b,j-1}(1-T_b)^\tau_{\text{leaf}})/\tau_L} + \rho_L
\]
Equations (2.20), (2.21) and (2.24) are the layer equations.

The first step to solve this set of equations is to assume that the component of the downward radiation above the canopy which is beam \( (I_{b,o}) \) is zero, and solve equation (2.24) for the ratio \( I'_{d,j-1}/I_{d,j-1} = \rho_{L} \). In this condition \( (I_{b,o} = 0) \) equation (2.24) becomes

\[
\rho_{L} = \frac{(\tau_{L}^{2} - \rho_{L}^{2})A_{j} + \rho_{L}}{(1-\rho_{L}A_{j})}
\]  

(2.25)

By setting the soil reflectance equal to \( \rho_{L} = 0 \) all \( A_{j} \) values can be found. Still considering \( I_{b,o} = 0 \) and solving equation (2.20) for \( I'_{d,j}/I_{d,j} = A_{j} \) yields an expression for all downward fluxes

\[
I_{d,j} = I_{d,j-1} \frac{\tau_{L}}{1 - \rho_{L}A_{j}}
\]  

(2.26)

where \( I_{d,o} \) in this case is the total downward flux above the canopy.

In this way a first approximation for the values of all up and down fluxes is calculated. For the second step \( I_{b,o} \) is set to its real value and equations (2.20) and (2.21) are applied in full, firstly equation (2.20) is used to calculate all downward fluxes and then these values are used in equation (2.21) to calculate the upward fluxes. This procedure is repeated until \( I_{d,j} \) do not change significantly. Only two or three iterations are necessary to obtain good estimates of the diffuse scattered fluxes (Norman and Jarvis, 1975; Norman, 1979).

The equation presented so far apply for visible (0.4 - 0.7 μm) and near-infrared radiation (0.7 - 3.0 μm).
Sunlit and shaded leaves

The equations presented so far for diffuse and direct radiation are averaged over the horizontal plane. However, this is not the same radiation that the foliage receives unless all its elements lie in the horizontal plane.

To calculate the direct beam radiation appropriated for leaves at different inclination angles, and the leaf area index of sunlit and shaded leaves at each layer \( j \) the approach proposed by Norman (1980) is used.

For a canopy with spherical leaf angle distribution the appropriate beam flux density to each leaf angle class is:

\[
I_{b,i}^* = \left( \frac{I_{b,0}}{\cos \theta} \right) \cos \alpha_i
\]

(2.27)

where \( \frac{I_{b,0}}{\cos \theta} \) is the beam flux density on a plane perpendicular to the direction of the sun, \( i \) is the arbitrary leaf angle class and \( \alpha_i \) is the angle between a plane normal to the leaf's plane and the direction of the sun.

Assuming that all leaves in a layer are exposed to the same diffuse flux as a horizontal leaf the total flux density incident on each class of sunlit leaves is given by:

\[
I_{bd,j}^* = I_{b,i}^* + I_{d,j}^*
\]

(2.28)

Shaded leaves receive only diffuse light and are treated as a single class of leaves.

The sunlit leaf area index in a layer is given by:

\[
\Delta F_j^* = (T_{b,j} - T_{b,j-1})^2 \cos \theta
\]

(2.29)
where $T_{D,0} = 1.0$; the shaded leaf area index is given by:

$$\Delta F_s = \Delta F - \Delta F^* \quad (2.30)$$

The sunlit leaves in the canopy are divided into leaf classes, each class being characterized by a particular angle ($\alpha_i$) between the plane normal to the leaf and the direction of the sun. For a canopy with spherical leaf angle distribution, the fraction of sunlit leaf area ($f_i$) exposed at various angles to the sun is independent of solar zenith angle and is given by:

$$f_i = \sin \alpha_i \, d\alpha \quad (2.31)$$

where $\alpha_1 = 5^\circ$, $\alpha_2 = 15^\circ$, ..., $\alpha_9 = 85^\circ$ for a distribution with nine angle class (Assumption 2).

The sunlit leaf area index for each angle class $i$ and layer $j$ is:

$$\Delta F^*_{ji} = f_i \Delta F^* \quad (2.32)$$

**Thermal radiation**

Because the scattered thermal fluxes within the canopy are small, the thermal fluxes at each layer take into account only the thermal radiation emitted by the foliage. The error that results by not considering the scattering of reflected thermal radiation is small since the emissivity and hence the absorption coefficient of leaves for thermal radiation is near 1.

Following Norman (1979) the downward flux of thermal radiation at layer $j$ is calculated from:
and the upward flux

\[ I'_{T,j-1} = I'_{T,j} \bar{T}_j + \sigma T_{1,j-1}',(1-\bar{T}_j) \]  

(2.34)

where \( \bar{T}_j \) is given by equation (2.17), \( \sigma \) is the Stefan-Boltzmann constant and \( T_{1,j} \) is the leaf temperature (°K) for a leaf at layer \( j \).

By setting \( I_{T,0} = \sigma T_{sky} \), where \( T_{sky} = (T_a - 21) + 0.2 T_a \) (Monteith, 1975), equation (2.33) is applied to obtain all downward thermal fluxes. Using \( I'_{T,N} = \sigma T_{soil} \) equation (2.34) can be applied up through the canopy (Norman personal communication), to yield all upward thermal fluxes.

Radiation load on single leaves

With this set of equations to calculate all radiation fluxes as a function of depth in the canopy, the total load of radiation for a single sunlit leaf in layer \( j \) and leaf angle class \( i \) is obtained from solar and thermal radiation both downward and upward

\[ R_{N,j,i} = R_{s,j} + R'_{s,j} + I_{T,j} + I'_{T,j} + I'_{s,j,i} \]  

(2.35)

where, \( R_{s,j} \) and \( R'_{s,j} \) are the downward and upward solar diffuse fluxes at layer \( j \) (obtained from the sum of visible and near-infrared radiation) respectively; \( I_{T,j} \) and \( I'_{T,j} \) are given by equations (2.33) and (2.34), and \( I'_{s,j,i} \) is the solar beam radiation appropriate for each leaf angle class.

For shaded leaves the total load of radiation is
The equations presented in this section define the radiation environment of individual leaves and will be used on the calculation of photosynthesis and transpiration as described in the following sections.

2.3 Modelling stomatal behaviour

The stomatae are the most important regulators of the diffusion process. By varying the width of the stomatal pores the plant simultaneously controls CO$_2$ entry into the leaf and release of water vapour. Although the mechanism of stomatal control is not yet fully understood, the manifestation of
stomatal movements has been correlated with environmental factors such as light, temperature and vapour pressure deficit. A comprehensive review of the relationship between individual environmental variables and stomatal conductance is presented by Ng (1979).

From knowledge of the stomatal response to environmental variables several models of stomatal conductance have been developed (Shawcroft et al 1973 (maize); Schulze et al 1974 (Prunus armenica); Jarvis 1976 (Sitka spruce); Ng 1979 (Scots pine); Thorpe et al 1980 (apple)). The parameters used in these models need to be determined from observations over a wide range of conditions or in controlled environment, and are specific to the species under study.

Jarvis (1976), working with Sitka spruce, determined the effects on stomatal conductance of five environmental variables (light, temperature, vapour pressure deficit, CO\textsubscript{2} concentration and water potential). Jarvis' model, with some alteration is applied in this work.

Assumptions

1. Stomatal conductance responds to the environmental variables independently except vapour pressure deficit, which interacts with temperature;
2. Stomatal conductance is given by the product of the functions describing the response to the environmental variables;
3. The responses of leaves of different ages and positions have the same general form.

The response of stomatal conductance to each environmental variable is described by dimensionless functions \( k_s \) with values between 0 and 1. Each \( k_s \) is a multiplier for maximum stomatal conductance \( g_s \text{ max} \), reducing stomatal conductance if the corresponding environmental variable is sub-optimum. In his work Jarvis (1976) uses the approach of multipliers. However, in his work the difference between stomatal conductance and multipliers is not clear, since the same symbol is used to describe both: stomatal conductance and multipliers.

Response to light

Stomata open in response to increasing photon flux density of visible radiation and close in declining photon flux density. Stomatal conductance increases rapidly over low flux densities, tending asymptotically to a maximum value at high photon flux densities. (Ludlow and Jarvis 1971; Turner 1973; Warrit et al 1980).

The relation between stomatal conductance \( g_s \) and photon flux density \( Q_p \) has been shown to be appropriately described by a rectangular hyperbola accounting for a finite value of \( g_s \) in the dark (Ng 1979).
Figure 2.3 The relation between stomatal conductance and photon flux density, as represented by the function $k_s(Q_p)$. $G_1$ is the asymptotic value of $k_s$ at infinite light, $G_2$ is $\Delta k_s/\Delta Q$ at the point where the hyperbola meets the abscissa and $G_3$ accounts for a finite value of $k_s$ in the dark.

The mathematical expression describing the rectangular hyperbola is:

$$k_s(Q_p) = \frac{G_2 (Q_p + AO)}{G_1 + G_2 (Q_p + AO)} \quad (2.37)$$

If $AB$ in Figure 2.3 is assumed to be a straight line, then

$$AO = \frac{G_3}{G_2} \quad (2.38)$$
From equations (2.37) and (2.38) it follows that the function describing the dependence of stomatal conductance upon photon flux density, when the other variables are not limiting is:

\[
k_s(Q) = \frac{G_2 (Q_p + (G_3/G_2))}{G_1 + G_2 (Q_p + (G_3/G_2))}
\]

Converting the range of \( k_s \) from 0 to \( G_1 \) to 0 to 1 we have

\[
k_s(Q) = \frac{G_2 (Q_p + (G_3/G_2))}{G_1 + G_2 (Q_p + (G_3/G_2))}
\]

Response to temperature

Stomatal conductance increases with increasing temperature reaching a maximum at intermediate temperature and thereafter declining (Neilson and Jarvis 1975).

The relation between \( g_s \) and leaf temperature can be represented by a bell shaped function (Figure 2.4).

![Figure 2.4](Image)

Figure 2.4 The relation between stomatal conductance and temperature, as represented by the function \( k_s(T) \). \( G_4 \) is the low temperature for \( k_s = 0 \), \( G_5 \) is the temperature for maximum \( k_s \) and \( G_6 \) is the high temperature for \( k_s = 0 \).
The function describing the relation between stomatal conductance and temperature is:

\[ k_s(T) = B_2 (T - G_4) (G_6 - T)^{B_1} \]  \hspace{1cm} (2.41)

where

\[ B_1 = \frac{(G_6 - G_5)}{(G_5 - G_4)} \]

and

\[ B_2 = \frac{1}{((G_5 - G_4)(G_6 - G_5)^{B_1})} \]

\( B_1 \) is the temperature ratio that describes whether the optimum temperature is biased towards the low temperature for \( k_s = 0 \) or towards the high temperature for \( k_s = 0 \).

Response to vapour pressure deficit

A linear reduction in \( g_s \) with increasing vapour pressure deficit (\( \delta e \)) has been found (Grace et al, 1975; Neilson and Jarvis, 1975; Watts et al, 1976).

Jarvis (1976) described the relation between \( g_s \) and \( \delta e \) with the following function:

\[ k_s(\delta e) = 1 - G \delta e \]  \hspace{1cm} (2.42)

where \( G = 1/G_v \) is the slope of the relation and \( G_v \) is the point at which the curve cuts the vapour pressure deficit axis.

\( G_v \) is assumed to depend linearly upon temperature (Ng 1979).

The equation describing the dependence of \( G_v \) upon temperature is

\[ G_v = G_7 (T - G_4) \]  \hspace{1cm} (2.43)

where \( G_7 \) is the slope of the relation and \( G_4 \) is as previously defined.
The function describing the response of \( g_s \) to vapour pressure deficit can be rewritten as:

\[
k_s(\delta e) = 1 - \frac{1}{S_G(T - S_G)} \cdot \delta e\tag{2.44}
\]

The complete model for stomatal conductance

Following Jarvis (1976), Ng (1979) and Thorpe et al. (1980) the response of stomatal conductance to environmental variables can be expressed as:

\[
q_s = g_s \max k_s(Q_p) k_s(T) k_s(\delta e)\tag{2.45}
\]

where \( g_s \max \) is the maximum stomatal conductance (m/s) and is dependent upon the leaf's age (Jarvis et al. 1976 - Table XII).

In its original form the model also related stomatal conductance with \( CO_2 \) concentration in the air and leaf-water potential.

The relationship between \( g_s \) and leaf-water potential demonstrate that there is a threshold level of water potential above which \( g_s \) remains constant and high, and below which the stomata conductance falls steeply (Turner and Waggoner 1968; Watts and Neilson 1978), but in forest canopy stomatal closure rarely occurs in response to leaf-water potential which stays above the threshold potential (Beadle et al. 1979).

Neilson and Jarvis (1975) have found that the stomata of Sitka spruce needles do not respond to \( CO_2 \) concentration in the atmosphere between 30 and 600 cm\(^3\)/m\(^3\).
Since field conditions for the threshold potential and CO$_2$ concentration are unlikely to occur, the functions relating $g_s$ to leaf water potential and CO$_2$ concentration are not considered in this model.

2.4 Modelling photosynthesis

Literally, photosynthesis means "synthesis with the help of light". Commonly the term is applied to describe the process by which plants synthesize organic compounds from inorganic raw materials in the presence of sunlight; this process is also called "carbon assimilation". Although much theoretical and experimental research have been done on the physiological aspects of photosynthesis (Rabinowitch and Gorindjee 1969; Beath 1970; Hall
and Rao 1978) our main concern will be primarily with the response
of photosynthesis to environmental variables such as light,
temperature and carbon dioxide concentration.

Several models of this response have been published. These
models consider photosynthesis at two levels; the whole leaf
level (Chartier 1970; Acock, Thornley and Warren Wilson 1971;
Lommen et al 1971; Charles-Edwards and Ludwig 1974; van Bavel
1975; Tenhunen, Yocum and Gates 1976) and at the plant and crop
level (de Wit 1965; Duncan et al 1967; Lemon, Stewart and
Shawcroft 1971; Proctor, Watson and Landsberg 1976; Reed et al
1976; Acock et al 1978; Thorpe et al 1978). Some of these
models are very simple and need only the knowledge of a few
parameters specific to the species in study and the weather
conditions as input. On the other hand, some are very complex and
the number of parameters required is so extensive that their use
is very limited.

A simple model for leaf photosynthesis in relation to environ-
mental and physiological factors is described here. The model
makes use of few parameters which can be easily found in the
published literature for particular species.

Assumptions
1. The function describing the response of photosynthesis
to photon flux density is a non-rectangular hyperbola;
2. Dark respiration decreases exponentially with light and
increases exponentially with temperature;
3. The relation between CO₂ compensation point and temperature is assumed linear over the whole range of temperature.

The photosynthetic rate increases linearly over low photon flux densities; this increase is followed by a gradual, but still substantial increase over high photon flux densities until saturation is reached and photosynthesis becomes independent of light. The response of photosynthesis to light is commonly described as a rectangular hyperbola (de Wit 1965; Duncan et al 1967; Lommen et al 1971; Proctor, Watson and Landsberg 1976; Thorpe et al 1978), but several authors prefer to use a non-rectangular hyperbola because such a curve would better represent the relation at low levels of photon flux density, at the point where the curve starts to bend (Prioul and Chartier 1977; Goudriaan 1978). In fact, Leverenz (1979) found that the non-rectangular hyperbola gives a better fit to the light response curves for Sitka spruce needles, than the commonly used rectangular hyperbola. For this reason a non-rectangular hyperbola was chosen to model the light response curve of photosynthesis.

According to Thornley (1976):

\[ MP^2_G - (\alpha Q_p + P_{max})P_G + \alpha Q_p P_{max} = 0 \]  

(2.46)

is the equation of a non-rectangular hyperbola relating gross photosynthesis \( (P_G) \) to photon flux density \( (Q_p) \). The parameter \( M \), called the convexity parameter, enables a family of curves to be produced, all with the same initial slope \( (\alpha) \) and final
asymptote ($P_{\text{max}}$).

The gross photosynthesis can be related to the CO$_2$ flux through the stomata or net photosynthesis ($P$) by

$$P_G = P + R_d$$  \hspace{1cm} (2.47)

where $R_d$ is the rate of dark respiration.

Combining equations (2.46) and (2.47) gives:

$$MP^2 + (2M R_d - \alpha Q)P + (\alpha Q - R_d - P)P_{\text{max}} + R_d^2 M - \alpha CR_d = 0$$  \hspace{1cm} (2.48)

On the basis of experimental data Watson, Landsberg and Thorpe (1978) made the assumption that

$$\frac{C_i}{r_m} - R_l$$  \hspace{1cm} (2.49)

where $r_m$ is the mesophyll resistance, $R_l$ is the photorespiration and according to Reed et al (1976) can be expressed as

$$R_l = \frac{r}{r_m}$$  \hspace{1cm} (2.50)

where $\Gamma$ is the CO$_2$ compensation point. $C_i$ is the concentration of CO$_2$ in the intercellular spaces and is described as:

$$C_i = C_a - P(r'_a + r'_s)$$  \hspace{1cm} (2.51)

where $C_a$ is the ambient CO$_2$ concentration, $r'_s$ is the diffusion resistance for CO$_2$ through the stomata and is obtained by multiplying $r_s$ for water vapour transfer by 1.606; $r'_a$ is the diffusion resistance for CO$_2$ transfer in the boundary layer and is given by multiplying the water vapour transfer resistance by 1.37 (Ludlow and Jarvis 1971).
Combining equations (2.49), (2.50) and (2.51) it yields:

\[ P_{\text{max}} = \frac{C_a - \Gamma - P(r' + r')}{r_m} \]  
(2.52)

Substituting the value of \( P_{\text{max}} \) in the right hand side of equation (2.48) and solving further it gives:

\[
(M + \frac{r' + r'}{r_m})P^2 + \{ (2M + \frac{r' + r'}{r_m})R_d - (1 - \frac{a_s}{r_m})Q_p \} P + \frac{C_a - \Gamma}{r_m} \}
= 0
\]  
(2.53)

Equation (2.53) has the form \( ax^2 + bx + C = 0 \) and can be solved for \( P \) by the quadratic formula.

\[ P = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a} \]  
(2.54)

where

\[ a = M + \frac{r' + r'}{r_m} \]  
(2.55a)

\[ b = (2M + \frac{r' + r'}{r_m})R_d - (1 - \frac{a_s}{r_m})Q_p - \frac{C_a - \Gamma}{r_m} \]  
(2.55b)

\[ c = \frac{C_a - \Gamma}{r_m} + (R_dM - \frac{a_s}{r_m})R_d \]  
(2.55c)

The result from equation (2.54) yields the photosynthetic rate for a single leaf for a given photon flux density and ambient \( \text{CO}_2 \) concentration. In this equation, except for \( \alpha \) and \( M \), all the remaining parameter are related to weather conditions, therefore, they must be calculated for each particular situation.
The dark respiration \( (R_d) \)

Reed et al (1976) assumed \( R_d \) to increase exponentially with temperature and to decrease exponentially with irradiance. The response to temperature in the dark is:

\[
R_d(T) = R_d(0) \exp (\delta T)
\]  

(2.56)

and the response to irradiance at a particular temperature \( T \) is:

\[
R_d(Q_P,T) = A_s + (R_d(T) - A_s) \exp (-\zeta Q_P)
\]  

(2.57)

Combining equations (2.56) and (2.57) and assuming \( A_s = 0 \) (Reed et al 1976)

\[
R_d = R_d(O,O) \exp (\delta T) \exp (-\zeta Q_P)
\]  

(2.58)

where \( \delta \) and \( \zeta \) are the temperature and radiation coefficients respectively, \( R_d(O,O) \) is the dark respiration at 0 °C and \( Q_P = 0 \), and \( A_s \) is the asymptote of the curve relating \( R_d \) to \( Q_P \) and its value can be taken as zero.

The CO\(_2\) compensation point (\( \Gamma \))

Neilson, Ludlow and Jarvis (1972) have shown that \( \Gamma \) increases linearly with temperature in the range of 8 to 30 °C. For convenience the relation is assumed linear for the whole range of temperature, and the relation is described by:

\[
\Gamma = 2.4 T + 27.5
\]  

(2.59)

The boundary layer resistance (\( r_a \))

According to Landsberg and Thom (1971) the boundary layer resistance for water vapour transfer for individual shoots can
be obtained with the equation:

\[ r_a = 7.77 \theta_1^{0.38} u(z)^{-0.58} \]  \hspace{1cm} (2.60)

where \( \theta_1 \) is the shoot density and \( u(z) \) is the wind speed at the height \( z \) within the canopy and can be evaluated according to the equation derived by Thom (1971):

\[ u(z) = u_h \left( 1 + \alpha' (1 - (z/h)) \right)^{-2} \]  \hspace{1cm} (2.61)

where \( u_h \) is the wind speed above the canopy, and \( \alpha' \) is related to the leaf area density at height \( z \), \( L_T(z) \), as (Landsberg and Jarvis 1973):

\[ \alpha'(z) = 6.85 \frac{\sqrt{L_T(z)}}{u_h} \]  \hspace{1cm} (2.62)

The mesophyll resistance \( r_m \)

The relation between mesophyll resistance and temperature can be represented by a U-shaped curve (Neilson, Ludlow and Jarvis (1972)) and can be described by:

\[ r_m = r_{\text{min}} \left\{ 1 / (R2(T - T_{\text{low}})(T_{\text{high}} - T)^{R1}) \right\} \]  \hspace{1cm} (2.63)

where

\[ R1 = (T_{\text{high}} - T_{\text{m}}) / (T_{\text{m}} - T_{\text{low}}) \]

\[ R2 = 1 / ((T_{\text{m}} - T_{\text{low}})(T_{\text{high}} - T_{\text{m}})^{R1}) \]

\( T_{\text{low}} \) and \( T_{\text{high}} \) are the low and high temperatures for maximum mesophyll resistance respectively, \( T_{\text{m}} \) is the temperature for minimum mesophyll resistance and \( r_{\text{min}} \) is the minimal \( r_m \).
A diagram for the interaction of equations (2.48) to (2.63) is summarised in Figure 2.5.

![Diagram](image)

Figure 2.5  Simplified diagram for the sub-model. The numbers in each box correspond to the number of the equation describing the variable in the text.

In section 2.2 the canopy is assumed to be divided into \( N \) layers of leaf area index 0.5. The photosynthetic rate for each layer can be calculated by integrating the rates for single leaves obtained from equation (2.54). The contribution of shaded and sunlit leaves, and of leaves of different age classes to the photosynthetic rate of layer \( j \) \( (P_j) \) can be calculated by:
\[ P_j = \sum_{i=1}^{M} \sum_{a=O}^{7} \left( P_{ji}(I_{d,i}) \Delta F^*_{ji} \rho_a \right) + P_j(I_{d,j}) \Delta F_s \rho_a \]  

(2.64)

where, \( P_{ji}(I_{d,i}) \) is the photosynthetic rate for a leaf at layer \( j \) and leaf angle class \( i \) calculated by equation (2.54) using the photon flux density appropriated for each angle class, \( \Delta F^*_{ji} \) is the sunlit leaf area index for leaves at layer \( j \) and leaf angle class \( i \), \( \rho_a \) is the proportion of the leaf area of layer \( j \) occupied by leaves of age class \( a \), \( P_j(I_{d,j}) \) is the photosynthetic rate for shaded leaves calculated with the appropriated photon flux, and \( \Delta F_s \) is the leaf area index of shaded leaves at layer \( j \).

The photosynthetic rate for the canopy can be calculated as the sum of the rates for each layer.

2.5 Modelling Transpiration
The importance of transpiration is recognised in studies of water balance of catchment areas and applied agriculture such as irrigation. It is also of physiological interest since transpiration influences both the water and energy budget of the plant.

The aim of a transpiration model is to predict the rate of water loss from a single leaf, plant or canopy as it is influenced by radiation, temperature, humidity and physiological parameters.

A number of simple models based on more or less empirical relations have been developed to provide estimates of evaporation from open water surfaces. Among the better known are those of Thornthwaite, Penman, Blaney and Criddle, Prescott, and Jensen-Haîse (see Slatyer (1967) and Rosemberg (1974) for references and details). Some of them have also been applied to plant community surfaces and bare soils. In general these approaches relate the evaporation to commonly measured meteorological elements and the empirical parameters used in the models are usually derived from statistical analysis on observed data during seasons or even years for a certain region. Therefore, reliable results are unlikely over shorter periods, say hours, as required by refined micrometeorological studies. Furthermore, since using climatic data only, they cannot be applied to actual field situation where crop and soil factors influence the evapotranspiration process.

The model developed by Penman (1948) was modified by Monteith (1965a) to account for the evaporation not only of wet surfaces, but from surfaces such as plants and soils. This is
known as the combination method or the Penman-Monteith equation. The equation can be applied to single leaves or extensive canopies (Monteith 1975) over short periods of time, such as weeks, days or hours.

To calculate the hourly transpiration rate of single leaves the Penman-Monteith equation is adopted in this work.

The Penman-Monteith equation relates transpiration rate to meteorological elements and physiological characteristics of the vegetation in studies as follows:

\[
\frac{\Delta A + c_p \delta e g_a}{\lambda e} = \frac{\Delta + \gamma (1 + (g_a/g_s))}{2.65}
\]

(2.65)

where \( \Delta \) is the available energy, \( \delta e \) is the saturation deficit of the air, \( g_a \) is the boundary layer conductance, \( g_s \) is the stomatal conductance, \( c_p, \rho, \gamma \) and \( \lambda \) are physical parameters, namely, the specific heat of air, the density of air, the psychrometric constant and the latent heat of vaporization of water, respectively, and are all weak functions of temperature (Monteith 1975, Table A.3), and \( \Delta \) is the slope of the curve relating the saturated vapor pressure of water to temperature and varies considerably with temperature (Monteith 1975, Table A.4).

As the dependence of \( c_p, \rho, \gamma \) and \( \lambda \) to temperature is very weak they are considered as constants in the sub-model, on the other hand as the value of \( \Delta \) varies from 0.83 at 10 °C to 1.53 at 20 °C its value is calculated for each temperature considered.

In order to calculate the slope of the curve relating the saturated vapor pressure of water to temperature from a given
temperature ($T_a$), the vapour pressure of saturated air was calculated at two temperatures ($T_a + 0.5$) °C and ($T_a - 0.5$) °C according to the equation described by Unwin (1980),

$$e_{s(T_a)} = 10^x$$

(2.66)

$$x = 9.24 - \frac{2305}{T} - \frac{500}{T^2} - \frac{100000}{T^3}$$

(2.67)

where $e_{s(T_a)}$ is the saturation vapour pressure at temperature $T_a$ in millibars, and $T$ is the temperature in degrees Kelvin. This formula gives a value of $e_{s(T_a)}$ to within ± 0.1 mbar of those given by Monteith (1975 - Table A.4) over the range of -5 to +34 °C.

The slope of the saturation curve was calculated as:

$$\Delta = \frac{e_{s(T_a + 0.5)} - e_{s(T_a - 0.5)}}{\Delta T}$$

(2.68)

and $\Delta T = (T_a + 0.5) - (T_a - 0.5) = 1$

Assuming that for this interval of 1 °C the relation between saturation vapour pressure and temperature is linear.

The values of transpiration calculated with equation (2.65) can be integrated to render the transpiration rates for a single layer and for the complete canopy as previously described in Section 2.4 for photosynthesis.

2.6 The Complete Model

The complete model may be briefly described as follows:
Using values for the weather variables above the canopy, the microclimate for each leaf within the canopy is evaluated; weighted mean hourly values of transpiration and CO₂ assimilation for each layer are then estimated and integrated to give the mean hourly values of transpiration and photosynthesis for the complete canopy.

Several sub-models were previously presented each one describing in detail the steps required to achieve the hourly rates for the canopy. The interaction between them is presented in this section.

Figure 2.6 shows the way in which the sub-models are linked together in order to calculate the hourly rate of photosynthesis.

For a particular day of the year the leaf area index for the canopy is calculated and distributed between several layers of equal leaf-area-index. The height of each layer, the proportion of leaves of different age classes and the leaf area density at each layer are also calculated. Once these variables related to the structure of the canopy have been defined they are transferred to the subsequent sub-models.

The number of layers in the canopy is transferred to the radiation sub-model and the flux of radiation relative to height is predicted for sunlit and shaded leaves. The visible and near-infrared portions of the spectrum are calculated independently. For each layer the leaf-area allocated for sunlit and shaded leaves is also calculated. The flux of visible radiation are later utilized to calculate photosynthesis.
Figure 2.6: Simplified diagram showing the links between the sub-models. Symbols are as described in the text.
The flux of CO$_2$ is diffused through the leaf boundary layer ($r_a$). The larger the leaf boundary layer, the greater the diffusion resistance; however the thickness of the leaf boundary layer is dependent upon the air flow over the leaf, therefore to calculate $r_a$, the windspeed at the height of each layer has to be known in order to calculate the appropriate $r_a$ for leaves at different height in the canopy. So, from the first sub-model the number of layers, the height of each layer and the leaf area density for each height are transferred to the boundary layer resistance sub-model where the wind profile within the canopy is estimated and then used on the calculation of $r_a$.

The flux of CO$_2$ has also to overcome an additional resistance, a physiological resistance imposed by the opening and closure of the stomata. As was mentioned earlier, the resistance for diffusion of CO$_2$ through the stomata is correlated to environmental variables, age and position inside the canopy. Temperature and vapour pressure deficit are given variables, but the visible radiation flux for each leaf is transferred from the radiation sub-model and the position of each leaf from the leaf area sub-model.

Finally the outputs so far mentioned and the values for the weather variables above the canopy are brought together to calculate the photosynthetic rate for single leaves according to whether they are sunlit or shaded, their age and position inside the canopy. Values of photosynthetic rate for single
leaves are then integrated rendering the hourly photosynthetic rates for each layer and for the complete canopy.

From Figure (2.6) it can be seen that the links between the sub-models are the same to calculate the transpiration rate, except that the outputs transferred from the radiation sub-model correspond to the total load of radiation for shaded and sunlit leaves instead of visible radiation.

2.7 The Structure of the Model

In the previous sections the main sub-models of the system to be simulated were treated in detail. The theory involved in the different processes was presented and the relations between the driving variables and the rate processes were described. The theoretical considerations of the previous sections can be quantitatively evaluated when they are formulated in terms of a computer program. A computer program was therefore developed in such a way that parts of the simulated system could be separately analysed or, when required, any function or any sub-model could easily be exchanged for more realistic ones describing the process being considered.

The program was written in FORTRAN 77 and consists of a control program and six subroutines. Figure 2.7 shows a simplified flowchart of the complete program, constructed according to the conventions described by Chapin (1974). A complete print out of the control program and of the subroutines is presented in Appendix A.

The program has four nested loops: the first loop accounts for the total period of the simulation in time steps of one hour, the second for the N layers being considered, the third accounts for the age classes and the last one for the leaf-angle classes.
Figure 2.7: Simplified flowchart for the complete programme
After reading the basic model parameters, the program reads for each hour the weather conditions variables and then for each layer, each age class and leaf-angle class, it computes, by calling the appropriated subroutines, the leaf area index and the vertical distribution of foliage, and hourly values of the radiation fluxes, the boundary layer resistance, the stomatal conductance, the photosynthetic and transpiration rates.

Finally, the print-out of the program consists of hourly photosynthesis and transpiration for each layer and for the whole canopy.

Although the leaf area index and the vertical distribution of foliage only need to be calculated once each day, these outputs need to be transferred hourly to all the sub-routines. As no arrays are transferred from one sub-routine to another, this sub-routine needs to be located inside the innermost DO-loop so that the appropriated outputs for each layer can be transferred to the other sub-routines.

Each sub-routine was written in such a way that they can be considered as black boxes, i.e. a complete sub-model can be replaced by another which simulates the same process in a different way, with only small alterations in the control program or in the other sub-routines. This feature provides flexibility for experimenting with new hypotheses and relationships even if the number of variables and parameters differ from those previously being considered.
CHAPTER 3

A MODULAR APPROACH FOR IMPLEMENTING THE MODEL

For each one of the sub-models described in the previous chapter a computer program was written which was composed of a control program and a sub-routine describing the process being simulated. Each program was written in order to analyse the performance of the sub-models and explore in full its capacity, extracting from each sub-routine as much information as possible. For the complete model all the sub-routines were linked together via a main program in order to calculate hourly rates of photosynthesis and transpiration for single leaves, convert these values to a leaf area basis and integrate them to render the photosynthetic and transpiration rates for layers and for the canopy. However, as with any model implemented as a compiled program, it was difficult, although able to experiment with the model by changing its structure (adding or removing sub-models), by switching between observed or arbitrary inputs for climatic variables, and by observing the response of the model to ranges of values for different parameters.

In order to achieve this flexibility, the sub-routines were incorporated into PRESTO, a package program developed by Dr. R. I. Muettzelfeldt.

Some of the features of PRESTO and examples of the versatility that is achieved by incorporating the sub-routines in this program are presented in the following sections.
3.1 PRESTO

Basically PRESTO is a control program that provides a number of data handling and modelling facilities in one program, using one set of conventions. The main features currently included in PRESTO are:

- information retrieval from numeric and alphanumeric data sets (e.g. bibliographic data);
- graphical and statistical analysis of data;
- mathematical modelling, including facilities for implementing models based on analytical equations (as in the present study), differential equations, compartment models and complete models of ecological systems.

Despite its scope, PRESTO is a simple program to use. The steps needed to achieve a specific objective (e.g. statistical analysis) consist of moving through a series of 'menu' type options. This simplicity enables access to PRESTO even to users with no previous knowledge of computing.

Although several of PRESTO's features, such as plotting graphs, have been used for the work described in this chapter, the following discussion is restricted to the modular modelling facility in PRESTO for implementing models based on analytical equations.

3.2 The modular approach

The modular approach is a facility provided by PRESTO to manipulate models described by analytical equations. The models
may be described by a single equation or by a complex set of equations. Either the simple or complex calculation is called a module, and PRESTO sees no basic difference between them.

Consider for example the equation given by Monteith (1975) to calculate the actual vapour pressure:

\[ \text{AVP} = \text{SVP} - 0.65 \times (\text{TEMP} - \text{TWET}) \]

The equation has as input the saturated vapour pressure at wet bulb temperature (SVP), air temperature (TEMP) and wet bulb temperature (TWET) and only one output (AVP). As a module, according to PRESTO conditions, this equation could be diagrammatically represented as:

\[ \begin{align*}
\text{SVP} &\quad \rightarrow \quad \text{AVP} = \text{SVP} - 0.65 \times (\text{TEMP} - \text{TWET}) \\
\text{TEMP} &\quad \rightarrow \\
\text{TWET} &\quad \rightarrow \\
\end{align*} \]

where AVP1 is the module's name.

By using the modular approach the value of AVP can be calculated from single values for all the inputs, or by varying the values of one or more of the inputs over a determined range, or by reading the input data straight from a file. The output
could then be analysed by plotting graphs of AVP against any of the inputs or by means of statistical analysis.

The modular approach allows experiments to be done for single modules or for a combination of modules. When two or more modules are combined PRESTO sorts them into the order in which they need to be calculated and links by name the input of one module which are provided as an output of another module. Figure 3.1 gives an example of the combination of two modules. Figure 3.1a represents two individual modules and Figure 3.1b represents the combination of the two modules with common inputs. For clarity only two of the modules, representing the sub-models of stomatal conductance and transpiration are presented.

The programs written for each one of the sub-models being considered in this study had to be modified so that they could be transformed into modules and incorporated into PRESTO. The major change was to make them completely independent of each other and to achieve the requirement that, despite the complex sequence of equations in each module, they would behave as a single equation.

3.3 Solving equations with single values for all inputs

For each module a set of typical input variables is stored in PRESTO. When the module is loaded, the name of the input variables are presented, one at a time, so that single values can be assigned to each of them. If no value is provided, for a particular input, the equations are solved using typical values
Figure 3.1 Combination of two modules. (a) two individual modules, (b) combination of two modules with common inputs.
for these inputs. A facility is provided to alter the value of a variable without going through the routine of attributing values to all variables.

The process of loading a module and solving the equations with the set of typical values kept in store, and for solving the equations with a new value for one of the input variables is presented in Example 1 for the module calculating transpiration as described in Section 2.5. The description of the variables is presented in Appendix A.

Example 1 - Solving the equations to calculate transpiration using single values for all the parameters.

:PRESTO
Hello, and welcome to PRESTO!

Type HELP and press the RETURN key if you are stuck.

1 Information retrieval.
2 Graphics.
3 Statistics.
4 Modelling.
5 Teaching material.
6 University information.
7 PRESTO information.

PRESTO : 4

4 Modelling.

1 Model is in the form of analytical equations.
2 Model is in the form of differential or difference equations.
3 Compartment modelling.
4 Matrix models of population dynamics (Leslie matrix).
5 Stochastic models.
6 Ecological Lego: building blocks for constructing models.
7 Complete self-contained models of ecological systems.
PRESTO : 1

1 Model is in the form of analytical equations.
2 Find out about the modules available.
3 Load one or more modules (mathematical function) from the library.
4 Assign values to all input variables and solve the set of equations.
5 Change the value of an input variable and solve the set of equations.
6 Print out the modules in hierarchical form.
7 Produce aggregated output variables.
8 Describe variables: means, min, max, SD, etc.
9 Graph one variable against another.

PRESTO : 2

2 Load one or more modules (mathematical function) from the library.

Press the RETURN key to finish.

Function : TRANSPIRE1
[ TRANSPIRE1 ]EVP,EVPL,EVPC = f( LAYER,CLASS,ANGLE,T,DL,RA,GS,QN,QAREA,AGELAI,H

Function :
2
1

Model is in the form of analytical equations.

1 Find out about the modules available.
2 Load one or more modules (mathematical function) from the library.
3 Assign values to all input variables and solve the set of equations.
4 Change the value of an input variable and solve the set of equations.
5 Print out the modules in hierarchical form.
6 Produce aggregated output variables.
7 Print values for selected variables.
8 Describe variables: means, min, max, SD, etc.
9 Graph one variable against another.

PRESTO : 3

3 Assign values to all input variables and solve the set of equations.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>VALUE</th>
</tr>
</thead>
<tbody>
<tr>
<td>LAYER</td>
<td>1.0000</td>
</tr>
<tr>
<td>CLASS</td>
<td>1.0000</td>
</tr>
<tr>
<td>ANGLE</td>
<td>0.0000</td>
</tr>
<tr>
<td>T</td>
<td>15.0000</td>
</tr>
<tr>
<td>DL</td>
<td>0.7000</td>
</tr>
<tr>
<td>RA</td>
<td>12.0000</td>
</tr>
<tr>
<td>GS</td>
<td>1.0000</td>
</tr>
<tr>
<td>QN</td>
<td>800.0000</td>
</tr>
<tr>
<td>QAREA</td>
<td>0.1700</td>
</tr>
<tr>
<td>AGELAI</td>
<td>0.8900</td>
</tr>
<tr>
<td>HOUR</td>
<td>6.0000</td>
</tr>
</tbody>
</table>
Model is in the form of analytical equations.

1 Find out about the modules available.
2 Load one or more modules (mathematical function) from the library.
3 Assign values to all input variables and solve the set of equations.
4 Change the value of an input variable and solve the set of equations.
5 Print out the modules in hierarchical form.
6 Produce aggregated output variables.
7 Print values for selected variables.
8 Describe variables: means, min, max, SD, etc.
9 Graph one variable against another.

PRESTO : 4

4 Change the value of an input variable and solve the set of equations.

Variable : DL
New value: 0.25

Input variable(s)  | LAYER = 1.00000  
| CLASS = 1.00000  
| ANGLE = 0.00000  
| T = 15.00000  
| DL = 0.25000  
| RA = 12.00000  
| GS = 1.00000  
| QN = 800.00000  
| QAREA = 0.17000  
| AGELAI = 0.89000  
| HOUR = 6.00000  

Output variable(s)  | EVP = 24.01854  
| EVPL = 24.01854  
| EVPC = 24.01854  

Press RETURN

PRESTO : Q
3.4 Studying responses

If instead of solving the equations to calculate transpiration using single values for all the input variables, the response of transpiration to changes in vapour pressure deficit (DL) over a specific range is desired, this can be achieved by defining the range over which DL is made to vary and the step interval for incrementing DL, i.e.:

\[
DL = 0 \text{ TO } 1 \text{ STEP } 0.05
\]

the same as it would be done in a DO-loop.

The difference between this process and the previously described is that when assigning values for all the input variables, no value is attributed to DL; instead its name is typed indicating that each value of vapour pressure deficit in the specified range is to be used. In Example 3.2 the response of transpiration to changes in vapour pressure deficit is presented.

This ability to specify a range of values can be done for any input, including those normally considered to be parameters. In addition, more than one input can be given a range of values, in which case the model is solved for every combination of input values.

When a set of values is specified for one or more inputs, PRESTO does not print the results of solving the model, but stores the results in PRESTO variables which can subsequently be printed or plotted.

Example 2 - Response of transpiration to changes in vapour pressure deficit.
Hello, and welcome to PRESTO!

Type HELP and press the RETURN key if you are stuck.

1 Information retrieval.
2 Graphics.
3 Statistics.
4 Modelling.
5 Teaching material.
6 University information.
7 PRESTO information.

PRESTO: 4 1 2

4 Modelling.

1 Model is in the form of analytical equations.
2 Load one or more modules (mathematical function) from the library.

Press the RETURN key to finish.

Function: TRANSPIRE1

[TRANSPIRE1]EVP,EVPL,EVPC = f(LAYER,CLASS,ANGLE,T,DL,RA,GS,QN,QAREA,AGELAI,H

Model is in the form of analytical equations.

1 Find out about the modules available.
2 Load one or more modules (mathematical function) from the library.
3 Assign values to all input variables and solve the set of equations.
4 Change the value of an input variable and solve the set of equations.
5 Print out the modules in hierarchical form.
6 Produce aggregated output variables.
7 Print values for selected variables.
8 Describe variables: means, min, max, SD, etc.
9 Graph one variable against another.

PRESTO: DL=0 TO 1 STEP 0.1
Variable DL has been calculated.

PRESTO: 3

3 Assign values to all input variables and solve the set of equations.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>VALUE</th>
</tr>
</thead>
<tbody>
<tr>
<td>LAYER</td>
<td>1.0000</td>
</tr>
<tr>
<td>CLASS</td>
<td>1.0000</td>
</tr>
<tr>
<td>ANGLE</td>
<td>0.0000</td>
</tr>
<tr>
<td>T</td>
<td>15.0000</td>
</tr>
<tr>
<td>DL</td>
<td>12.0000</td>
</tr>
<tr>
<td>RA</td>
<td>800.0000</td>
</tr>
<tr>
<td>QN</td>
<td>0.1700</td>
</tr>
<tr>
<td>QAREA</td>
<td>0.8900</td>
</tr>
<tr>
<td>HOUR</td>
<td>6.0000</td>
</tr>
</tbody>
</table>
9 Graph one variable against another.

1 Plot one or more graphs.
2 Select plotting devices (this terminal is the standard device).
3 Select type of graph (scatter diagram is the standard type).
4 Set plotting options, if you are unhappy with standard settings.

PRESTO : 1

1 Plot one or more graphs.

X variable(s): DL
Y variable(s): EVP.1

Symbol Y variable X variable
+ EVP.1 vs DL

45.000+
I
I
39.000+
I
I
33.000+
I
I
27.000+
I
I
21.000+
+I
I
15.000+
-----+-------------------0.000
0.200 0.400 0.600 0.800 1.000

Press RETURN

PRESTO : Q
3.5 Input of climatic variables

As with many models, the present model has climatic inputs, and we need to be able to solve the model with observed values for these inputs. For the transpiration module considered in the previous examples these data consist of air temperature (T), vapour pressure deficit (DL) and the load of radiation (QN). To calculate the transpiration rate, PRESTO reads the input data from a file set to certain conventions, i.e., the first line of the file contains the number of climatic variables (in this case 3) and the number of measurements made, the following lines give the name of each variable, and the remaining lines contain the values of the variables. The name given to a climatic variable in the file does not need to be the same as the name in PRESTO, but when assigning values to the input variables the new name must be attributed to the corresponding input variable (see Example 3).

When more than one input variable have a range of values, PRESTO needs to know at which sequence they are to be made to vary. This sequence is controlled by a series of nested DO-loops, which are numbered in ascending order starting from the innermost loop.

If only one variable has a range of values, all external DO-loops are skipped and only the innermost loop is considered. The same occurs when more than one variable have a range of values and need to be made to vary at the same time, for example the same DO-loop number is attributed to all climatic inputs, since they must be used together on an hourly basis.

Example 3 - Response of transpiration to climatic data
Hello, and welcome to PRESTO!

Type HELP and press the RETURN key if you are stuck.

1 Information retrieval.
2 Graphics.
3 Statistics.
4 Modelling.
5 Teaching material.
6 University information.
7 PRESTO information.

PRESTO: 2 1 2 TRANS

2 Graphics.
1 Input data from the terminal or a file.
2 Input data from a file set up to PRESTO conventions.

The following variables are in the file:
HOUR QN T VPD

13 cases picked up successfully.
Press RETURN

PRESTO: F 4 1 2

Hello, and welcome to PRESTO!
4 Modelling.
1 Model is in the form of analytical equations.
2 Load one or more modules (mathematical function) from the library.

Press the RETURN key to finish.
Function: TRANSPIRE1
[ TRANSPIRE1 ]EVP, EVPL, EVPC = f( LAYER, CLASS, ANGLE, T, DL, RA, GS, QN, QAREA, AGELAI, H

Function:
Model is in the form of analytical equations.

1 Find out about the modules available.
2 Load one or more modules (mathematical function) from the library.
3 Assign values to all input variables and solve the set of equations.
4 Change the value of an input variable and solve the set of equations.
5 Print out the modules in hierarchical form.
6 Produce aggregated output variables.
7 Print values for selected variables.
8 Describe variables: means, min, max, SD, etc.
9 Graph one variable against another.

PRESTO: 3
3 Assign values to all input variables and solve the set of equations.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>LAYER</td>
<td>1.0000</td>
</tr>
<tr>
<td>CLASS</td>
<td>1.0000</td>
</tr>
<tr>
<td>ANGLE</td>
<td>0.0000</td>
</tr>
<tr>
<td>RA</td>
<td>12.0000</td>
</tr>
<tr>
<td>GS</td>
<td>1.0000</td>
</tr>
<tr>
<td>QAREA</td>
<td>0.1700</td>
</tr>
<tr>
<td>AGELAI</td>
<td>0.8900</td>
</tr>
<tr>
<td>HOUR</td>
<td>1.0000</td>
</tr>
</tbody>
</table>

Now enter the DO-loop number for each input variable which has a range of values.

T 1
DL 1
QN 1
HOUR 1

PRESTO : 9 1

9 Graph one variable against another.

1 Plot one or more graphs.

X variable(s): HOUR.1
Y variable(s): EVP.1

Symbol Y variable X variable
+ EVP.1 vs HOUR.1

<table>
<thead>
<tr>
<th>Value</th>
<th>Symbol</th>
<th>X Variable</th>
</tr>
</thead>
<tbody>
<tr>
<td>35.000</td>
<td>+</td>
<td>HOUR.1</td>
</tr>
<tr>
<td>28.000</td>
<td>+</td>
<td>HOUR.1</td>
</tr>
<tr>
<td>21.000</td>
<td>+</td>
<td>HOUR.1</td>
</tr>
<tr>
<td>14.000</td>
<td>+</td>
<td>HOUR.1</td>
</tr>
<tr>
<td>7.000</td>
<td>+</td>
<td>HOUR.1</td>
</tr>
<tr>
<td>0.000</td>
<td>+</td>
<td>HOUR.1</td>
</tr>
</tbody>
</table>

Press RETURN

PRESTO : Q
3.6 Using a combination of modules to calculate transpiration

In the previous sections the module to calculate transpiration was used individually in order to illustrate the facilities and the flexibility to experiment with modules. In this section five modules are combined in order to calculate transpiration for single leaves, transform these values to a leaf area basis and integrate them to produce the transpiration rate for different layers throughout the canopy. The modules loaded are AMOUNT 1 (calculating the leaf area index and vertical distribution of foliage), RADIATION 1 (calculating the radiation regime in the canopy), BOUNDARY 1 (calculating the boundary layer resistance), STOMATA 1 (calculating the stomatal resistance) and TRANSPIRE 1 which calculates transpiration.

Values of transpiration have to be calculated for 17 layers. Inside each layer 4 age classes have to be considered and a distinction between shaded and sunlit leaves that are exposed at different angles to the sun has to be made. So, these 3 input variables have specific ranges that are described as follows:

\[
\begin{align*}
\text{LAYER} &= 1 \text{ TO } 17 \text{ STEP } 1 \\
\text{CLASS} &= 1 \text{ TO } 4 \text{ STEP } 1 \\
\text{ANGLE} &= 0 \text{ TO } 9 \text{ STEP } 1
\end{align*}
\]

where ANGLE = 0 accounts for leaves that are shaded. In this case the DO-loop number for each variable is:

\[
\begin{align*}
\text{DO-loop over LAYER} &= 3 \\
\text{DO-loop over CLASS} &= 2 \\
\text{DO-loop over ANGLE} &= 1
\end{align*}
\]
The module for transpiration has an output for transpiration integrated over angles, and another for transpiration integrated over angle and classes, as well as transpiration itself. So, in order to avoid producing a large amount of output, CLASS and ANGLE are marked with an asterix: this is a signal to PRESTO to solve the model for these inputs but only to store the results for each new value of the unmarked inputs.

Values of transpiration integrated for different layers in the canopy, calculated using the procedure described above is presented in Example 4.

Example 4 - Integrated values of transpiration calculated by using a combination of modules.
Hello, and welcome to PRESTO!

Type HELP and press the RETURN key if you are stuck.

1 Information retrieval.
2 Graphics.
3 Statistics.
4 Modelling.
5 Teaching material.
6 University information.
7 PRESTO information.

PRESTO : 4 1 2

4 Modelling.

1 Model is in the form of analytical equations.
2 Load one or more modules (mathematical function) from the library.

Press the RETURN key to finish.

Function : AMOUNT1
[ AMOUNT1 ] LAI, AGERAI, Z, AREAD = f( LAYER, CLASS, ANGLE, DN, HEIGHT1, HEIGHT2, HEIG

Function : RADIATION1
[ RADIATION1 ] QV, QN, QAREA, NETLAI = f( LAYER, CLASS, ANGLE, LAI, THETA, IT, FRAC, T, TSO

Function : BOUNDARY1
[ BOUNDARY1 ] RA = f( ANGLE, UZ1, Z1, HZ, Z, AREAD, HOUR )

Function : STOMATA1
[ STOMATA1 ] GS, GSL, GSC = f( LAYER, CLASS, ANGLE, G2, G3, G4, G5, G6, G7, GMAX1, GMAX2, G

Function : TRANSPIRE1
[ TRANSPIRE1 ] EVP, EVPL, EVPC = f( LAYER, CLASS, ANGLE, T, DL, RA, GS, QN, QAREA, AGERAI, H

Model is in the form of analytical equations.

1 Find out about the modules available.
2 Load one or more modules (mathematical function) from the library.
3 Assign values to all input variables and solve the set of equations.
4 Change the value of an input variable and solve the set of equations.
5 Print out the modules in hierarchical form.
6 Produce aggregated output variables.
7 Print values for selected variables.
8 Describe variables: means, min, max, SD, etc.
9 Graph one variable against another.

PRESTO : LAYER=1 TO 17 STEP 1
Variable LAYER has been calculated.

PRESTO : CLASS=1 TO 4 STEP 1
Variable CLASS has been calculated.

PRESTO : ANGLE=0 TO 9 STEP 1
Variable ANGLE has been calculated.
Assign values to all input variables and solve the set of equations.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>LAYER</td>
<td>3</td>
</tr>
<tr>
<td>CLASS</td>
<td>1</td>
</tr>
<tr>
<td>ANGLE</td>
<td>1</td>
</tr>
<tr>
<td>DN</td>
<td>166</td>
</tr>
<tr>
<td>HEIGHT1</td>
<td>8.5000</td>
</tr>
<tr>
<td>HEIGHT2</td>
<td>7.7500</td>
</tr>
<tr>
<td>HEIGHT3</td>
<td>7.0000</td>
</tr>
<tr>
<td>HEIGHT4</td>
<td>6.2500</td>
</tr>
<tr>
<td>HOUR</td>
<td>6.0000</td>
</tr>
<tr>
<td>THETA</td>
<td>53</td>
</tr>
<tr>
<td>IT</td>
<td>355</td>
</tr>
<tr>
<td>FRAC</td>
<td>0.3</td>
</tr>
<tr>
<td>T</td>
<td>14</td>
</tr>
<tr>
<td>TSOIL</td>
<td>10.0000</td>
</tr>
<tr>
<td>TV</td>
<td>0.0230</td>
</tr>
<tr>
<td>RV</td>
<td>0.0780</td>
</tr>
<tr>
<td>TN</td>
<td>0.3290</td>
</tr>
<tr>
<td>RN</td>
<td>0.2770</td>
</tr>
<tr>
<td>RVSOIL</td>
<td>0.1700</td>
</tr>
<tr>
<td>TVSOIL</td>
<td>0.2500</td>
</tr>
<tr>
<td>UZ1</td>
<td>2.9</td>
</tr>
<tr>
<td>Z1</td>
<td>18.5000</td>
</tr>
<tr>
<td>HZ</td>
<td>12.0000</td>
</tr>
<tr>
<td>G2</td>
<td>0.0300</td>
</tr>
<tr>
<td>G3</td>
<td>0.0100</td>
</tr>
<tr>
<td>G4</td>
<td>5.0000</td>
</tr>
<tr>
<td>G5</td>
<td>15.0000</td>
</tr>
<tr>
<td>G6</td>
<td>40.0000</td>
</tr>
<tr>
<td>G7</td>
<td>0.0800</td>
</tr>
<tr>
<td>GMAX1</td>
<td>1.0000</td>
</tr>
<tr>
<td>GMAX2</td>
<td>0.2500</td>
</tr>
<tr>
<td>GMAX3</td>
<td>0.1850</td>
</tr>
<tr>
<td>GMAX4</td>
<td>0.0850</td>
</tr>
<tr>
<td>DL</td>
<td>0.25</td>
</tr>
</tbody>
</table>

Now enter the DO-loop number for each input variable which has a range of values.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>LAYER</td>
<td>3</td>
</tr>
<tr>
<td>CLASS</td>
<td>2</td>
</tr>
<tr>
<td>ANGLE</td>
<td>1</td>
</tr>
</tbody>
</table>
7 Print values for selected variables.

Variable name: LAYER.1, EVPC.1

<table>
<thead>
<tr>
<th>Case</th>
<th>LAYER.1</th>
<th>EVPC.1</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.0000</td>
<td>10.9274</td>
</tr>
<tr>
<td>2</td>
<td>2.0000</td>
<td>9.2268</td>
</tr>
<tr>
<td>3</td>
<td>3.0000</td>
<td>7.8717</td>
</tr>
<tr>
<td>4</td>
<td>4.0000</td>
<td>6.7626</td>
</tr>
<tr>
<td>5</td>
<td>5.0000</td>
<td>5.8187</td>
</tr>
<tr>
<td>6</td>
<td>6.0000</td>
<td>4.9761</td>
</tr>
<tr>
<td>7</td>
<td>7.0000</td>
<td>4.2245</td>
</tr>
<tr>
<td>8</td>
<td>8.0000</td>
<td>3.5530</td>
</tr>
<tr>
<td>9</td>
<td>9.0000</td>
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<td>0.4903</td>
</tr>
</tbody>
</table>

Press RETURN

PRESTO : 9 1

1 Plot one or more graphs.

X variable(s): LAYER.1
Y variable(s): EVPC.1

Symbol Y variable X variable
+ EVPC.1 vs LAYER.1

12.000+
   I   +
   I   
9.600+
   I   +
   I   
7.200+
   I   +
   I   
4.800+
   I   +
   I   
2.400+
   I   +
   I   
0.000+
   I   +
   I   +
   I   +
   I   +
   I   

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PRESTO : Q
CHAPTER 4

PERFORMANCE OF THE SUB-MODELS

The sub-models presented in the last chapter were constructed to obtain a quantitative description of important aspects of photosynthesis and transpiration with the use of a minimum amount of field data. Before linking them to form the complete model, each sub-model was validated by checking the internal consistency and units used in the computer program and by comparison of the sub-model's output with experimental data found in the published literature.

If needed, the performance of a model, as measured by the agreement between observed and calculated values for the output variables, can in general be improved by calibrating it against the data. This is known as parameter optimisation, and involves adjusting weak or unknown parameters until an optimum agreement between the model's output and real data is achieved. Although useful, this technique can lead to perfect but meaningless goodness-of-fit, since the new values for the parameters may not be of real significance. When applied, the calibration, should be guided by a sensitivity analysis, which is a test on the relative influence of realistic changes in input data and parameters on the relevant output of the model.

The output of each one of the sub-models described in Chapter 2 was tested against published data in order to be validated. A sensitivity analysis was made for each sub-model to be used as a guide in case an optimisation of parameters was needed. Responses
of the sub-models to climatic variables and parameters were studied. The results of these analysis are presented in this chapter.

4.1 Leaf area index

The value of the leaf area index calculated for a complete year was in the range of 8 to 10. Starting with a value of 9.3 at 1st January it steadily declined to a minimum of 8.3 on 1st June when the contribution of current-year needles for the total leaf area index was nil. During the period of growth of new needles the leaf area index increased steeply until a maximum of 10 was reached, after which the leaf area index steadily declined, reaching by the end of the year the same value it started on 1st January. This behaviour of the sub-model results directly from the assumption that the same leaf area of new leaves is added to the tree each year (section 2.1).

The calculated values for the canopy's leaf area index are in agreement with values found in the literature for Sitka spruce, which ranges from 8 to 10 (Landsberg et al., 1973; Jarvis et al., 1976; Watts et al., 1976; James, 1977).

The largest contribution to the total leaf area (accounting for 50 to 70% of LAI) is that of young needles: current-year, 1-year and 2-year-old. Because the contribution from the older needles is small, needles older than 2-years were grouped into a single class, referred here as ≥3-year-old class (see Table 4.1).

The vertical distribution for the total leaf area was negatively skewed, a consequence of being calculated by summing the vertical distributions of individual age classes (Figure 4.1). The peak of the vertical distribution for the total leaf area varied during the year between 0.7 m and 1.0 m below the canopy's mean depth (Figure 4.2).
TABLE 4.1: Leaf area density and proportion of leaf area occupied by different age classes at different depths in the canopy.

<table>
<thead>
<tr>
<th>Layer No</th>
<th>Height interval (m)</th>
<th>Leaf area density</th>
<th>Proportion of leaf area occupied by leaves of different age classes</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>12.0-9.3</td>
<td>0.034</td>
<td>Current year 1-year-old 2-year-old &gt;3-year-old</td>
</tr>
<tr>
<td>2</td>
<td>9.3-8.8</td>
<td>0.060</td>
<td>0.58 0.30 0.09 0.03</td>
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<tr>
<td>3</td>
<td>8.8-8.4</td>
<td>0.081</td>
<td>0.50 0.30 0.14 0.06</td>
</tr>
<tr>
<td>4</td>
<td>8.4-8.1</td>
<td>0.099</td>
<td>0.45 0.30 0.16 0.09</td>
</tr>
<tr>
<td>5</td>
<td>8.1-7.9</td>
<td>0.112</td>
<td>0.40 0.30 0.18 0.11</td>
</tr>
<tr>
<td>6</td>
<td>7.9-7.7</td>
<td>0.123</td>
<td>0.39 0.29 0.19 0.13</td>
</tr>
<tr>
<td>7</td>
<td>7.7-7.5</td>
<td>0.132</td>
<td>0.37 0.28 0.20 0.15</td>
</tr>
<tr>
<td>8</td>
<td>7.5-7.3</td>
<td>0.139</td>
<td>0.35 0.28 0.20 0.17</td>
</tr>
<tr>
<td>9</td>
<td>7.3-7.1</td>
<td>0.143</td>
<td>0.33 0.27 0.21 0.19</td>
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<td>7.1-7.0</td>
<td>0.144</td>
<td>0.31 0.27 0.22 0.20</td>
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<td>11</td>
<td>7.0-6.8</td>
<td>0.141</td>
<td>0.30 0.26 0.22 0.22</td>
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<tr>
<td>12</td>
<td>6.8-6.6</td>
<td>0.137</td>
<td>0.29 0.26 0.22 0.23</td>
</tr>
<tr>
<td>13</td>
<td>6.6-6.4</td>
<td>0.128</td>
<td>0.28 0.25 0.22 0.25</td>
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<tr>
<td>14</td>
<td>6.4-6.2</td>
<td>0.116</td>
<td>0.27 0.25 0.23 0.26</td>
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<tr>
<td>15</td>
<td>6.2-6.0</td>
<td>0.099</td>
<td>0.26 0.25 0.23 0.27</td>
</tr>
<tr>
<td>16</td>
<td>6.0-5.7</td>
<td>0.080</td>
<td>0.25 0.24 0.23 0.28</td>
</tr>
<tr>
<td>17</td>
<td>5.7-5.3</td>
<td>0.052</td>
<td>0.24 0.24 0.23 0.29</td>
</tr>
<tr>
<td>18</td>
<td>5.3-4.6</td>
<td>0.017</td>
<td>0.24 0.23 0.23 0.30</td>
</tr>
</tbody>
</table>
Figure 4.1 - Vertical distribution for the total area of foliage and different age classes. For clarity needles 3-years and older are grouped into one class. The distribution is calculated for 1st January.
Figure 4.2 - Variation in the vertical distribution for the total leaf area of foliage at 1st January, 1st June and 1st August, and the variation of the mean height for the distribution. $\bar{h}$ is the mid point in the live crown, $\bar{h}_1$, $\bar{h}_2$ and $\bar{h}_3$ are the mean height for the distribution on 1st January, 1st June and 1st August respectively.
Gary (1976) found a negatively skewed distribution of needles dry weight plus branchwood for *Pinus contorta* Dougl. On the other hand, Stephens (1969) found a normal distribution of needly dry weight with height for *Pinus resinosa*. Quoting Beadle et al (1981): "The mean midpoint of foliage amount should generally be lower for leaf area than for leaf dry weight because of the increase in specific leaf area with depth in the canopy". Therefore the distributions found by Gary (1976) and Stephens (1969) would be negatively skewed if expressed in terms of leaf area, in agreement with the skewed distribution described by the sub-model.

**Sensitivity analysis**

An analysis of the sensitivity of the total leaf area index for variations in the parameters required by the sub-model was carried out for an arbitrary day in the year (1st July, day 181). The inputs required by the sub-model are given in the folded table at the end of the thesis.

The most important parameter is $L_o$, representing the leaf area index for current year needles, which varied from +53% to -48% of the total LAI for a variation of ±50% on the value of the parameter. This strong dependence was expected since the leaf area index for the different age classes is defined in terms of the area of current year needles (equations (2.1) to (2.8)), and LAI is calculated by adding up the individual contributions, resulting in a linear relationship of the form $\text{LAI} = \text{slope} \cdot L_o$.

Variation of LAI related to the chosen day of the year (D) is not negligible if compared with the effects of the parameters.
concerned with rates of fall of old needles (Table 4.2). However, the parameter D will always have lesser influence on the total LAI than the leaf area index of current-year needles.

4.2 Radiation penetration

Goodness-of-fit

The transmittance of visible and near-infrared radiation at four levels within the canopy calculated by the sub-model were compared with the values presented by Norman and Jarvis (1975). The model accounted for 99% of the variation in the data (Figure 4.3).

Plotting of responses

Figure 4.4 contains profiles of downward visible and near-infrared radiation as well as net thermal radiation plotted against cumulative leaf area index.

Radiation penetrates deep into the canopy, but at the level where the leaf area index amounts to 5 (approximately 5 m below the top of the canopy) most of the radiation has already been absorbed, and only a very small fraction of it reaches the ground. At all levels the flux of near-infrared radiation is higher than the flux of visible radiation, this being a consequence of the large values of the leaf's transmittance and reflectance for near-infrared radiation*.

The net radiation at each layer \((Rn_j)\) was calculated and hourly profiles of \(Rn_j/Rn_{top}\) have been plotted on a logarithmic scale against cumulative leaf area index (Figure 4.5). The curves show that the

* For a list of the parameters required by the sub-model and the values used see folded table at the end of the thesis.
TABLE 4.2: Variation in the sub-model's output in relation to increase or decrease in the inputs and parameters.

<table>
<thead>
<tr>
<th>Increment for parameters (%)</th>
<th>D</th>
<th>L₀</th>
<th>Rₙ₃</th>
<th>Rₙ₄</th>
<th>Rₙ₅</th>
<th>Rₙ₆</th>
<th>Rₙ₇</th>
</tr>
</thead>
<tbody>
<tr>
<td>-50</td>
<td>-8.7</td>
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<td>0.4</td>
<td>0.4</td>
<td>0.2</td>
<td>0.1</td>
<td>0.0</td>
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<tr>
<td>-40</td>
<td>-9.6</td>
<td>-38.0</td>
<td>0.3</td>
<td>0.3</td>
<td>0.2</td>
<td>0.1</td>
<td>0.0</td>
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<tr>
<td>-30</td>
<td>-10.7</td>
<td>-28.4</td>
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<td>-11.8</td>
<td>-18.9</td>
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<td>0.2</td>
<td>0.1</td>
<td>0.1</td>
<td>0.0</td>
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<td>-10</td>
<td>-6.9</td>
<td>-9.4</td>
<td>0.1</td>
<td>0.1</td>
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<td>+10</td>
<td>7.0</td>
<td>9.7</td>
<td>0.0</td>
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<td>0.0</td>
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<td>19.3</td>
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<td>-0.1</td>
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<td>+40</td>
<td>4.0</td>
<td>38.3</td>
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<td>+50</td>
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<td>-0.3</td>
<td>-0.2</td>
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</table>
Figure 4.3 - Agreement between values of transmittance calculated with the sub-model ($\tau_M$) and published values ($\tau_D$) from Norman and Jarvis (1975): (a) for visible transmittance, (b) for near-infrared transmittance
Figure 4.4 - Profiles of downward visible (X), downward near-infrared (O) and net thermal radiation (■) against cumulative leaf area index. All points above each layer.
Figure 4.5 - Attenuation of net radiation in the canopy:

\[
\frac{R_{n_j}}{R_{n_{top}}} \text{ against cumulative leaf area index.}
\]
rate of extinction of radiation varied with time of the day and
that at low levels in the canopy a marked increase in net
radiation occurs. The curve start to bend upwards at a height
when the cumulative leaf area index is in the range of 5 to 7.5.
From Figure 4.4 it can be seen that at the point where the leaf
area equals 5 the thermal radiation starts to contribute positively
to the net radiation, this is because leaves deep within the canopy
are protected from loosing thermal radiation, since leaves above
them obscure their view of the "cold" sky. As the fluxes of
visible and near-infrared radiation became almost completely extinct
deep in the canopy the net thermal radiation increases considerably
causing an increase on net radiation at the lower levels of the
canopy.

Profiles of net radiation with similar shape as the ones
calculated by the sub-model have been described by Landsberg et al
(1973) for a spruce canopy.

Sensitivity analysis

The influence of inputs and parameters upon fluxes of visible
and near-infrared radiation as well as the load of radiation
received by leaves at an arbitrary layer was determined with a
sensitivity analysis.

For visible radiation, the solar radiation above the canopy (St),
the fraction of solar radiation above the canopy which is beam (fb)
and the solar zenith angle (θ) are the strongest variables. The
dependence of the flux of visible radiation upon the transmittance
of the leaf for visible radiation (τ_{lv}) is small (-4 to 4.5 % for
changes of ± 50 % in the initial value of the parameter) but not negligible when compared with leaf and soil reflectance for visible radiation (Table 4.3).

For near-infrared radiation, St, f_b, and θ are strong variables when determining the radiation flux, but the strongest parameter determined by the analysis was the leaf transmittance (τ_{1N}) which produced a variation of -51 to 100 % on the flux of near-infrared radiation for a variation of ± 50 % on the initial value of the parameter.

The marked difference on the dependence of fluxes of visible and near-infrared radiation upon the appropriate leaf transmittance can be explained by the fact that a 50 % increase in (τ_{1N}) would imply 50 to 60 % of the income near-infrared radiation being transmitted by the leaf; while for visible radiation the same 50 % increase for τ_{1V} would account for only 3 to 5 % of the incoming visible radiation being transmitted by the leaf.

Table 4.3 shows that the total load of radiation on a single leaf is strongly dependent on St, θ, f_b and τ_{1N}, and less sensitive to the remaining parameters.

4.3 Stomatal conductance

Goodness-of-fit

The relationship between stomatal conductance and temperature calculated with the sub-model was tested against data published by Neilson and Jarvis (1975). Figure 4.6 shows the agreement reached. The sub-model accounted for 94 % of the variation in the data. This agreement was obtained after optimising the values of maximum stomatal
TABLE 4.3: Variation in the outputs of the radiation sub-model in relation to increase or decrease in the inputs and parameters.

<table>
<thead>
<tr>
<th>Increment for parameters (%)</th>
<th>Visible radiation</th>
<th>Near-infrared radiation</th>
<th>Total load of radiation on leaves at layer j</th>
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<td></td>
<td>Photon flux (W/m²)</td>
<td>Photon flux (W/m²)</td>
<td>Photon flux (W/m²)</td>
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<td>φf_b</td>
<td>φf_t</td>
<td>φf_t_in</td>
</tr>
<tr>
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<td></td>
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<td>φf_t</td>
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<th>φf_t</th>
<th>φf_t_in</th>
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</table>

Note: The table shows the variation in outputs with changes in inputs and parameters.
conductance \( (G_1) \), temperature for maximum stomatal conductance \( (G_5) \) and the slope of the curve relating stomatal conductance to vapour pressure and temperature \( (G_7) \) by trial-and-error.

The final value obtained for \( G_1 \) was 0.71 cm s \(^{-1} \), which is the value of maximum stomatal conductance found independently by Watts and cited by Jarvis et al (1976). The value of 10 °C obtained for \( G_5 \) is in the range of temperature for optimal stomatal conductance published by Neilson and Jarvis (1975). No value of \( G_7 \) was found in the literature for Sitka spruce, therefore starting with the value of 0.08 published by Ng (1979) for Scots pine, \( G_7 \) was optimized by trial-and-error until with the value of 0.06 the agreement shown in Figure 4.6 was obtained.

Plotting of responses

Stomatal conductance saturated at approximately 200 \( \mu \text{E m}^{-2} \text{s}^{-1} \).

The model predicts that the photon flux density needed for saturation varies with vapour pressure deficit \( (\delta e) \): decreasing at high values of \( \delta e \) and increasing at low values of \( \delta e \) (Figure 4.7). Ng (1979) found the same sort of response for young needles of Scots pine.

The low temperature for minimal stomatal conductance and the temperature for optimal stomatal conductance are shifted towards higher values by large vapour pressure deficits (Figure 4.8). This is a consequence of the interaction between vapour pressure deficit and temperature assumed for the sub-model as described in Sections 2.3.

Sensitivity analysis

The sensitivity of stomatal conductance to changes in inputs and parameters is shown in Table 4.4. Stomatal conductance is highly dependent upon air temperature \( (T) \) and vapour pressure deficit,
Figure 4.6 - Agreement between values of stomatal conductance calculated with the sub-model (X) and data published by Neilson and Jarvis (1975) (O). δe in the range of 0.5 to 2.5 kPa and $Q_p = 1000 \, \mu E \, m^{-2} \, s^{-1}$. 
Figure 4.7 - Relation between stomatal conductance at 3 levels of vapour pressure deficit and photon flux density.

Temperature at 15 °C.
Figure 4.8 - Relation between stomatal conductance at 3 levels of vapour pressure deficit and temperature. Photon flux density at 750 μE m⁻² s⁻¹.
TABLE 4.4: Variation in the output of the stomatal conductance sub-model in relation to increase or decrease in the inputs and parameters.

<table>
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<th>T</th>
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and the parameters \( G_1, G_5 \) and \( G_7 \). The extremely low dependence upon photon flux density \( (Q_p) \) shown in Table 4.4 results from using a standard value of 750 \( \mu \text{E} \text{ m}^{-2} \text{ s}^{-1} \) for \( Q_p \) whereas saturation is reached at 200 \( \mu \text{E} \text{ m}^{-2} \text{ s}^{-1} \). At a value for \( Q_p \) of 50 \( \mu \text{E} \text{ m}^{-2} \text{ s}^{-1} \) a variation of -28% to 16% occurs for a variation of \( \pm 50\% \) in the value of \( Q_p \).

4.4 Photosynthesis

Goodness-of-fit

The sub-model's output as a function of photon flux density was compared with values of photosynthesis of shaded needles of Sitka spruce published by Leverenz (1978). The agreement between the data and the values calculated with the sub-model is presented in Figure 4.9. The sub-model accounted for 96% of the variation in the data. No calibration between sub-model and data was needed.

Plotting of responses

Figure 4.10 shows the effect of the convexity parameter \( (M) \) on the shape of the curve describing the dependence of photosynthesis upon photon flux density. The curves were derived by using equation (2.54). For description and values of parameters required see folded table at the end of the thesis. The curves calculated with \( M = 1 \) and \( M = 0 \) represent the limiting cases, i.e. for \( M = 1 \) a Blackman's response curve is achieved and for \( M = 0 \) a rectangular hyperbola describes the relationship.
Figure 4.9 - Agreement between photosynthesis of shaded needles of Sitka spruce calculated by the sub-model (X) and data published by Leverenz (1978) (O).
Figure 4.10 - Light response curve of photosynthesis calculated for 3 values of convexity parameter.
Sensitivity analysis

Because photosynthesis of Sitka spruce saturate at low values of photon flux density, the sensitivity of the sub-model to $Q_p$ presented in Table 4.5 is small. At low values of $Q_p$ a much higher dependence is found. The low sensitivity of the sub-model to changes in the value of $M$ was expected since the values of $M$ appropriated for sunlit and shaded leaves are too close to the upper limit value of $M$. The concentration of CO$_2$ in the air, the stomatal resistance and mesophyll resistance are the strongest parameters.

4.5 Transpiration

Goodness-of-fit

The output from the transpiration sub-model was compared with measured values taken at the Forest of Ae Station #2 (Jarvis personal communication). The data was collected by an automatic weather station and processed by the Meteorological Office. All the inputs required for the sub-model were available on the data. The agreement between the sub-model's output and data is shown in Figure 4.11.

Sensitivity analysis

The sensitivity analysis have shown that the sub-model's output is highly sensitive to the value of stomatal conductance ($r_s$). An increase on the output of 58% was calculated for a decrease of 50%
TABLE 4.5: Variation in the output of the photosynthesis sub-model
in relation to increase or decrease in the inputs and
parameters.

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Figure 4.11 - Agreement between values of transpiration calculated with the sub-model ($\lambda E_M$) and experimental observations ($\lambda E_D$).

This is only a calibration exercise.
in the initial value of $r_s$. Weather variables also have a large influence on the output but their influence are not comparable to the effect of $r_s$. The boundary layer resistance ($r_a$) was of minor importance (Table 4.6).

The performance of each sub-model was evaluated by comparing the outputs produced by them with values of published data. The agreement reached in these tests were good, with the sub-models accounting for 94 to 99% of the variation in the data.

The poorest agreement was reached by the sub-model describing the response of stomatal conductance to weather variables. The performance of the sub-model was greatly improved by calibration against the data. The new values of the parameters achieved with the calibration are acceptable in view of the large range of possible values for a same parameter existent in the literature.
TABLE 4.6: Variation in the output of the transpiration sub-model in relation to increase or decrease in the outputs and parameters.

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CHAPTER 5
THE PERFORMANCE OF THE COMPLETE MODEL

Once the performance of the individual sub-models had been assessed (Chapter 4), they were combined into the complete model with the structure illustrated in Figure 2.6. This complete model was constructed using the modular modelling facility of PRESTO, by loading the six modules corresponding to the six sub-models (Chapter 3).

Three types of analysis were undertaken with the complete model:

- Testing the model, by comparing the hourly values for photosynthesis and transpiration calculated by the module for measured values from representative days.
- Describing the contribution of sub components within the canopy to the total canopy photosynthesis and transpiration.
- Analysing the response of photosynthesis and transpiration to changes in input and parameters.

For the first two of these analysis, hourly mean values of photosynthesis and transpiration were calculated for four summer days. The model's outputs were compared with data provided by James (1977) which also included hourly values of temperature, solar radiation, vapour pressure deficit and wind speed. The measurements were taken during the summer of 1973 above a Sitka spruce stand at Fetteresso Forest (30 km S.W. of Aberdeen). Transpiration fluxes were calculated using the energy-budget technique and the hourly mean fluxes of CO₂ above the Sitka spruce canopy were calculated from measurements of the gradients of CO₂ concentration above the forest and making use of
the transfer coefficient for CO\textsubscript{2} obtained from the energy-budget technique.

5.1 Testing the model

From all the climatic inputs required by the complete model, only the fraction of radiation above the canopy which is beam (fb) was not in the data presented by James (1977). Since no measurements of fb were available for this particular data set (James personal communication) the following method was used to estimate fb.

Using values provided by Gates (1980 - Table 6.1) a graph of direct solar flux (horizontal surface) against solar zenith angle was plotted. From this graph the expected value of the direct beam for each hour (assuming clear atmosphere) was determined. This value was then multiplied by the hourly value of sunshine duration and divided by the income solar radiation provided by James (1977). The tables containing the hourly values of sunshine duration were provided by the Meteorological Office.

The values of fb calculated by this method were used as input for the model, even aware that they may not represent the true values of fb at the site, since the hourly values of sunshine duration were collected at Dyce, 35 km from Fetteresso Forest.

Simulated and published values of photosynthesis and transpiration for 4 days in 1973 are presented in Figures 5.1 to 5.4. The hatched band in the figures represents the range of values for photosynthesis and transpiration for fb varying between 0.0 (all radiation is diffuse) to 1.0 (all radiation is direct). In all cases the upper limit was reached by assuming that all radiation above the canopy was diffuse. The large difference between photosynthesis at full sunlight and overcast conditions
Figure 5.1 - Comparison between simulated (—) and measured (—-—) values of photosynthesis (a) and transpiration (b).
Figure 5.2 - Comparison between simulated (-) and measured (---) values of canopy photosynthesis (a) and tranpiration (b).
10 July

Figure 5.3 - Comparison between simulated (—) and measured (---) values of canopy photosynthesis (a) and transpiration (b).
Figure 5.4 - Comparison between simulated (--) and measured (---) values of canopy photosynthesis (a) and transpiration (b).
occurs because the radiation load in shaded areas of the canopy is lower for full sunlight than it is for overcast condition. An increase in photosynthetic rate with increasing fraction of diffuse radiation above the canopy has been reported for *Goethalsia meianta* (Donn. Smith) Burret and *Cecropia piltata* L. by Allen *et al* (1974) and for soybean (*Glycine max* (L.) Merrill) by Kumura *et al* (1978).

The agreement between the simulated and measured values of photosynthesis and transpiration varied considerably. For example, for 15 June (Figure 5.1) the model only accounted for 13% of the variation on the data for photosynthesis and 35% for transpiration. In contrast, for 12 September (Figure 5.4) the model accounted for 85% of the variation of the data for photosynthesis and 77% for transpiration. In general, the agreement for transpiration was more uniform, usually accounting for about 72% of the variation on the data.

The simulated values of photosynthesis and transpiration followed reasonably well the gross daily pattern, and the daily totals were within 12% for photosynthesis and 5% for transpiration, except for 15 June. However, the hourly mean values did not always follow the peaks present in the data. The discrepancies between simulated and measured values may arise from erroneous estimates of $f_b$ being used as inputs for the model, and also for measurement errors in the fluxes which in James' data amounted to 20% for most of the time (James 1977), and probably larger errors are likely to occur near dusk and dawn. For example, in the early morning on 15 June an increase from -0.09 to 1.32 mg m$^{-2}$ s$^{-1}$ was recorded by James for photosynthesis, which is unlikely to be real. The considerable underestimation of the fluxes on 15 June may be due to an underestimation of the leaf area index of current year needles, which were assumed to start growing on 1st June.
5.2 The contribution of canopy sub-components

- Contribution of individual layers

The contribution of individual layers to photosynthesis and transpiration of the complete canopy is shown in Figure 5.5. For clarity, only a few layers are included in the diagrams. Figure 5.5a shows that the largest contribution to the total photosynthetic rate is made by the first 7 layers. Needles on layers lower than the 12th only occasionally photosynthesize. Respiration exceeding photosynthesis in the lower layers of the canopy have been reported for a young spruce forest by Baumgartner (1967) and Schuelze et al (1977) reported that for lower levels inside a Norway spruce canopy the net CO₂ exchange is approximately zero. The same has been observed by Mr. J. H. Griffiths on his measurements of photosynthesis of Sitka spruce at Rivox Forest (personal communication). It seems that low radiation levels deep in the canopy (Figure 4.4) is the principal factor limiting photosynthesis.

Figure 5.5b shows the contribution of individual layers to the transpiration of the canopy. The figure shows that most of the contribution is made by the upper layers as for photosynthesis. The very low values of transpiration at lower levels are also a consequence of the low radiation fluxes deep in the canopy.

- Contribution of individual age classes

Figure 5.6 shows the contribution of individual age classes of needles to the photosynthetic and transpiration rates for the complete canopy. Current year needles contribute more than 50 % of the total photosynthesis (Figure 5.6a) and 60 % of the total transpiration (Figure 5.6b). The contribution of 1-year-old plus 2-year-old needles to
Figure 5.5 - Contribution of different layers to photosynthesis (a) and transpiration (b) for 10 July 1973.
Figure 5.6 - Contribution of current year (o), 1-year-old (1), 2-year-old (2), ≥3-year-old needles (≥3) to the canopy photosynthesis (a) (-----) and transpiration (b) (----), for 10 July 1973.
photosynthesis and transpiration are similar, being 40 and 30 %, respectively. Needles 3-years and older add only a minor contribution for both fluxes.

- Contribution of sunlit and shaded leaves

The contribution of sunlit and shaded needles to photosynthesis can be seen from Figure 5.7a and to transpiration from Figure 5.7b. The fluxes shown were calculated for mid-day conditions on 28 June 1973: solar zenith angle ($\theta$) = 35°; solar radiation = 593 Wm$^{-2}$; fraction of direct beam radiation above the canopy ($fb$) = 0.75; air temperature ($T$) = 18°C; vapour pressure deficit ($s_e$) = 0.76 kPa.

The shapes of the curves are mainly determined by the proportion of shaded and sunlit leaves in each layer within the canopy. The leaf area of sunlit leaves in each layer depends on the solar zenith angle ($\theta$) and the transmittance of the layer to the direct beam radiation ($T_{b,j}$) (Eq. 2.29). Because the transmittance ($T_{b,j}$) declines exponentially with depth within the canopy, the contribution of the sunlit leaves to photosynthesis and transpiration also declines exponentially from the top (LAI = 0) downwards in the canopy. The solar zenith angle determines the magnitude of the sunlit leaf area in each layer, and hence the magnitude of the contribution of the sunlit fluxes in the course of the day.

Since the leaf area of shaded leaves in each layer is calculated by subtracting the sunlit area from the total leaf area in that particular layer (Eq. 2.30), the contribution of shaded leaves rapidly increases as the sunlit leaf area decreases with depth within the canopy, until a level is reached in which the radiation level is formed by diffuse radiation alone.

For the example in Figure 5.7, sunlit needles contribute about 43 % to the total of the canopy photosynthesis and about 38 % to the
Figure 5.7 - Contribution of sunlit (○) and shaded (■) leaves to:
(a) photosynthesis of each layer (X)
(b) transpiration of each layer (X)
total of the hourly mean transpiration. The contribution of sunlit needles predominates over that of shaded needles only in the two first layers on the top of the canopy (LAI = 0 to 1). Thereafter, shaded needles are of primary importance to photosynthesis and transpiration.

As the total solar radiation above the canopy becomes mainly diffuse, the contribution of shaded needles becomes even more important. In this case, photosynthesis may reach saturation throughout the top four layers of the canopy (LAI = 0 to 2), moreover, in the middle layers an increase of about 25% on photosynthesis may also occur. The increase on the proportion of diffuse radiation above the canopy, may also affect the loss by respiration in the deeper layers: the higher the fraction of diffuse radiation the lower the level at which respiration starts to occur (Figure 5.8a). Respiration starts at a leaf area index of about 6, depending on the climatic conditions above the canopy such as solar radiation, temperature and vapour pressure deficit.

The effect of changes in the fraction of diffuse radiation are not so prominent in transpiration as opposed to photosynthesis, and the layers mainly affected are those in the middle of the canopy, as shown in Figure 5.8b.

5.3 Response of photosynthesis and transpiration to change in input variables and parameters.

It is difficult to analyse in a realistic way the extent at which the changes in a single climatic variable or parameter may affect the photosynthetic and transpiration rates because the climatic variables are interdependent.

An attempt to demonstrate the effects of some of the climatic variables and parameters on the computation of photosynthesis and
Figure 5.8 - Effect of the increase of fraction of diffuse radiation upon
(a) photosynthesis of individual layers
(b) transpiration of individual layers

\[ S_t = 593 \text{ Wm}^{-2}, T = 18 \text{ °C}, \delta e = 0.76 \text{ kPa}, \theta = 34 \text{ °C}, \]

\[ fb = 0.75 \text{ (X)}, 0 \text{ (O) and 1 (■)} \]
transpiration fluxes for the complete canopy is presented in this section.

For this analysis, two variables were allowed to change in a certain range: one varying continuously and the other by step changes, usually ± 10 % and ± 50 % of its standard value. All the other climatic variables and parameters are held constant. The standard values of climatic variables used through the analysis are:

- Solar radiation \((St) = 590 \text{ Wm}^{-2}\)
- Fraction of direct beam \((fb) = 0.5\)
- Solar zenith angle \((\theta) = 34^\circ \text{ (midday)}\)
- Air temperature \((T) = 18 \text{ °C}\)
- Vapour pressure deficit \((\delta e) = 0.76 \text{ kPa}\)
- Wind speed \((u) = 3.2 \text{ m s}^{-1} \text{ (2 m above the canopy)}\)

Responses were plotted for all possible combinations of the variables presented above. Some were discarded because although mathematically they were correct, physically they had no meaning at all, as for example plotting the response of photosynthesis and transpiration to changes in solar zenith angles while keeping the value of solar radiation constant. Others were discarded because photosynthesis and transpiration had shown no variation over the complete range of values for that particular variable. The six graphs presented in this section are for those variables which have shown the largest influence on the fluxes.

- Response to the fraction of direct beam above the canopy \((fb)\) for different levels of solar radiation \((St)\).

Figure 5.9 shows the variations on photosynthesis \((a)\) and on transpiration \((b)\) to changes in the fraction of direct beam above the canopy at five levels of solar radiation. It is shown that both fluxes
Figure 5.9 - The effect of the fraction of direct beam radiation (fb) at four levels of solar radiation (St) upon:
(a) canopy photosynthesis
(b) transpiration for the complete canopy
decrease with increases in the value of the fraction \(fb\), markedly photosynthesis. At the higher level of solar radiation \((St = 889 \text{ Wm}^{-2})\) the photosynthesis at \(fb = 1\) is about 57% less than that for \(fb = 0\). At the lower level \((St = 297 \text{ Wm}^{-2})\) the decrease in photosynthesis is about 69%. Therefore, on average the photosynthetic rate is about 60% lower in situations of clear sky \((fb = 1)\) as opposed to conditions of overcast sky \((fb = 0)\).

In contrast, the reduction in transpiration is on average about 15%, being as much as 22% at the higher level of \(St\) and 7% at the lower level.

Although the extreme situations are unlikely to occur, it seems that, in general, the canopy will benefit more in conditions where the proportion of diffuse radiation exceeds that of direct beam radiation.

- Response to solar radiation \((St)\) for different levels of vapour pressure deficit \((\delta e)\).

Figure 5.10 describes the effects of different vapour pressure deficits in photosynthesis \((a)\) and transpiration \((b)\) where \(St\) is in the range of 0 to 900 \text{ Wm}^{-2}.

As expected both fluxes increase with increasing solar radiation. Saturation does not occur because even at \(St = 900 \text{ Wm}^{-2}\) the radiation in the lower layers within the canopy do not reach the level required to saturate photosynthesis.

Photosynthesis is higher for low values of vapour pressure deficit (Figure 5.10a), this is because as vapour pressure deficit increases stomatal conductance decreases (viz. Figure 4.7). At radiation levels above the canopy lower than 100 \text{ Wm}^{-2}, the photosynthetic rate of the first layers is not enough to compensate the loss by respiration of the remaining layers, which is indicated by negative values of photosynthesis.
Figure 5.10 - The effect of solar radiation \( (S_t) \) at four levels of vapour pressure deficit \((\delta_e)\) upon:

(a) canopy photosynthesis
(b) transpiration for the complete canopy
Transpiration tends to increase as vapour pressure deficit and solar radiation increases (Eq. 2.65). For a fixed value of vapour pressure deficit, transpiration would increase linearly with solar radiation if the stomatal conductance remained constant. However, the stomatal conductance changes with solar radiation, in a non-linear way, and vapour pressure, therefore in the example of Figure 5.10b, the transpiration rate rapidly increases over low levels of solar radiation and then a nearly linear increase happens, though less steep. A perfect linear increase of transpiration in relation to solar radiation is not reached because the stomatal conductance for needles deep in the canopy never saturates. It should be remembered that in practice the air temperature usually increases with increasing solar radiation and this may affect the vapour pressure deficit, and consequently the shape of Figures 5.10a and 5.10b may not be considered as the usual trends of photosynthesis and transpiration.

- Response of photosynthesis and transpiration to temperature (T) for different levels of vapour pressure deficit (δe).

Figure 5.11 shows the variations on photosynthesis (a) and transpiration (b) to changes in temperature at five levels of vapour pressure deficit.

The shape of the curve of photosynthesis plotted against temperature (Figure 5.11a) is similar to the response of the stomatal conductance to temperature (viz. Figure 4.8). At high temperatures (T = 30 °C) the effect of vapour pressure deficit is much less than it is for lower temperatures (T = 5 °C). The optimum temperature for photosynthesis is shifted towards lower values for lower values of
Figure 5.11 - Effect of temperature (T) at five levels of vapour pressure deficit (se) upon
(a) canopy photosynthesis
(b) transpiration for the complete canopy
vapour pressure deficit, and photosynthetic rates are considerably higher for lower values of vapour pressure deficit.

It is shown that there is no photosynthesis when $T = 8^\circ C$ and vapour pressure deficit = 1.14 kPa, however this situation is unlikely to occur in the natural environment. Usually at low temperatures (near dusk and dawn) the air is nearly saturated and therefore the vapour pressure deficit would be much lower, say about 0.38 kPa.

Vapour pressure deficit affects the stomatal conductance and also is a driving force for transpiration, therefore the interpretation of Figure 5.11b is more difficult. When vapour pressure deficit is small ($\delta e = 0.38$ kPa) the stomatal conductance is higher throughout the range of temperature, but in this case the low value of $\delta e$ is limiting the maximum transpiration attainable. As the value of $\delta e$ increases the stomatal conductance decreases and becomes then the limiting factor for transpiration.

The graphical analysis was also carried out to assess the effect of wind speed upon photosynthesis and transpiration. The results have shown that changes in wind speed, which affects the boundary layer resistance, could be considered negligible as compared to the effects of the climatic variables described above.
CHAPTER 6

GENERAL DISCUSSION

6.1 Discussion of the model

The objective of this work was to model hourly photosynthetic and transpiration rates for a Sitka spruce canopy, and the relative importance of different leaf age classes, and sunlit and shaded needles to the total rates. The level of detail considered in this work was determined by the aim of the modelling effort and the relative importance of the various processes affecting the behaviour of the system.

The model consists of five sub-models which describe the leaf area distribution; radiation interception; stomatal conductance; photosynthesis; and transpiration.

Although all effort was made to consider all factors influencing the photosynthetic rate for the complete canopy, the model does not simulate the respiration of trunk, branches and roots. Very little information is available in this subject for conifers (Linder 1979, 1980). Nevertheless, some information is available for Picea jezonensis, Picea glehnii (Kira 1968); Pinus densiflora (Negisi 1975); Picea abeis (Yoda et al, 1965) and Pinus silvestris (Linder and Troeng 1980; Ågren et al, 1980).

The only information available for Sitka spruce was given by Jaes• (1977) which states that respiration of the roots is about 3 % of the hourly value of the photosynthetic rate for the canopy. On the other hand, Ågren et al (1980) reported that the respiration of the woody parts of a Scots pine stand in Sweden was in the range of 4 to 15 % of the annual net photosynthesis.
Three models were found to simulate the respiration rate of woody organs for *Picea glehnii*, *Picea jezoensis* and *Pinus densiflora* (Yoda *et al.*, 1965); *Picea glehnii* and *Picea jezoensis* (Kira 1968) and *Pinus taeda* (Kinerson 1975). These models are based upon the dry weight and diameter of the woody organs and make use of parameters derived from experimental data and are specific to the species in study.

In view of the absence of information needed to properly model this respiration for Sitka spruce and the relative small contribution of respiration in any case, it was decided not to include this process in the complete model.

- Use of leaf age classes

In the present model, leaves were divided into age classes. This enabled the values for stomatal conductance to be age-specific. Several models to calculate the photosynthetic and transpiration rates for the canopy as a whole take into account the effect of age on these fluxes. de Wit (1965) and Duncan *et al.* (1967) for example consider the effect of age upon photosynthesis by assuming that the maximum rate of photosynthesis decreases linearly from a constant value at the top of canopy to zero at a specified leaf area index at the bottom of the canopy. This approach may well simulate the effects of leaf age on photosynthesis, but can not be applied to calculate transpiration.

Landsberg (1981) states that the mesophyll conductance and the initial slope of the curve relating photosynthesis to light also vary with age class, but because of insufficient data these parameters are always considered the same for all age classes. In fact, Thorpe *et al.* (1978) used the same values of the parameters for all leaf ages and successfully simulated the net photosynthesis by an apple.
tree. Also, in the present study the sensitivity analysis has shown that photosynthesis is fairly insensitive to these two parameters, being altered by ± 15% for variations of ± 50% on the standard values of the mesophyll resistance and hardly altered by the same sort of variation in the slope of the response curve of photosynthesis to light. In addition the agreement reached for the daily total of the fluxes suggests that the difference in these parameters with age classes may have little influence on estimates of canopy photosynthesis.

- Use of layers

Models considering different layers of the canopy are widely used, since dividing the canopy into very thin layers is a requirement for models describing the radiation interception by canopies. Generally the rates are calculated for each layer, but the results are presented as the integrated rates for the canopy as a whole (see for example de Wit 1965; Duncan et al. 1967; Lemon et al. 1971; Sinclair et al. 1976). Only a few authors present the rates as the contribution of individual layers (Allen et al. 1974; Norman 1980). Usually, the major interest is the prediction of photosynthesis for analysis of growth and productivity, but as shown later, knowledge of the sources and sinks of CO₂ and water vapour within the canopy can be of great help in planning crop and forest management.

Although the approach of dividing the canopy in extensive horizontal layers is widely accepted to represent a closed canopy, the approach described by Thorpe et al. (1978), based on the shape of individual crowns, is more appropriate to describe the radiation interception by single trees and may be extended to represent rows
of trees or open stands.

6.2 Performance of the whole model

In general a good agreement was obtained between the outputs of each sub-model and published data. The sub-models accounted for 95% of the variation in the data. The only sub-model which required to be calibrated against the experimental data was the one describing the stomatal conductance. The final values achieved for the parameters were well inside the range of possible values. Despite the good agreement reached with each sub-model when tested against experimental data, usually carried out in controlled conditions for single leaves or shoots, the agreement between simulated and measured fluxes of photosynthesis and transpiration for the complete canopy was not nearly so good.

The agreement between simulated and measured values of photosynthesis and transpiration varied considerably. The model accounted for as little as 13% of the variation on the data for photosynthesis ($r^2 = 0.13$) on 15 June to 85% ($r^2 = 0.85$) on 12 September. Excluding the poor agreement on 15 June the agreement for transpiration was more uniform, usually accounting for 72% of the variation on the data. Generally simulated values of photosynthesis and transpiration followed reasonably well the gross daily pattern, and daily totals were within 12% for photosynthesis and 5% for transpiration, except for 15 June. However, simulated values did not follow very well the hourly trends in the fluxes.

By comparing the simulated fluxes of photosynthesis and transpiration with those measured by James (1977) it was clear that the fluxes could be better estimated if the fraction of direct beam radiation above the
canopy was known. This parameter has been shown to be of great
importance especially for the computation of photosynthesis, as
indicated by the width of the hatched areas in Figures 5.1 to 5.4.
A marked increase in photosynthesis for high levels of diffuse
radiation has been reported by Allen et al. (1974) and by Kumura
(1978). Unfortunately, James (1977) did not measure the fraction
of direct beam radiation. The fractions were then estimated by
using hourly values of sunshine duration obtained from a meteor-
ological station located 35 km distant from the experimental site
as described in Chapter 5. When it was evident from James' data
that the sky was overcast, as for example in Figure 5.4, a good
agreement between photosynthesis was obtained ($r^2 = 0.85$). Another
situation in which the agreement is acceptable is that presented in
Figure 5.2 for photosynthesis ($r^2 = 0.71$) and transpiration ($r^2 = 0.74$).
If the actual values of the fraction of direct beam radiation on the
site were known a better validation of the model would be possible.

However, for the simulation at the beginning of June, the
hatched area did not overlap most of the experimental curve. It is
possible that the discrepancy was caused by an erroneous prediction
of the leaf area index of the current year needles by assuming that
current year needles start to grow to late in the year. It has been
shown that the current year needles may account for more than 50 % of
total photosynthesis and 60 % of transpiration.

The underestimation of the photosynthetic and transpiration rates
may also be caused by an erroneous assumption on the total leaf area
index. In the case of photosynthesis, loss by respiration starts to
occur at a level where the leaf area index reaches a value of
approximately 6, therefore an overestimation of the total leaf area
would cause an underestimation on photosynthesis.

It is possible that the loss by respiration in the lower layers was caused by an underestimation of the light penetration into the canopy. Norman and Jarvis (1975) suggest that for Sitka spruce a better simulation of light distribution inside the canopy could be achieved by a non-random distribution of foliage, i.e.: by grouping the needles into shoots and also considering the woody elements of the canopy. If only the shoots are considered the grouping theory substantially overestimates the light transmittance. As stated by the authors: "One of the difficulties in dealing with non-random foliage distribution is the determination of the effective shoot spectral properties, since needle properties are not directly applicable". Another alternative may be to consider three different leaf distributions throughout the depth of the canopy: vertical on the top, spherical in the middle and horizontal at the bottom, as observed by Büsgen and Münch (1929). In any case the radiation model would need to be much more complex than the one presented in this study in order to allow a significant increase in the radiation reaching the lower layers of the canopy.

It is possible that an error in computing the stomatal conductance and transpiration rate could result from assuming that the leaf temperature is equal to the air temperature on the top of the canopy and constant throughout the canopy. However, this assumption is unlikely to cause serious errors since the air temperature inside the canopy rarely exceeds that above the canopy by more than 2 °C (Jarvis et al 1976). In addition, the difference between leaf temperature and surrounding air seldom exceeds 0.2 °C for conifers because of its small leaves and low boundary layer resistances.
(Rutter 1967; Jarvis et al. 1976). Therefore, the errors caused by assuming a constant leaf temperature would not explain the discrepancy usually found in the hourly estimates of transpiration rates. The same could be said of the assumption that vapour pressure deficit is constant throughout the canopy. Measurements inside a Sitka spruce stand have shown that the difference between vapour pressure deficit at the top and within the canopy is usually less than 0.1 kPa (Jarvis et al. 1976). Thus, the discrepancies are likely to be related to an underestimation of the load of radiation on the needles within the canopy, or errors on the determination of the total leaf area index, or measurement errors, or all added together.

6.3 Insights from the model

The model has shown that the largest contribution for the photosynthetic and transpiration rates for the complete canopy is that of current year needles, amounting to more than 50% of both rates. In contrast, 3-years and older needles provide a minor contribution, of about 10%, to the total photosynthetic and transpiration rates.

Shaded needles are of primary importance to the total photosynthetic and transpiration rates, except in the top layers (LAI = 1) where the contribution of sunlit needles predominates. In general, shaded needles contribute approximately 60% to either photosynthesis or transpiration.

The comparison of simulated fluxes with experimental data suggests that not only the amount of solar radiation but also the quality of this radiation (in terms of the fraction of direct radiation above the canopy) is important for photosynthesis. This
The effect has been found in detached shoots of Sitka spruce (Ludlow and Jarvis 1971) and seedlings (Hodges and Scott 1968), but has not been reported for natural canopies of Sitka spruce.

At lower levels in the canopy a marked increase in net radiation was observed. The same behaviour was observed by Landsberg et al (1973) for a Sitka spruce stand. The marked increase in net radiation was attributed to a marked increase in the flux of thermal radiation below a leaf area index of approximately 6.

The maximum rate of photosynthesis simulated was about $1 \text{ mg m}^{-2} \text{s}^{-1}$. This maximum rate of photosynthesis is comparable in magnitude to rates of *Pinus taeda* (Sinclair et al) and *Picea abies* (Puller and Baumgartner) presented by Jarvis et al (1976). The contribution of shaded needles to this rate was more than 50%. Below a height at which the total leaf area index was about 6 (6.5 m above the ground for a stand of 12 m high) net photosynthesis was negative indicating that loss by respiration occurred. This loss amounted to approximately 13% of the total photosynthesis. Respiration losses of about the same magnitude were reported by Baumgartner (1967) for a young spruce forest.

If the lower layers of the canopy are respiring for most of the time, pruning these layers of the canopy would give a gain in dry matter production and it would minimize the water loss by transpiration by approximately 40%. It should be remembered however that no field data was available to allow the validation of the contribution of the canopy sub-components to the total photosynthesis and transpiration.

6.4 Final remarks

The outputs from the model have provided a new insight into the
relative contribution of different age classes of needles, sunlit or shaded needles and different layers of the canopy for the complete photosynthetic and transpiration rates of a Sitka spruce stand.

Although the model makes use of a large number of parameters, once they have been determined the model only requires hourly values of climatological variables measured above the canopy. In addition the model also requires hourly values of the fraction of direct beam radiation which is not very commonly measured.

Where the information was not fully available to allow a precise formulation of the process being simulated assumptions had to be made. With the new advances in the proper instrumentation for field work, and new experiments in controlled environments, soon some of the assumptions made when developing the sub-models may be confirmed or refuted. Also, some new functions describing, in a more realistic way, the processes being simulated may be available. The validation of these new assumptions and functions may easily be achieved by using the modular modelling approach described in this work. Also, this facility will permit additional sub-models and alternative versions of particular sub-models to be incorporated into the complete model.
APPENDIX A

This appendix contains the symbols used in the FORTRAN program and a listing of each sub-routine.

A - Description of variables

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description of variables</th>
<th>Unity</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Initial slope of the curve relating photosynthesis to quantum irradiance</td>
<td>mg / μE</td>
</tr>
<tr>
<td>AGELAI</td>
<td>Fraction of the leaf area index of a specific layer occupied by leaves of each age class</td>
<td></td>
</tr>
<tr>
<td>AN</td>
<td>Albedo of layer j for near-infrared radiation</td>
<td></td>
</tr>
<tr>
<td>AREAD</td>
<td>Leaf area density at height z</td>
<td>m² m⁻³</td>
</tr>
<tr>
<td>AV</td>
<td>Albedo of layer j for visible radiation</td>
<td></td>
</tr>
<tr>
<td>CA</td>
<td>CO₂ concentration in the air</td>
<td>mg m⁻³</td>
</tr>
<tr>
<td>CCP</td>
<td>CO₂ saturation point</td>
<td>mg m⁻³</td>
</tr>
<tr>
<td>CF1</td>
<td>Convexity coefficient for the curve relating photosynthesis to light; for shaded leaves</td>
<td></td>
</tr>
<tr>
<td>CF2</td>
<td>Convexity coefficient for the curve relating photosynthesis to light; for sunlit leaves</td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>Zero plane displacement</td>
<td>m</td>
</tr>
<tr>
<td>DELTA</td>
<td>integration interval</td>
<td></td>
</tr>
<tr>
<td>DIFN</td>
<td>Energy balance for leaves that are shaded at layer j</td>
<td>Wm⁻²</td>
</tr>
<tr>
<td>DIRN</td>
<td>Energy balance for leaves that are sunlit at layer j</td>
<td>Wm⁻²</td>
</tr>
<tr>
<td>DL</td>
<td>Vapour pressure deficit</td>
<td>kPa</td>
</tr>
<tr>
<td>DN</td>
<td>Day number</td>
<td></td>
</tr>
<tr>
<td>DNET</td>
<td>Net radiation at layer j</td>
<td>Wm⁻²</td>
</tr>
<tr>
<td>EDN</td>
<td>Downward near-infrared radiation at layer j</td>
<td>Wm⁻²</td>
</tr>
<tr>
<td>EDV</td>
<td>Downward visible (diffuse) radiation at layer j</td>
<td>Wm⁻²</td>
</tr>
<tr>
<td>EUN</td>
<td>Upward near-infrared (diffuse) radiation at layer j</td>
<td>Wm⁻²</td>
</tr>
<tr>
<td>EUV</td>
<td>Upward visible (diffuse) radiation at layer j</td>
<td>Wm⁻²</td>
</tr>
<tr>
<td>Symbol</td>
<td>Description of variables</td>
<td>Unity</td>
</tr>
<tr>
<td>--------</td>
<td>--------------------------</td>
<td>-------</td>
</tr>
<tr>
<td>EVP</td>
<td>Transpiration on a leaf area basis</td>
<td>Wm⁻²</td>
</tr>
<tr>
<td>EVPC</td>
<td>Transpiration integrated over layer</td>
<td>Wm⁻²</td>
</tr>
<tr>
<td>EVPL</td>
<td>Transpiration integrated over age class</td>
<td>Wm⁻²</td>
</tr>
<tr>
<td>FH</td>
<td>Leaf area density at a specific height for each individual age class</td>
<td>m⁻¹</td>
</tr>
<tr>
<td>FRAC</td>
<td>Fraction of solar radiation which is beam</td>
<td></td>
</tr>
<tr>
<td>FR</td>
<td>Fraction of the leaf area index of a specific layer occupied by leaves of each age class</td>
<td></td>
</tr>
<tr>
<td>FRV</td>
<td>Leaf area density of a specific layer</td>
<td>m²·m⁻³</td>
</tr>
<tr>
<td>FSA</td>
<td>Fraction of sunlit leaf area for leaves at angle class i</td>
<td></td>
</tr>
<tr>
<td>GA</td>
<td>Boundary layer conductance</td>
<td>m·s⁻¹</td>
</tr>
<tr>
<td>GMAX</td>
<td>Maximum stomatal conductance for each age class</td>
<td>m·s⁻¹</td>
</tr>
<tr>
<td>GDL</td>
<td>Function describing the dependence of stomatal conductance upon vapour pressure deficit</td>
<td></td>
</tr>
<tr>
<td>GM</td>
<td>Mesophyll conductance</td>
<td>m·s⁻¹</td>
</tr>
<tr>
<td>GQV</td>
<td>Function describing the dependence of stomatal conductance upon photon flux density</td>
<td></td>
</tr>
<tr>
<td>GS</td>
<td>Stomatal conductance</td>
<td>m·s⁻¹</td>
</tr>
<tr>
<td>GT</td>
<td>Function describing the dependence of stomatal conductance upon temperature</td>
<td></td>
</tr>
<tr>
<td>G2</td>
<td>Initial slope of the curve relating stomatal conductance to photon flux density</td>
<td>m·s⁻¹/µE·m⁻²·s⁻¹</td>
</tr>
<tr>
<td>G3</td>
<td>Value of stomatal conductance in the dark</td>
<td>m·s⁻¹</td>
</tr>
<tr>
<td>G4</td>
<td>Low temperature for stomatal conductance = 0</td>
<td>°C</td>
</tr>
<tr>
<td>G5</td>
<td>Temperature for maximum stomatal conductance</td>
<td>°C</td>
</tr>
<tr>
<td>G6</td>
<td>High temperature for stomatal conductance = 0</td>
<td>°C</td>
</tr>
<tr>
<td>G7</td>
<td>Slope of the curve relating stomatal conductance to vapour pressure deficit and temperature</td>
<td>kPa·°C⁻¹</td>
</tr>
<tr>
<td>IBA</td>
<td>Direct visible radiation appropriated for leaves at layer j and leaf angle class i</td>
<td>Wm⁻²</td>
</tr>
<tr>
<td>Symbol</td>
<td>Description of variables</td>
<td>Unity</td>
</tr>
<tr>
<td>--------</td>
<td>--------------------------</td>
<td>-------</td>
</tr>
<tr>
<td>IBJ</td>
<td>Direct visible radiation at layer j</td>
<td>Wm(^{-2})</td>
</tr>
<tr>
<td>IBN1</td>
<td>Direct near-infrared radiation appropriated for leaves at layer j and angle class i</td>
<td>Wm(^{-2})</td>
</tr>
<tr>
<td>IDJ</td>
<td>Visible diffuse radiation at layer j</td>
<td>Wm(^{-2})</td>
</tr>
<tr>
<td>IT</td>
<td>Solar radiation above canopy</td>
<td>Wm(^{-2})</td>
</tr>
<tr>
<td>HEIGHT</td>
<td>Height occupied in the live crown by leaves of each specific age class</td>
<td>m</td>
</tr>
<tr>
<td>HE</td>
<td>Height from the ground, of each layer</td>
<td>m</td>
</tr>
<tr>
<td>HS</td>
<td>Tree height</td>
<td>m</td>
</tr>
<tr>
<td>LAI</td>
<td>Total leaf area index</td>
<td></td>
</tr>
<tr>
<td>LD</td>
<td>Downward thermal radiation at layer j</td>
<td>Wm(^{-2})</td>
</tr>
<tr>
<td>LJ</td>
<td>Thermal radiation for leaves at layer j</td>
<td>Wm(^{-2})</td>
</tr>
<tr>
<td>LK</td>
<td>Maximum number of integrations for the vertical distribution</td>
<td></td>
</tr>
<tr>
<td>LNIC</td>
<td>Layer non-interception coefficient</td>
<td></td>
</tr>
<tr>
<td>LU</td>
<td>Upward thermal radiation at layer j</td>
<td>Wm(^{-2})</td>
</tr>
<tr>
<td>NIR</td>
<td>Downward near-infrared radiation at layer j</td>
<td>Wm(^{-2})</td>
</tr>
<tr>
<td>NP</td>
<td>Number of points for the vertical distribution</td>
<td></td>
</tr>
<tr>
<td>P</td>
<td>Photosynthesis on a leaf area basis</td>
<td>mg m(^{-2}) s(^{-1})</td>
</tr>
<tr>
<td>PC</td>
<td>Photosynthesis integrated over layer</td>
<td>mg m(^{-2}) s(^{-1})</td>
</tr>
<tr>
<td>PL</td>
<td>Photosynthesis integrated over each age class</td>
<td>mg m(^{-2}) s(^{-1})</td>
</tr>
<tr>
<td>QAREA</td>
<td>Leaf area index of shaded or sunlit leaf at layer J</td>
<td></td>
</tr>
<tr>
<td>QC</td>
<td>Radiation coefficient for dark respiration</td>
<td>((\mu E) m(^{-2}) s(^{-1}))(^{-1})</td>
</tr>
<tr>
<td>QN</td>
<td>Radiation balance</td>
<td>W/m(^{-2})</td>
</tr>
<tr>
<td>QV</td>
<td>Photon flux density</td>
<td>(\mu E) m(^{-2}) s(^{-1})</td>
</tr>
<tr>
<td>RA</td>
<td>Boundary layer resistance</td>
<td>s/m</td>
</tr>
<tr>
<td>RD</td>
<td>Dark respiration</td>
<td>mg m(^{-2}) s(^{-1})</td>
</tr>
<tr>
<td>RD1</td>
<td>Dark respiration at temperature and photon flux density = 0, for shaded leaves</td>
<td>mg m(^{-2}) s(^{-1})</td>
</tr>
<tr>
<td>RD2</td>
<td>Dark respiration at temperature and photon flux density = 0, for sunlit leaves</td>
<td>mg m(^{-2}) s(^{-1})</td>
</tr>
<tr>
<td>Symbol</td>
<td>Description of variables</td>
<td>Unity</td>
</tr>
<tr>
<td>--------</td>
<td>-----------------------------------------------------------------------------------------</td>
<td>-----------</td>
</tr>
<tr>
<td>RF3</td>
<td>Daily rate of fall for 3-year-old leaves</td>
<td>LAI/day</td>
</tr>
<tr>
<td>RF4</td>
<td>Daily rate of fall for 4-year-old leaves</td>
<td>LAI/day</td>
</tr>
<tr>
<td>RF5</td>
<td>Daily rate of fall for 5-year-old leaves</td>
<td>LAI/day</td>
</tr>
<tr>
<td>RF6</td>
<td>Daily rate of fall for 6-year-old leaves</td>
<td>LAI/day</td>
</tr>
<tr>
<td>RF7</td>
<td>Daily rate of fall for 7-year-old leaves</td>
<td>LAI/day</td>
</tr>
<tr>
<td>RL4</td>
<td>Leaf-area-index of 4-year-old leaves remaining on the tree</td>
<td></td>
</tr>
<tr>
<td>RL5</td>
<td>Leaf-area-index of 5-year-old leaves remaining on the tree</td>
<td></td>
</tr>
<tr>
<td>RL6</td>
<td>Leaf-area-index of 6-year-old leaves remaining on the tree</td>
<td></td>
</tr>
<tr>
<td>RL7</td>
<td>Leaf-area-index of 7-year-old leaves remaining on the tree</td>
<td></td>
</tr>
<tr>
<td>RM</td>
<td>Mesophyll resistance</td>
<td>s m⁻¹</td>
</tr>
<tr>
<td>RN</td>
<td>Leaf reflectivity for near-infrared radiation</td>
<td></td>
</tr>
<tr>
<td>RN SOIL</td>
<td>Soil reflectivity for near-infrared radiation</td>
<td></td>
</tr>
<tr>
<td>RV</td>
<td>Leaf reflectivity for visible radiation</td>
<td></td>
</tr>
<tr>
<td>RV SOIL</td>
<td>Soil reflectivity for visible radiation</td>
<td></td>
</tr>
<tr>
<td>S</td>
<td>Standard deviation of the mean height</td>
<td></td>
</tr>
<tr>
<td>SC</td>
<td>Psychrometer constant</td>
<td>kPa °C⁻¹</td>
</tr>
<tr>
<td>SCA</td>
<td>Leaf area cumulated from the top to a specific height for each age class</td>
<td></td>
</tr>
<tr>
<td>SCT</td>
<td>Leaf area cumulated from the top for all age classes</td>
<td></td>
</tr>
<tr>
<td>SHLAI</td>
<td>Shaded leaf area index at layer j</td>
<td></td>
</tr>
<tr>
<td>SLAA</td>
<td>Sunlit leaf area for leaves at layer j and leaf angle class i</td>
<td></td>
</tr>
<tr>
<td>SLAI</td>
<td>Sunlit leaf area index at layer j</td>
<td></td>
</tr>
<tr>
<td>SLAI1</td>
<td>Total leaf-area-index for leaves older than 2-years</td>
<td></td>
</tr>
<tr>
<td>SLOPE</td>
<td>Slope of the curve relating saturated vapour pressure to temperature</td>
<td>kPa °C⁻¹</td>
</tr>
<tr>
<td>STH</td>
<td>Leaf area density at a specific height for the total leaf area</td>
<td></td>
</tr>
<tr>
<td>Symbol</td>
<td>Description of variables</td>
<td>Unity</td>
</tr>
<tr>
<td>--------</td>
<td>----------------------------------------------------------------------------------------</td>
<td>-------</td>
</tr>
<tr>
<td>T</td>
<td>Air temperature</td>
<td>°C</td>
</tr>
<tr>
<td>TAIR</td>
<td>Air temperature</td>
<td>°K</td>
</tr>
<tr>
<td>TC</td>
<td>Temperature coefficient for dark respiration</td>
<td>°C⁻¹</td>
</tr>
<tr>
<td>TEST</td>
<td>Leaf area increment</td>
<td></td>
</tr>
<tr>
<td>THETA</td>
<td>Solar zenith angle</td>
<td></td>
</tr>
<tr>
<td>TLAI0</td>
<td>Leaf-area-index of current year leaves at day DN</td>
<td></td>
</tr>
<tr>
<td>TLAI1</td>
<td>Leaf-area-index of 1-year-old leaves at day DN</td>
<td></td>
</tr>
<tr>
<td>TLAI2</td>
<td>Leaf-area-index of 2-year-old leaves at day DN</td>
<td></td>
</tr>
<tr>
<td>TLAI3</td>
<td>Leaf-area-index of 3-year-old leaves at day DN</td>
<td></td>
</tr>
<tr>
<td>TLAI4</td>
<td>Leaf-area-index of 4-year-old leaves at day DN</td>
<td></td>
</tr>
<tr>
<td>TLAI5</td>
<td>Leaf-area-index of 5-year-old leaves at day DN</td>
<td></td>
</tr>
<tr>
<td>TLAI6</td>
<td>Leaf-area-index of 6-year-old leaves at day DN</td>
<td></td>
</tr>
<tr>
<td>TLAI7</td>
<td>Leaf-area-index of 7-year-old leaves at day DN</td>
<td></td>
</tr>
<tr>
<td>TLN</td>
<td>Layer transmissivity for near-infrared radiation</td>
<td></td>
</tr>
<tr>
<td>TLV</td>
<td>Layer transmissivity for visible radiation</td>
<td></td>
</tr>
<tr>
<td>TN</td>
<td>Leaf transmissivity for near-infrared radiation</td>
<td></td>
</tr>
<tr>
<td>TNEW</td>
<td>Leaf area of current year leaves</td>
<td></td>
</tr>
<tr>
<td>TSKY</td>
<td>Sky temperature</td>
<td>°K</td>
</tr>
<tr>
<td>TSOIL</td>
<td>Soil temperature</td>
<td>°C</td>
</tr>
<tr>
<td>TSOILL</td>
<td>Soil temperature</td>
<td>°K</td>
</tr>
<tr>
<td>TV</td>
<td>Leaf transmissivity for visible radiation</td>
<td></td>
</tr>
<tr>
<td>UH</td>
<td>Wind speed at the top of canopy</td>
<td>m s⁻¹</td>
</tr>
<tr>
<td>UZ</td>
<td>Wind speed at height Z</td>
<td>m s⁻¹</td>
</tr>
<tr>
<td>UZ1</td>
<td>Wind speed at a reference height above the canopy</td>
<td>m s⁻¹</td>
</tr>
<tr>
<td>VIS</td>
<td>Downward visible radiation at layer j</td>
<td>W m⁻²</td>
</tr>
<tr>
<td>Z</td>
<td>Height of each layer</td>
<td>m</td>
</tr>
<tr>
<td>Z0</td>
<td>Roughness parameter</td>
<td>m</td>
</tr>
<tr>
<td>Z1</td>
<td>Reference height above the canopy</td>
<td>m</td>
</tr>
</tbody>
</table>

**Note:** The table above is a representation of the symbols and their descriptions from the image. The values in the 'Unity' column are provided for context and do not correspond to the symbols listed.
B - FORTRAN program for each sub-routine

LEAFAREA calculates the daily leaf area index; the vertical distribution of foliage; the number of layers with a leaf area index of 0.5; and also the proportion of this area occupied by needles of different ages.

SUBROUTINE LEAFAREA(ILAYER,ICLASS,ITANGLE,DN,HEIGHT,LAI,AGELAI, * Z,AREAD)
DIMENSION LLAI(4),HEIGHT(4),S(4),NP(4),H(200),
1FH(200,4),STH(200),STC(200),XA(200),FHI(200,4),
1HF(30),STHI(200),SCA(200,4),FR(30,4),FHV(25)
REAL LAI,LAI
IF(ICLASS.NE.1) GOTO 999
IF(ILAYER.EQ.1.AND.ITANGLE.EQ.0) THEN

DAILY AMOUNT OF LEAVES

TLAI=9.0
TNEW=2.1

daily rate of fall for each age class

RF3=0.38/365
RF4=0.58/365
RF5=0.78/365
RF6=0.98/365
RF7=1.00/365

leaf area of each age class that remain on the tree on 1st January.

RL4=0.62*TNEW
RL5=0.26*TNEW
RL6=0.06*TNEW
RL7=0.01*TNEW

calculating the leaf area index of each age class at any day D between 1st January and 31 May.

IF(DN.GT.151) GO TO 101
DAY=214+DN
TLAI0=TNEW
TLAI1=TNEW
TLAI2=TNEW
TLAI3=(1.-RF3*DAY)*TNEW
TLAI4=(1.-RF4*DAY)*RL4
TLAI5=(1.-RF5*DAY)*RL5
TLAI6=(1.-RF6*DAY)*RL6
TLAI7=(1.-RF7*DAY)*RL7
GOTO 105

101 IF(DN.GT.151.AND.DN.LE.201) GOTO 102
GOTO 103
calculating the leaf area of current year needles between 1st June and 20 July.

102 DAY=DN-152
TLAI0=(DAY/50)*TNEW
GOTO 104

calculating the leaf area index of each age class between 1st June and 31 December.

103 DAY=DN-152
TLAI0=TNEW
104 TLAI1=TNEW
TLAI2=TNEW
TLAI3=(1.-RF3*DAY)*TNEW
TLAI4=(1.-RF4*DAY)*RL4
TLAI5=(1.-RF5*DAY)*RL5
TLAI6=(1.-RF6*DAY)*RL6
TLAI7=(1.-RF7*DAY)*RL7
105 SLAI1=TLAI3+TLAI4+TLAI5+TLAI6+TLAI7
LAI=TLAI0+TLAI1+TLAI2+SLAI1
NLAYER=(LAI/0.5)

THE VERTICAL DISTRIBUTION OF FOLIAGE

LAI(1)=TLAI0
LAI(2)=TLAI1
LAI(3)=TLAI2
LAI(4)=SLAI1
DELTA=0.05
LK=ANINT(HEIGHT(1)/DELTA)+1
106 DO 1 I=1,LK
107 DO 2 J=1,4
108 CONTINUE
1 CONTINUE

calculating the leaf area density for each age class

DO 2 J=1,4
S(J)=HEIGHT(J)/6,
L1=ANINT(HEIGHT(J)/DELTA)+1
NP(J)=L1
106 DO 4 I=1,L1
107 IF(I-1)106,106,107
108 H(I)=0.0
GOTO 108
107 H(I)=H(I-1)+DELTA

PV1=0.05*LAI(J)*(1./SQRT(6.2832)*(1./S(J)))
PV2=(H(I).HEIGHT(J)/2.)**2/(2.*(S(J)**2))

4 CONTINUE
3 CONTINUE
calculating the total leaf area density

DO 5 I=1,LK
  STH(I)=0,
  DO 6 J=1,4
    STH(I)=STH(I)+FH(I,J)
  CONTINUE
  6 CONTINUE
DO 5 CONTINUE
DO 7 J=1,4
  DO 8 I=1,LK
    STHI(I)=STH(LK-I+1)
    FH(I,J)=FH(LK-I+1,J)
  CONTINUE
  7 CONTINUE

calculating the leaf area cumulated from the top for each leaf age class

DO 9 J=1,4
  DO 10 I=1,LK
    IF(I-1).LE.109,110
      XA(I)=HEIGHT(I)
      SCA(I,J)=FH(I,J)
      GOTO 10
    ELSE
      XA(I)=XA(I-1)-DELTA
      SCA(I,J)=SCA(I-1,J)+FH(I,J)
    END IF
  CONTINUE
  9 CONTINUE

calculating the leaf area cumulated from the top for the total leaf area and the height of each layer

TEST=0.5
K=0
DO 11 I=1,LK
  IF(I-1).LE.111,112,112
    XA(I)=HEIGHT(I)
    SCT(I)=STHI(I)
    GOTO 11
  ELSE
    XA(I)=XA(I-1)-DELTA
    SCT(I)=SCT(I-1)+STHI(I)
    SS=TEST-SCT(I)
    IF(SS.GT.0.025) GOTO 11
    K=K+1
    HF(K)=XA(I)
  END IF
  11 CONTINUE

calculating the leaf area density and the proportion of leaves at each layer

DO 12 J=1,4
  FR(K,J)=SCA(I,J)/SCT(I)
  CONTINUE
  FRV(K)=STHI(I)
  TEST=TEST+0.5
  12 CONTINUE
  CONTINUE
END IF

999 IF(ILAYER.GT.NLAYER) STOP
Z=HF(ILAYER)
AREAD=FRV(ILAYER)
AGELAI=FR(ILAYER,ICLASS)
RETURN
END
BOUNDARY determined the wind profile inside the canopy and calculates the shoot boundary layer resistance in each layer.

SUBROUTINE BOUNDARY(IANGLE, UZ1, Z1, HZ, Z, AREACI, RA)

IF(IANGLE.NE.0) RETURN
D=0.89*HZ
Z0=0.03*HZ

calculating the windspeed at the top of the canopy
UH=UZ1*(ALOG((HZ-D)/Z0)/ALOG((Z1-D)/Z0))

calculating the windspeed at layer J
ZZ=Z+3.5
ALPHA=6.85*SQR(AREACI/UH)
SHOOTD=0.5*ZZ
UZ=UH/((1.+(ALPHA*(1.-((ZZ/HZ))))))**2

calculating the boundary layer resistance
RA=7.77*(SHOOTD*0.38)*(UZ**(-0.58))
RETURN
END

RADIATION determines the beam and diffuse flux densities through the depth of the canopy, considering separately visible and near-infrared radiation. It calculates the incident radiation, thermal radiation and the radiation balance for sunlit and shaded leaves taking into account the different leaf-sun angles.

SUBROUTINE RADIATION(ILAYER, ICLASS, IANGLE, LAI, THETA, IT, FRAC, T, *TSOIL, TV, RV, TN, RN, RVSOIL, RNSOIL, GV, GN, GAREA, NETLAI)

DIMENSION AV(30), AN(30), EDU(30), EDN(30), EUV(30), EUH(30)
*BJV(30), BJN(30), SLAI(30), SHLAI(30), FSA(30), SLAA(3)
*0, 9, 1BA(30), 9, 1BN1(30), 9, LD(30), LU(30), LJ(30), F(30), IDJ(30),
*VIS(30), NIR(30), DN(30), DIFN(30), IBJ(30), 9, DIRN(30)

REAL NETLAI
REAL LAI, LNIC, IT, IBA, IBN1, LD, LU, LJ, IDJ, IBJ, NIR

IF(ICALSS.NE.1) GOTO 999
IF(ILAYER.EQ.1 AND IANGLE.EQ.0) THEN
NLAYER=(LAI/0.5)+1
N2=NLAYER+1
N=NLAYER-1
calculating the layer non interception coefficient

\[ \text{SUME} = 0, \]
\[ \text{SUMSC} = 0, \]
\[ \text{DANG} = 1.573 \]
\[ \text{DO } 1 \ I = 1, 89 \]
\[ \text{ANG} = I/57.3 \]
\[ \text{SC} = \sin(\text{ANG}) \times \cos(\text{ANG}) \times \text{DANG} \]
\[ \text{E} = \exp(-0.25/\cos(\text{ANG})) \times \text{SC} \]
\[ \text{SUME} = \text{SUME} + \text{E} \]
\[ \text{SUMSC} = \text{SUMSC} + \text{SC} \]

1 CONTINUE

\[ \text{LNIC} = \text{SUME} / \text{SUMSC} \]
\[ \text{TLV} = \text{TV} \times (1. - \text{LNIC}) + \text{LNIC} \]
\[ \text{RLV} = \text{RV} \times (1. - \text{LNIC}) \]
\[ \text{TLN} = \text{TN} \times (1. - \text{LNIC}) + \text{LNIC} \]
\[ \text{RLN} = \text{RN} \times (1. - \text{LNIC}) \]

calculating the albedo

\[ \text{AV}(N2) = \text{RVSOIL} \]
\[ \text{AN}(N2) = \text{RNSOIL} \]
\[ \text{DO } 2 \ J = 1, \text{NLAYER} \]
\[ \text{J1} = \text{NLAYER} + 1 - J \]
\[ \text{J2} = \text{NLAYER} + 2 - J \]
\[ \text{AV}(J1) = ((\text{TLV} \times 2 - \text{RLV} \times 2) \times \text{AV}(J2) + \text{RLV}) / (1. - \text{RLV} \times \text{AV}(J2)) \]
\[ \text{AN}(J1) = ((\text{TLN} \times 2 - \text{RLN} \times 2) \times \text{AN}(J2) + \text{RLN}) / (1. - \text{RLN} \times \text{AN}(J2)) \]

2 CONTINUE

first iteration to calculate the diffuse radiation - assumes beam = 0

100 \[ \text{EDV}(1) = \text{IT} \times 0.53 \]
\[ \text{EDN}(1) = \text{IT} \times 0.47 \]
\[ \text{EUV}(1) = \text{EDV}(1) \times \text{AV}(1) \]
\[ \text{EUN}(1) = \text{EDN}(1) \times \text{AN}(1) \]
\[ \text{DO } 3 \ J = 2, N2 \]
\[ \text{EDV}(J) = (\text{EDV}(J-1) \times \text{TLV}) / (1. - \text{RLV} \times \text{AV}(J)) \]
\[ \text{EDN}(J) = (\text{EDN}(J-1) \times \text{TLN}) / (1. - \text{RLN} \times \text{AN}(J)) \]
\[ \text{EUV}(J) = \text{EDV}(J) \times \text{AV}(J) \]
\[ \text{EUN}(J) = \text{EDN}(J) \times \text{AN}(J) \]

3 CONTINUE

second and third iterations

\[ \text{BI} = \exp(-0.25/\cos(\text{THETA}/57.3)) \]
\[ \text{BJV}(1) = 1, \]
\[ \text{BJN}(1) = 1, \]
\[ \text{DO } 4 \ J = 2, N2 \]
\[ \text{BJV}(J) = \exp((-0.25 \times (J-1)) / \cos(\text{THETA}/57.3)) \]
\[ \text{BJN}(J) = \text{BJV}(J) \]

4 CONTINUE

\[ \text{DO } 5 \ L = 1, 2 \]
\[ \text{EDV}(1) = (1. - \text{FRAC}) \times \text{IT} \times 0.53 \]
\[ \text{EDN}(1) = (1. - \text{FRAC}) \times \text{IT} \times 0.47 \]
\[ \text{DO } 6 \ J = 2, N2 \]
\[ \text{EDV}(J) = \text{EDV}(J-1) \times \text{TLV} + \text{EUV}(J) \times \text{RLV} + \text{FRAC} \times 0.53 \times \text{IT} \times \text{BJV}(J-1) \times \text{IT} \times \text{BI} \times \text{TV} \]
\[ \text{EDN}(J) = \text{EDN}(J-1) \times \text{TLN} + \text{EUN}(J) \times \text{RLN} + \text{FRAC} \times 0.47 \times \text{IT} \times \text{BJN}(J-1) \times \text{IT} \times \text{BI} \times \text{TN} \]

6 CONTINUE
EUV(N2) = (EDV(NLAYER) + FRAC*0.53*IT*BJV(NLAYER)) * RVS
EUN(N2) = (EDN(NLAYER) + FRAC*0.53*IT*BJN(NLAYER)) * RNVS

DO 7 J=1,NLAYER
   J1=NLAYER+1-J
   J2=NLAYER+2-J
   EUV(J1) = EUV(J2) * TLN + EDV(J1) * RLV + FRAC*0.53*IT*BJV(J1) * 
           (1.-BI)*RV
   EUN(J1) = EUN(J2) * TLN + EDN(J1) * RLN + FRAC*0.47*IT*BJN(J1) * 
           (1.-BI)*RN
   CONTINUE

7 CONTINUE 5 CONTINUE

calculating the ‘shaded’ and ‘sunlit’ leaf area
indices at layer J

SLAI(1)=0.
SHLAI(1)=0.
DO 9 J=2,NLAYER
   SLAI(J)=(BJV(J-1)-BJV(J)) * 2.*COS(THETA/57.3)
   SHLAI(J)=0.5-SLAI(J)

calculating the fraction of sunlit leaf area occupied
by leaves of different angles and the direct beam flu

density appropriate to each leaf angle class

*  AI=5.0
  AM=5.0
  DO 9 I=1,9
     FS(A(J,I))=COS((AM-AI)/57.3)-COS((AM+AI)/57.3)
     SLAA(J,I)=FS(A(J,I))*SLAI(J)
     IBA(J,I)=FRAC*0.53*IT*(COS(AM/57.3)/COS(THETA/57.3)) + 
               EDV(J)+EUV(J)
     IBN1(J,I)=FRAC*0.47*IT*(COS(AM/57.3)/COS(THETA/57.3)) + 
               EDN(J)+EUN(J)
     AM=AM+5.0
  CONTINUE

8 CONTINUE

calculating the thermal radiation at layer J

TSOIL1=TSOIL+273.2
SIGMA=0.00000006
TAIR=T+273.2
TSKY=((T-21.0)+0.2*T)+273.2
IF(FRAC.LT.0.25) TSKY=(T+273.1)
TS=SIGMA*(TSKY**4)
LD=(1)=TS
F(1)=0.
DO 10 J=2,NLAYER
   F(J)=SIGMA*(TAIR**4)*(1.-LNIC)
   LD(J)=LD(J-1)*LNIC+F(J)
 CONTINUE

10 CONTINUE
LU(N2)=SIGMA*(TSOIL1**4)
LU(1)=0.
DO 11 J=1,NLAYER
   J1=NLAYER+1-J
   J2=NLAYER+2-J
   LU(J1)=LU(J2)*LNIC+F(J1)
   LJ(J1)=LD(J1)-LU(J1)
 CONTINUE
DO 12 J=2,NLAYER
   IDJ(J-1)=4.2*(EDV(J)+EUV(J))
   VIS(J-1)=EDV(J)+FRAC*0.53*IT*BJV(J)
   NIR(J-1)=EDN(J)+FRAC*0.47*IT*BJN(J)
   DNET(J-1)=VIS(J-1)+NIR(J-1)+LJ(J)-(EUV(J)+EUN(J))
   DIFN(J-1)=EDV(J)+EDN(J)+EUV(J)+EUN(J)+LJ(J)
12 CONTINUE
DO 13 J=2,NLAYER
   DO 14 I=1,9
      IBJ(J-1,I)=4,2*IBA(J,I)
      DIRN(J-1,I)=IBA(J,I)+IBN1(J,I)+LJ(J)
14 CONTINUE
13 CONTINUE
END IF
999 IF(IANGLE-.EQ.0.)156,156,157
156 QV=IDJ(ILAYER)
   QN=DIFN(ILAYER)
   QAREA=SHLA(Ilayer+1)
   NETLAI=DNET(ILAYER)
   GO TO 158
157 QV=IBJ(ILAYER,IANGLE)
   QN=DIRN(ILAYER,IANGLE)
   QAREA=SLAA(Ilayer+1,IANGLE)
   NETLAI=DNET(ILAYER)
158 RETURN
END
STOMATA calculates the stomatal conductance for individual leaves as a function of weather conditions, leaf age class and position inside the canopy.

SUBROUTINE STOMATA(ILAYER, ICLASS, IANGLE, G2, G3, G4, G5, G6, G7, GMAX, T, * DL, QV, QAREA, AGLAI, GS, GSL, GSC)

DIMENSION GMAX(4)

IF (G4, GT, 0) G4 = -1*G4

response to temperature

RT=(G6-G5)/(G5-G4)
BT=1./(G5-G4)*((G6-G5)**RT))
GT=BT*(T-G4)*((G6-T)**RT)

response to vapour pressure deficit

GV=G7*(T-G4)
GDL=0.
IF((1.:-(1./GV)*DL),GE.0.) GDL=1.-((1./GV)*DL

response to age

G1=GMAX(ICLASS)

RESPONSE TO LIGHT

GQV=(G2*(QV+(G3/G2)))/(G1+G2*(QV+(G3/G2)))

Calculating the stomatal conductance

GSS=G1*GT*GDL*GQV

Calculating the integrated values of stomatal conductance

GS=GSS*QAREA*AGELAI
IF(IANGLE, EQ, 0.,) GSL=0.
IF(IANGLE, EQ, 0., AND., ICLASS, EQ, 1.) GSC=0.
GSL=GSL+GS
GSC=GSC+GS
RETURN
END
PHOTO calculates the hourly photosynthetic rate for single leaves according to their age, orientation angle and position inside the canopy; converts these values to a leaf area bases and integrate them to produce the photosynthetic rate for each layer and for the complete canopy.

SUBROUTINE PHOTO(ILAYER, ICLASS, IANGLE, TC, QC, A: RD1, RD2, CF1, CF2 *

IF (QC.GT.0) QC = -1*QC

calculating the mesophyll conductance

GM=0.17*(0.0049*(T+5.)*(40.-T)**0.698))
RM=(1./GM)*100

calculating the CO2 compensation point

CCF=27.5+2.4*T

calculating dark respiration

R=(1./GS)*100.
IF (IANGLE.EQ.0) THEN
  RD0 = RD1
  CF = CF1
ELSE
  RD0 = RD2
  CF = CF2
END IF
RD=RD0*EXP(TC*T)*EXP(QV*QC)

calculating photosynthesis

C1=(CA-CCF)/RM
R2=(RA*1.37+R1.606)/RM
A1=CF+R2
B=RD*(2.*CF+R2)-A*QV*(1.+R2)-C1
C=RD*(CF*RD-A*QV-C1)+A*QV*C1
PP=((-1.)*B-SQRT((B**2)-4.*A1*C))/2.*A1

calculating the integrated values of photosynthesis

P=PP*QAREA*AGELAI
IF (IANGLE.EQ.0.) PL=0.
IF (IANGLE.EQ.0. AND. ICLASS.EQ.1) PC=0.
PL=PL+P
PC=PC+P
RETURN
END
TRANSPIRE determines the transpiration rate for single leaves according to age, orientation angle and position in the canopy, converts these values to a leaf area basis and integrates them to produce the rates for single layers and for the complete canopy.

SUBROUTINE TRANSPIRE(ILAYER,ICLASS,IANGLE,T,DL,RA,GS,QN,*QAREA,AGELAI,EVP,EVL,EVPC)
SC=0.065

calculating the slope of the vapour pressure saturation curve

T1=(T+0.5)+273.2
T2=(T-0.5)+273.2
EST1=10.*((9.24349-(2305./T1)-(500./(T1**2)))-(100000./((T1**3)))
EST2=10.*((9.24349-(2305./T2)-(500./(T2**2)))-(100000./((T2**3)))
S=0.1*(EST1-EST2)

calculating the flux of latent heat

GA=1./RA
RN=QN
EVPF=(S*RN+1230*DL*GA)/(S+SC*(1.+GA/(0.01*GS)))

calculating the integrated value of transpiration

EVP=EVPF*QAREA*AGELAI
IF(IANGLE.EQ.0.) EVPL=0.
IF(IANGLE.EQ.0.,AND.ICLASS.EQ.1) EVPC=1
EVPL=EVPL+EVP
EVPC=EVPC+EVP
RETURN
END
REFERENCES


MONTEITH, J.L. (1975). "Principles of Environmental Physics".
Edward Arnold, London.


### TABLE OF PARAMETERS

#### A) Leaf area index

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Value</th>
<th>Unity</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>$L_0$</td>
<td>Leaf area index of current year needles</td>
<td>2.0</td>
<td></td>
<td>Dr. D.E. Ford pers. corn.</td>
</tr>
<tr>
<td>$R_{23}$</td>
<td>Rate of fall of 3-year-old needles</td>
<td>$1.04 \times 10^{-3}$</td>
<td>LA/Year</td>
<td>Dr. D.E. Ford pers. corn.</td>
</tr>
<tr>
<td>$R_{24}$</td>
<td>Rate of fall of 4-year-old needles</td>
<td>$1.59 \times 10^{-3}$</td>
<td>LA/Year</td>
<td>Dr. D.E. Ford pers. corn.</td>
</tr>
<tr>
<td>$R_{25}$</td>
<td>Rate of fall of 5-year-old needles</td>
<td>$2.14 \times 10^{-3}$</td>
<td>LA/Year</td>
<td>Dr. D.E. Ford pers. corn.</td>
</tr>
<tr>
<td>$R_{26}$</td>
<td>Rate of fall of 6-year-old needles</td>
<td>$3.68 \times 10^{-3}$</td>
<td>LA/Year</td>
<td>Dr. D.E. Ford pers. corn.</td>
</tr>
<tr>
<td>$R_{27}$</td>
<td>Rate of fall of 7-year-old needles</td>
<td>$2.74 \times 10^{-3}$</td>
<td>LA/Year</td>
<td>Dr. D.E. Ford pers. corn.</td>
</tr>
</tbody>
</table>

#### B) Radiation Penetration

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Value</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\rho_{\text{soil}}$</td>
<td>Soil reflectance for near-infrared radiation</td>
<td>0.25</td>
<td>Goudriaan (1977)</td>
</tr>
<tr>
<td>$\rho_{\text{soil}}$</td>
<td>Soil reflectance for visible radiation</td>
<td>0.17</td>
<td>Goudriaan (1977)</td>
</tr>
<tr>
<td>$\rho_{L,N}$</td>
<td>Leaf reflectance for near-infrared radiation</td>
<td>0.277</td>
<td>Norman and Jarvis (1975)</td>
</tr>
<tr>
<td>$\rho_{L,V}$</td>
<td>Leaf reflectance for visible radiation</td>
<td>0.078</td>
<td>Norman and Jarvis (1975)</td>
</tr>
<tr>
<td>$\tau_{L,N}$</td>
<td>Leaf transmittance for near-infrared radiation</td>
<td>0.33</td>
<td>Norman and Jarvis (1975)</td>
</tr>
<tr>
<td>$\tau_{L,V}$</td>
<td>Leaf transmittance for visible radiation</td>
<td>0.023</td>
<td>Norman and Jarvis (1975)</td>
</tr>
</tbody>
</table>

#### C) Stomatal conductance

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Value</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>$G_1$</td>
<td>Maximum stomatal conductance</td>
<td>1.0</td>
<td>Jarvis et al. (1976)</td>
</tr>
<tr>
<td>$G_2$</td>
<td>Initial slope of the curve relating stomatal conductance to photon flux density</td>
<td>0.03</td>
<td>cm s^{-1}/(muE m^{-2} s^{-1})</td>
</tr>
<tr>
<td>$G_3$</td>
<td>Value of stomatal conductance of photon flux density = 0</td>
<td>0.01</td>
<td>cm s^{-1}</td>
</tr>
<tr>
<td>$G_4$</td>
<td>Low temperature for stomatal conductance = 0</td>
<td>-5.0</td>
<td>°C</td>
</tr>
<tr>
<td>$G_5$</td>
<td>Temperature for maximum stomatal conductance</td>
<td>15.0</td>
<td>°C</td>
</tr>
<tr>
<td>$G_6$</td>
<td>High temperature for stomatal conductance = 0</td>
<td>40.0</td>
<td>°C</td>
</tr>
<tr>
<td>$G_7$</td>
<td>Slope of the curve relating stomatal conductance to vapour pressure and temperature</td>
<td>0.08</td>
<td>kPa/°C</td>
</tr>
</tbody>
</table>

#### D) Photosynthesis

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Value</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>$m$</td>
<td>Convexity factor</td>
<td>0.86</td>
<td>Leverenz and Jarvis (1979)</td>
</tr>
<tr>
<td>$R_{N(0,0)}$</td>
<td>Dark respiration at temperature = 0 and photon flux density = 0</td>
<td>0.0122</td>
<td>mg m^{-2} s^{-1}</td>
</tr>
<tr>
<td>$F_{\text{min}}$</td>
<td>Minimum resistance</td>
<td>6 s cm^{-1}</td>
<td>Neilson et al. (1972)</td>
</tr>
<tr>
<td>$T_{\text{low}}$</td>
<td>Low temperature for minimal mesophyll resistance</td>
<td>5.0</td>
<td>°C</td>
</tr>
<tr>
<td>$T_{\text{high}}$</td>
<td>High temperature for minimal mesophyll resistance</td>
<td>40.0</td>
<td>°C</td>
</tr>
<tr>
<td>$T_{\text{opt}}$</td>
<td>Optimum temperature for minimum mesophyll resistance</td>
<td>21.5</td>
<td>°C</td>
</tr>
<tr>
<td>$\Phi$</td>
<td>Quantum efficiency</td>
<td>$2.44 \times 10^{-2}$</td>
<td>mmol E m^{-2} s^{-1}</td>
</tr>
<tr>
<td>$\delta$</td>
<td>Temperature coefficient for dark respiration</td>
<td>0.082</td>
<td>°C^{-1}</td>
</tr>
<tr>
<td>$z$</td>
<td>Radiation coefficient for dark respiration</td>
<td>-0.07</td>
<td>(muE m^{-2} s^{-1})^{-1}</td>
</tr>
</tbody>
</table>