

Simulation of forest hydrology: model description

4.1 Introduction

The water balance of a forest system consists of the water fluxes as precipitation, evapotranspiration from soil and vegetation, interception of precipitation, and change in soil water content by drainage. The one-dimensional, time dependent forest water balance model, used in this study, is divided into three sub-models. Each sub-model describes one of the above named water fluxes, except for precipitation, which is an input variable. The daily water balance is simulated from hourly measured meteorological data.

Transpiration is calculated with the Penman-Monteith (PM) equation (Monteith, 1965, Rijtema, 1965). From the pilot study, described in chapter 2, it was concluded that transpiration of forests was strongly determined by stomatal conductance. Stomatal conductance often is sensitive to an increase in the atmospheric CO₂ concentration (Morison, 1987), and a change in water use of a forest will strongly depend on the sensitivity of the stomatal conductance to increasing atmospheric CO₂. Therefore, it was important to select a model, which simulates the stomatal conductance and which also includes its sensitivity to elevated CO₂. In chapter 3, the responses of trees to elevated CO₂ concentration were summarized and several possible models for determination of the stomatal conductance were given. A process-based model of the stomatal conductance is not yet available (Kearns and Assmann, 1993) and until now the models are empirical. As concluded in chapter 3, the assimilation-stomatal conductance ($A-g_s$) based models are preferable, as they give a good description of the stomatal functioning, including its sensitivity to CO₂.

The primary process of the CO₂-assimilation (A) at leaf and cellular scale are reasonably well understood for C₃-plants (Reynolds *et al.*, 1993), although the knowledge of the processes is largely phenomenological. Nowadays assimilation models can be used to evaluate the possible effects of increasing atmospheric CO₂ and climate change. However, the models only give an understanding of the short-term process. The long-term process, which lasts several decades for forests, is complex: the secondary effects of the CO₂ change on growth, photosynthetic capacity, nutrient cycle, acclimatization, species competition and forest tree composition are difficult to analyse. So, the model only simulates primary effects of CO₂ on the water balance.

Soil water content is calculated by a simple bucket type model. The model may suffice for forests on sandy soils with a deep water table.

Several one-dimensional models are available for simulation of rainfall interception (Rutter, 1971; Gash, 1979; Mulder, 1985; Calder, 1986). Direct measurements of water storage of the canopy by Bouten *et al.* (1991) suggest, that bucket type models of interception underestimate water storage and this is usually compensated by an overestimation of evaporation during rain (Klaassen *et al.*, 1996b). Application of a lowered evaporation rate in the model resulted in an improved simulation of the interception for two forest sites (Lankreijer *et al.*, 1993). Based on those findings, Klaassen *et al.* (1996b) described a new concept of interception simulation, using an exponential and higher saturation of the canopy and a lower evaporation rate.

In this study interception is still simulated by the common bucket-like model as the recent developments, described by Klaassen *et al.* (1996b), are still insufficient for specific simulations and they need further validation.

Abbreviations and units are explained in the text as well as in the list at the beginning of the thesis.

4.2 Simulation of the forest water balance

The water balance of a forest can be described by:

$$P = E_T + I + U + \Delta\Theta \quad (4.1)$$

with P = precipitation, E_T = evapotranspiration from soil and vegetation, I = interception of rainfall, U = drainage of water from the system and $\Delta\Theta$ = the change in soil water storage. An overview of the water system of a forest is given in figure 2.1. Precipitation, often referred to as gross precipitation, may fall on the canopy or directly onto the soil. The last part is called free throughfall. The intercepted water may drip from the leaves (canopy drip) or flow along stems to the soil (stem flow). A large part of the intercepted water remains on the canopy and evaporates directly into the atmosphere. This part is referred to as interception.

Interception of precipitation by the forest canopy can be very large. In deciduous forests values of 20 to 30 % interception of the total precipitation during the leaf period were found and 10-20 % during the leafless period. For coniferous forests the average value for interception was between 30 and 40 % of the total precipitation (Roestel, 1984).

In tropical forests these values ranged from 9 to 23 % (Raiche, 1983). Interception of rain (I) is especially important for tall vegetation as forests (Rutter, 1967; Stewart, 1978), because of the strong coupling between canopy and the atmosphere. The fast evaporation of the stored water in the canopy *after* a storm is important (Klaassen *et al.*, 1996b). The difference in interception between forests and low vegetation like agricultural crops causes the main difference in the water use of these ecosystems. The reason for this difference in interception is, that the forests canopy dries more quickly and the transpiration starts sooner after the end of the storm.

Net precipitation, that is water reaching the soil, is the sum of free throughfall, canopy drip and stem flow. In most forests, stem flow is only 0-5 % of the precipitation, and therefore it is often neglected. In trees with a smooth bark, however, it can reach up to 20 % of the precipitation during leafless periods (Hiege, 1985). At the forest floor, the water can be stored in layers of dead leaves and humus, or evaporate before infiltrating the soil. According to Schaap & Bouten (1995) and Kelliher *et al.* (1995), the amount of evaporated water from the forest floor can be 3 to 21 %, if the tree canopy density is low. Overland flow of water is possible, but many forest soils are covered with leaves or humus, and for this reason overland flow of water is often negligible in regions with a flat topography.

Precipitation, which reaches the upper layer of the soil, is available for the vegetation. In areas with a high water table, water can also be supplied by capillary rise from ground water. Water, taken up by the roots of plants, is transpired by leaves into the atmosphere. A small and negligible part of the absorbed water is used for growth. Water in the unsaturated soil zone percolates to the ground water and drains from the forest soil or is taken up by the vegetation for transpiration.

4.3 Simulation of soil water content

In the present study, the forest soil is represented by a single layer, a bucket type of model. The single layer represents the rooting depth of the vegetation. As long as the soil water content (θ) is below field capacity (θ_{FC}), the drainage is considered as nihil. When the soil water content rises above field capacity, the surplus water is considered as drainage, and the actual soil water content is set to field capacity. This procedure presents a simplification of the reality, but the procedure is considered satisfactory for sandy soils with a deep water table (Dolman, 1988; Hendriks *et al.*, 1990). For other soil types, it is recommended to calculate drainage on the basis of soil characteristics, and to take into

account the effect of capillary rise as well.

Soil water content was calculated on a daily basis from the soil water content of the previous day (θ_{T-1}), total precipitation (P), drainage from the system (U), interception (I) and transpiration (E_t), using equation 4.1. Values for the field capacity and the maximum soil water deficit were taken from *in situ* measurements for a sandy soil by Hendriks *et al.*(1990). The total amount of available water to the forest trees was taken as equal to the difference between field capacity and wilting point of the soil, the wilting point being set to the maximum soil water deficit.

4.4 Rainfall interception model

Interception of precipitation was calculated, using a model derived from the model of Gash (1979). This model was chosen, because it yields accurate estimates and it only needs a few measured parameters to describe interception. Lankreijer *et al.* (1993) successfully applied the model to deciduous and coniferous forests.

The interception process is divided into three phases. The first phase, the wetting up phase (w), ranges from the start of the storm up to saturation of the canopy. During the second phase, the saturation phase (s), the canopy surface is assumed to be completely wet. The last phase is the drying phase after the rainfall event (d). It is assumed that canopy drip and stem flow are zero, when the amount of water in the canopy is below storage capacity, according to the applied concept of 'bucket' type.

The total amount of intercepted water, evaporated from the canopy (I), is the summation of the intercepted water, evaporated during the above mentioned three phases:

$$I=I_w+I_s+I_d \quad (4.2)$$

When the precipitation (P) is too small to saturate the canopy, the total interception is equal to the amount of rainfall minus the throughfall, given by:

$$I=I_w+I_d=P(1-p) \quad (4.3)$$

The variable p is the free throughfall coefficient, which is related to the proportional ratio of open space area and total canopy area.

When the amount of rainfall is sufficient to saturate the canopy, and the average evaporation rate (\bar{E}) during the storm is zero, total interception (I) is equal to the saturation capacity (S). On the other hand, when \bar{E} during the storm is above zero and larger than $(1-p)R$, - where R is the average rainfall intensity -, then the canopy will never reach saturation

and total interception I equals the amount of rainfall on the canopy, given by equation 4.3.

The amount of rainfall, necessary to saturate the canopy (P') is given by (Gash, 1979):

$$P' = \left(-\frac{\bar{R}S}{\bar{E}}\right) \ln\left(1 - \left(\frac{\bar{E}}{\bar{R}}\right)(1-p)^{-1}\right) \quad (4.4)$$

where S is the storage capacity of the canopy. S is generally assumed to be constant, and it is related to the leaf area index and structure of leaves and stems (Herwitz, 1985).

The canopy parameters, S and p , are derived from the daily totals of precipitation and interception through the Leyton analysis (Leyton *et al.*, 1967). The values are taken as constant for periods with no change in the leaf area.

Storms, with an amount of rainfall larger than P' , yield a total evaporation of intercepted water, which depends on the evaporation rate and rainfall intensity during all three phases of the storm. Interception during these phases is given by:

$$I_w = P'(1-p) - S \quad (4.5)$$

$$I_s = \left(\frac{\bar{E}}{\bar{R}}\right)(P - P') \quad (4.6)$$

$$I_d = S \quad (4.7)$$

The rainfall interception was calculated on a daily basis. Daily precipitation rate was averaged from hourly measured values and daily evaporation rate from hourly calculated values. The evaporation rate was calculated from the slightly modified Penman-Monteith (PM) equation:

$$\lambda E = \frac{sQ_{AC} + \rho_a c_p D / r_{a,H}}{(s + \gamma)} \quad (4.8)$$

Note that, compared with the original PM equation, $r_{a,H}$ replaced $r_{a,M}$, the aerodynamic resistance for momentum and r_s is set to zero.

The aerodynamic resistance for heat ($r_{a,H}$) is calculated by:

$$r_{a,H} = \frac{1}{k^2 u} \ln\left\{\frac{(z-d)}{z_{0,M}}\right\} \ln\left\{\frac{(z-d)}{z_{0,H}}\right\} \quad (4.9)$$

where k is von Kármán constant (=0.4). In equation 4.9 the corrections for stability have

been neglected, as their influence generally is small for forests under wet conditions. The aerodynamic resistance is calculated, assuming a similarity in the resistance for latent and sensible heat respectively.

For closed canopies, the roughness length for momentum ($z_{0,M}$) can easily be estimated from the canopy height h_c . Shuttleworth (1989) gives the average of 15 studied coniferous forests: $z_{0,M} h_c^{-1} = 0.076$ (based on values presented by Jarvis *et al.*, 1976). Gash (1979) used $z_{0,M} h_c^{-1} = 0.1$ to estimate $\bar{z}_{0,M}$. Dolman (1986) also found a value of $\bar{z}_{0,M} h_c^{-1} = 0.1$ for a deciduous forest. A higher accuracy of $z_{0,M}$ can be obtained from *in situ* wind profile measurements.

Determination of the roughness length for heat ($z_{0,H}$) is much more difficult. An overview of the relation between $z_{0,H}$ and $z_{0,M}$ is given by Mölder (1993). Estimation of $\bar{z}_{0,H}$ from the radiation surface temperature suggests, that $z_{0,H}$ is three orders of magnitude smaller than $z_{0,M}$ in heterogeneous terrain (Beljaars and Holtslag, 1991). Brutsaert (1982) summarizes several relations, which suggest that $z_{0,H}$ varies between 4 orders to only one order of magnitude smaller than $z_{0,M}$, depending on the surface type. Kustas *et al.* (1989) found from radiation measurements a range in $\ln(z_{0,M}/z_{0,H})$ from 1 to 10, confirming that the range was larger in cases of heterogeneous surfaces. A $z_{0,H}$ value is found for forests, which in general is only one magnitude below $z_{0,M}$.

It is questionable, whether this value of $z_{0,H}$ can be used to describe the evaporation of a wet forest canopy. Lindroth (1993) directly analysed the roughness length for latent heat ($z_{0,V}$) from flux measurements above a wet canopy of a willow short-rotation stand and he found that $z_{0,V} \approx 0.1h_c$ has the same magnitude as $z_{0,M}$.

Given the uncertainty in the relation $z_{0,H}/z_{0,M}$ in this study, a simple relation is used, as proposed by Garratt and Francey (1978), which relation also is in agreement with the value, found by Brutsaert (1982) for pine forest:

$$\ln\left(\frac{z_{0,M}}{z_{0,H}}\right) = 2.0 \pm 0.35 \quad (4.10)$$

or

$$z_{0,H} = z_{0,M} e^{-2} = 0.14 z_{0,M} \quad (4.11)$$

The zero plane displacement for heat might also deviate from the value for momentum, for instance when water evaporates from levels in the forest, which differ from the levels of mean momentum absorption. Following Raupach and Thom (1981), the value of d is taken identical for heat and for momentum exchange.

4.5 Simulation of transpiration

The most difficult water flux to simulate in a forest system probably is the transpiration of water from the leaves: the flux depends on both atmospheric and plant specific characteristics. The rate of transpiration is determined by the evaporative demand of the air, the available net radiation, the opening of the stomata in the leaves, by the availability of water to the plant and by the storage of water in the plant.

Transpiration was calculated on an hourly basis with the PM-equation:

$$\lambda E = \frac{s Q_{AC} + c_p \rho_a D G_{a,H}}{s + \gamma(1 + G_{a,H} / G_s)} \quad (4.12)$$

where $G_{a,H}$ is the aerodynamic conductance for heat and G_s is the surface conductance. Note, that conductance is equal to the reciprocal value of resistance ($g = 1/r$).

The specific humidity deficit, D , is calculated from measured actual air humidity and the saturated vapour pressure.

Available energy Q_{AC} is calculated from net radiation, Q_N and soil heat flux, H_s :

$$Q_{AC} = Q_N - H_s \quad (4.13)$$

where H_s might be taken from measured data or it may be estimated from Q_N , H ranges from 2 % of net radiation under a dense canopy to more than 30 % under sparse canopy (Monteith *et al.*, 1990). Baldocchi *et al.* (1984) assumed that the soil heat flux was equal to the net flux radiation, available at the forest floor, since latent and sensible fluxes are small near the floor. Based on this relationship, the soil heat flux (H_s) was computed as 3.6 % of the net radiation above canopy, as found by Baldocchi *et al.* (1984).

The aerodynamic conductance, $G_{a,H}$, was calculated, using equations 4.9 and 4.10. $G_{a,H}$ in general was much larger than G_s , and the correction for the difference between the aerodynamic conductance for momentum and for heat is only of minor importance in the simulation of the transpiration.

Transpiration will be suppressed when the canopy is wetted by rain. Some transpiration takes place during the first part of the storm, when the canopy is not yet saturated. Therefore, the amount of transpiration during the wet leaf period was larger in a period with many small storms than in a long period of rainfall. Based on sapflow measurements, Klaassen *et al.* (1996b) estimated transpiration as 10 % of total evaporation during rain.

In this study transpiration during the wet leaf period was neglected in a following indirect way. After calculation of transpiration for all 24 hours, the daily transpiration was corrected for wet leaf periods by subtraction of part of the interception from the total transpiration, following Gash and Stewart (1977) and Gash (1978):

$$E_t(\text{corrected}) = E_t - c \cdot I \quad (4.14)$$

where c is the quotient of transpiration and potential evaporation. The simulated values for transpiration and potential evaporation were averaged over the rainfall hours.

4.5.1 The stomata - photosynthesis model

The surface conductance (G_s) in the PM-equation is assumed to be fully determined by the stomatal conductance (g_s) of the leaves in the canopy. CO_2 is taken up in the leaf through the stomata to be used in assimilation. Water vapour is lost through the stomata at the same time. The stomatal conductance for water vapour (g_{sw}) is therefore directly related to the stomatal conductance for CO_2 (g_{sc}), given by:

$$g_{sw} = 1.6g_{sc} \quad (4.15)$$

The factor 1.6 is the approximate ratio of the molecular diffusion coefficients for water vapour and CO_2 in the air respectively.

The stomatal conductance is simulated by the $A-g_s$ based model of Leuning (1995), which incorporates the sensitivity of the stomatal conductance to changes in ambient CO_2 and to plant physiological characteristics. Leuning (1990) adapted the stomatal conductance model of Ball, Berry and Woodrow (1987), using the humidity function by Lohammar (1980).

Stomatal conductance for CO_2 (g_{sc} , in $\text{mol m}^{-2}\text{s}^{-1}$) depends on the assimilation rate A ($\text{mol m}^{-2}\text{s}^{-1}$), the air humidity deficit D (in this equation given in mol m^{-1}) and the CO_2 concentration at the leaf surface C_s (mol m^{-3}). In this version of the model, the concentration of CO_2 at the leaf surface, ζ , is set to the ambient concentration. Stomatal conductance is given by Leuning (1995):

$$g_{sc} = g_0 + \frac{a_1 A}{(C_s - \Gamma)(1 + D/D_{s,0})} \quad (4.16)$$

The assimilation rate A can be derived from (i) the supply of CO_2 through diffusion from the leaf surface to the interior cells and (ii) the demand of CO_2 by the biochemical CO_2 fixation in the leaf cells. When the stomata close, the assimilation process stops, because CO_2 is no longer available. On the other hand, when assimilation stops because of leaf internal processes, the stomata may close to prevent loss of water.

The relation between A and g_{sc} depends on the CO_2 supply through the stomata and it can be described by:

$$A = g_{sc} (C_s - C_i) \quad (4.17)$$

The assimilation rate A was simulated (at the single leaf scale) according to Farquhar *et al.* (1980), following Friend (1991, 1995) and Jones (1992).

The assimilation rate is a function of absorbed photosynthetically active radiation (PAR), leaf temperature (T_L), intercellular CO_2 concentration (C) and intercellular O_2 concentration (O_i). The net assimilation rate is assumed to be the minimum of the assimilation rate limited by Rubisco activity (A_c) and the regeneration of RuBP (A_r), expressed by:

$$A = \text{Min} \{A_c, A_r\} \quad (4.18)$$

The regeneration of RuBP is limited by the electron transport. The electron transport J (in $\text{mol m}^{-2}\text{s}^{-1}$) depends on the light absorption by chlorophyll. A_r (in $\text{mol m}^{-2}\text{s}^{-1}$) is given by:

$$A_r = \frac{J(C_i - \Gamma_*)}{(C_i + 2\Gamma_*)} - R_d \quad (4.19)$$

The assimilation rate as limited by Rubisco, A_c ($\text{mol m}^{-2}\text{s}^{-1}$), depends on Rubisco activity, C_i and O_i (mol m^{-3}):

$$A_c = \frac{V_{c,\text{max}}(C_i - \Gamma_*)}{C_i + K_c(1 + O_i/K_o)} - R_d \quad (4.20)$$

where Γ_* = CO_2 compensation concentration in absence of mitochondrial respiration (mol m^{-3}), J = potential electron transport rate ($\text{mol m}^{-2}\text{s}^{-1}$), K_c = Michaelis-Menten constant of ribulose bis-phosphate carboxylase (Rubisco) for carboxylation (mol m^{-3}), K_o = Michaelis-Menten constant of Rubisco for oxygenation (mol m^{-3}), $V_{c,\text{max}}$ = maximum catalytic capacity of Rubisco ($\text{mol m}^{-2}\text{s}^{-1}$) and R_d = respiration rate ($\text{mol m}^{-2}\text{s}^{-1}$).

Given the similarities between 4.19 and 4.20, the net assimilation can be written as:

$$A = \alpha \left[\frac{(C_i - \Gamma_*)}{(C_i + \beta)} \right] - R_d \quad (4.21)$$

where α is $V_{c,max}$ or J , and β is $c K (1 + O_0/K)$ or 2Γ . Simultaneous solution of the three equations 4.16, 4.17 and 4.21 results in a quadratic equation for C_i :

$$b_2 C_i^2 + b_1 C_i + b_0 = 0 \quad (4.22)$$

where

$$b_2 = g_0 + X(\alpha - R_d) \quad (4.23)$$

$$b_1 = (1 - C_s X)(\alpha - R_d) + g_0(\beta - C_s) - X(\alpha \Gamma_* + \beta R_d) \quad (4.24)$$

$$b_0 = -(1 - C_s X)(\alpha \Gamma_* + \beta R_d) - g_0 \beta C_s \quad (4.25)$$

$$X = \frac{a_1 f(D)}{(C_s - \Gamma)} \quad (4.26)$$

and

$$f(D) = \frac{1}{\left(1 + \frac{D}{D_{s,0}}\right)} \quad (4.27)$$

Equation 4.22 gives two solutions for C_i . The C_i , resulting in the lowest A , was chosen and g_{sc} was calculated. C_i is an estimation of the C_0 , available to the cell within the leaf. Farquhar and von Caemmerer (1982) assume that differences between C_i and the fraction of CO_2 at the site of carboxylation are small. During high rates of photosynthesis, however, a significant gradient in the CO_2 concentration from the intracellular spaces to the carboxylation site in the cells can be expected. This effect is neglected because of simplicity reasons.

The assimilation rate is temperature dependent. The calculation of the assimilation rate was started at the assumption of a leaf temperature (T_L) to be 5° above air temperature (T_A). The leaf temperature was recalculated with the function, adapted from Jones (1992, equation 9.5), using the simulated value of g_{sc} :

$$T_L = T_A + \frac{(\gamma(r_{a,H} + r_s)/(\rho_a c_p)) Q_{AC}}{s + \gamma(1 + r_s/r_{a,H})} - \frac{D}{s + \gamma(1 + r_s/r_{a,H})} \quad (4.28)$$

where T_A = air temperature, r_s = stomatal resistance ($=1/g_s$), $r_{a,H}$ = aerodynamic resistance for heat.

The temperature dependent parameters were calculated resulting in new values for the assimilation rate and stomatal conductance. The calculation was iterated, until the leaf temperature was constant within 0.001 K. The calculation was also stopped, when T_L reached values below 0 °C, since it is assumed that the assimilation was nihil, when leaf temperature becomes below 0 °C.

Transpiration of water from the leaf was determined by calculation of the stomatal resistance (or its reciprocal stomatal conductance). The resistances to vapour transport of the leaf mesophyll (internal) and of the leaf boundary layer were small and could be neglected, compared with the resistance of the stomata. The stomatal conductance depended on leaf temperature, which again depended on the heat resistance of the leaf boundary layer. The resistance of the leaf boundary layer is determined by several factors, as e.g. the leaf width. With increasing resistance, the leaf temperature changed and it influenced the assimilation and transpiration rates.

In equation 4.28 the leaf temperature was calculated from the aerodynamic resistance for heat, $r_{a,H}$. The aerodynamic resistance, $r_{a,H}$, was calculated with equation 4.9. The leaf temperature was assumed to be constant through the canopy and the effect of the leaf boundary layer resistance on the latent heat flux was approximated by using $r_{a,H}$ instead of $r_{a,M}$.

4.5.2 Calculation of the canopy conductance

In the present calculation the canopy is regarded as a single 'big leaf', meaning that environmental variables, as air temperature, atmospheric CO₂-concentration, wind speed, air humidity and leaf temperature are assumed to be constant throughout the entire canopy. The only exception to this single 'big leaf assumption' is the variable solar radiation. This variable is a major and decisive factor, governing photosynthesis and stomatal conductance (Goudriaan, 1986). The available solar radiation decreases with canopy depth and it strongly depends on leaf density. The relation between the assimilation rate and solar radiation is not linear, and therefore, the available solar radiation is calculated for different

canopy layers, depending on the LAI of the canopy, following the Beer-Bouguer law. The canopy is divided into n layers, with each layer (i) having its own LAI. Default value for n is 5.

Solar radiation, available in each layer, Q_{ci} ($W\ m^{-2}$), is calculated from leaf area and extinction coefficient (k), by:

$$Q_{ci} = Q_s \text{Exp}\left(-k \left(\frac{i-0.5}{n}\right) LAI\right) \quad (4.29)$$

The density of the leaves, the canopy structure, the leaf angle distribution, but also azimuth of the sun, determine together the value of k . The value of k was found to vary between 0.2 and 1.5 (Baldocchi *et al.*, 1984; Jones, 1992). In this study the value was set constant at 0.75 and it is assumed to be independent of solar elevation. The value of k implicates a canopy with a clumped-leaf distribution. The relation between solar radiation and LAI for different canopy layers is given in figure 4.1.

PAR is derived from solar radiation. About 45% of the total solar radiation is PAR (Monteith *et al.*, 1990). Total PAR (in molquanta $m^{-2}\ s^{-1}$) is given by:

$$PAR = 0.45 Q_{ci} \frac{4.75}{1.0E6} \quad (4.30)$$

PAR, absorbed by the leaf, is calculated from:

$$PAR_{\alpha} = \alpha_{PAR} PAR \quad (4.31)$$

where α_{PAR} is the absorption coefficient of the leaf, which slightly depends on thickness of the leaf, age, water content, surface morphology and orientation. The value is set at 0.85 in the model, according to Jones (1992).

LAI distribution influences canopy radiation and thus total assimilation and transpiration. The date of leaf unfolding can be simulated, using periods of chilling and forcing temperatures (Kramer, 1994). To calculate the day of leaf fall is more difficult, since it is determined by several factors, like water availability during the season. Given the uncertainties of the simulation of the LAI distribution over time, functions based on LAI-measurements are used in the model for deciduous and coniferous types of forests

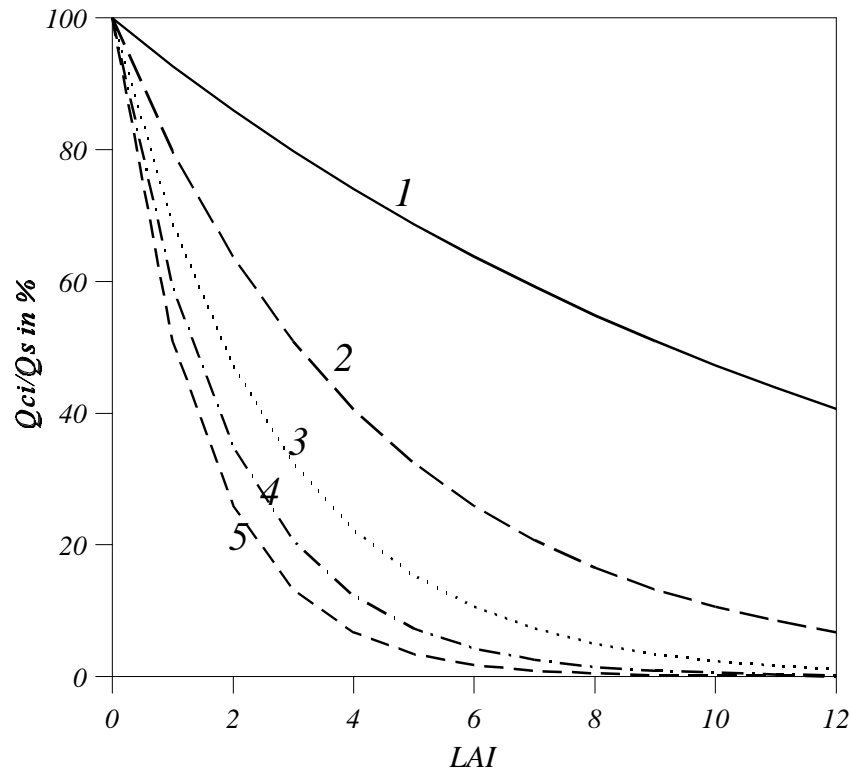


Figure 4.1 Relation between the percentage of radiation in the center of each canopy layer relative to the total radiation at the top of the canopy and the total canopy LAI. The number of canopy layers is set to 5.

(Beadle *et al.*, 1982; Hendriks *et al.*, 1990).

In summary, for each canopy layer the available solar radiation was determined. From the last value the PAR for each layer was calculated and the assimilation rate A of the concerned canopy layer ($\text{mol m}^{-2}\text{s}^{-1}$). Total A for the entire canopy was then determined by multiplication of the average A of the n layers by the total LAI. The found value of A is used in equation 4.16 and resulted in the surface conductance for the whole canopy.

Soil water deficit function

In this study, the simulation of the water balance is given for periods, when soil water may be temporarily limiting. Therefore, a relation between stomatal conductance and soil water availability is needed, since both stomatal opening and photosynthesis are reduced by soil

water limitation. These processes are regulated by the production of the phytohormone ABA in the roots under water limitation (Kearns and Assmann, 1993).

To account for the effect of water deficit in the soil, it is assumed that the stomatal conductance, as simulated with the Leuning-model (equation 4.16), presents the optimal conductance without any leaf water and soil water limitation.

To incorporate the influence of soil water content on canopy conductance, the relation, described by Stewart (1988), is used:

$$f(\theta) = 1 - \text{Exp}(a_{\theta} (\theta_D - \theta_{\max})) \quad (4.32)$$

where $f(\theta)$ is the soil moisture factor, varying between 0 and 1, θ_D is the actual soil moisture deficit, θ_{\max} is maximum soil moisture deficit and a_{θ} is a fitted constant. Leuning (1995) concluded, that the A versus g_{sc} model needs to be corrected for water-stressed plants. An independent multiplicative factor to describe the relation between ABA production and stomatal conductance is not realistic (Dewar, 1995), because the sensitivity of the stomata to atmospheric CO_2 concentration can increase with increasing soil moisture deficit, but is applied as a first approach.

Finally, the surface conductance (G_s) is calculated by multiplication of the canopy conductance for CO_2 (G_{sc}) with the factor 1.6 (see equation 4.15) and the soil water reducing factor:

$$G_s = 1.6 G_{sc} f(\theta) \quad (4.33)$$

In the calculation of the stomatal conductance for CO_2 , the interaction between the diffusing molecules of CO_2 and water vapour with each other and with the cell walls is neglected. Leuning (1983), following Jarman (1974), gave an extensive overview of the influence of CO_2 and H_2O pressure differences between leaf and air and the collision of the CO_2 and H_2O molecules with the cell walls. Both the effects of pressure gradients of CO_2 and H_2O between leaf interior and outside on the diffusion of CO_2 and water vapour and of CO_2 diffusion on the diffusion of H_2O , are very small and should be neglected. However, according to Jacobs (1994), the effect of diffusion of water molecules, to the outside, on the diffusion of CO_2 molecules, to the leaf interior, can not be neglected, considering the transport of gases through the stomata. The effect depends on the rate of transpiration and the assimilation rate and it is large, when the assimilation rate is small. On the other hand, Leuning (1990) stated, that under most conditions the introduced error is $<2\%$ in the estimation of A and C_i . In this study both effects are neglected for reasons of simplicity.

4.5.3 Derivation of CO₂ assimilation parameters

The simulation of the assimilation rate, given in equations 4.19 and 4.20, uses several parameters. Most parameters were calculated, according to Farquhar *et al.* (1980) and Friend (1993) and they are given below. Constants and site dependent variables are given in appendix A.

Photorespiratory compensation point

The compensation point in absence of mitochondrial respiration, Γ_* , depends on the rates of oxygenation and carboxylation of Rubisco (von Caemmerer and Farquhar, 1981):

$$\Gamma_* = \frac{0.5V_{o,\max}K_c O_i}{V_{c,\max}K_o} \quad (4.34)$$

Respiration rate R_d

The mitochondrial respiration rate, R_d , was simulated as a function of the nitrogen content of the leaf (Friend, 1995):

$$R_d = R_{dt} N \quad (4.35)$$

R_{dt} is the rate of dark respiration (mitochondrial respiration) in mol (CO₂) kg⁻¹(N) s⁻¹; it is temperature dependent.

Rubisco-parameters

The maximum rate of carboxylation of Rubisco ($V_{c,\max}$) has been derived from gas exchange measurements, and it was empirically calculated from the nitrogen content of the leaf (Farquhar *et al.*, 1980; Friend, 1993). It is a function of the carboxylation turnover number, k_c , of Rubisco:

$$V_{c,\max} = k_c R_c \quad (4.36)$$

where R_c is the leaf Rubisco catalytic site content, k_c is a given input value and it is temperature dependent.

Similarly, the maximum rate of oxygenation of Rubisco, $V_{o,\max}$, is calculated from R_c

and the oxygenation turnover number k_o . R_c is calculated from the Rubisco concentration, where complete activation of Rubisco is assumed. The molar mass of the enzyme Rubisco is 550 kg mol^{-1} with 8 active sites, resulting in:

$$R_c = \frac{8\sigma}{550} \quad (4.37)$$

where σ is the Rubisco content of the leaf (g m^{-2}). Rubisco content is on its turn, derived from nitrogen content of the leaf, assuming $0.16 \text{ kg N kg}^{-1}$ Rubisco (Farquhar *et al.*, 1980):

$$\sigma = f_{N,\text{Rub}} N / 0.16$$

$f_{N,\text{Rub}}$ is the fraction of leaf nitrogen, bound in Rubisco, and N is the total leaf nitrogen content in kg m^{-2} . The fraction of leaf nitrogen, bound in Rubisco, is assumed to be 22% (Friend, 1991). The N -content per unit one-sided leaf area, appears to be fairly constant for a broad range of leaf types, with an average of 1.57 g N m^{-2} ; it ranges between 1 and 4 g m^{-2} . The N content of conifers is above the average of 1.57, namely 3.02 g m^{-2} (Schulze *et al.*, 1994). In this study the total leaf nitrogen content is set default to 2 g m^{-2} .

Physiological research has shown, that leaf photosynthesis is related to leaf nitrogen concentration. The dependency of the actual assimilation rate on the nitrogen content of the leaf is incorporated, according to Friend (1991). The relation between A and N is determined by the total leaf concentration of N , the partitioning of N in Rubisco and chlorophyll, and by the dark respiration rate. The relation between A and N results in an almost linear increase in the assimilation rate with N (figure 4.2), and it slightly decreases with higher nitrogen concentrations, also resulting in a linear relation between the stomatal conductance and nitrogen content. Schulze *et al.* (1994) also derived a linear relation between maximum assimilation rate and leaf nitrogen concentration.

Light dependent and electron transport related parameters

The electron transport, J , depends on the absorbed PAR and on the potential rate of electron transport during light saturation, J_{max} ($\text{mol m}^{-2}\text{s}^{-1}$); for details see Farquhar and von

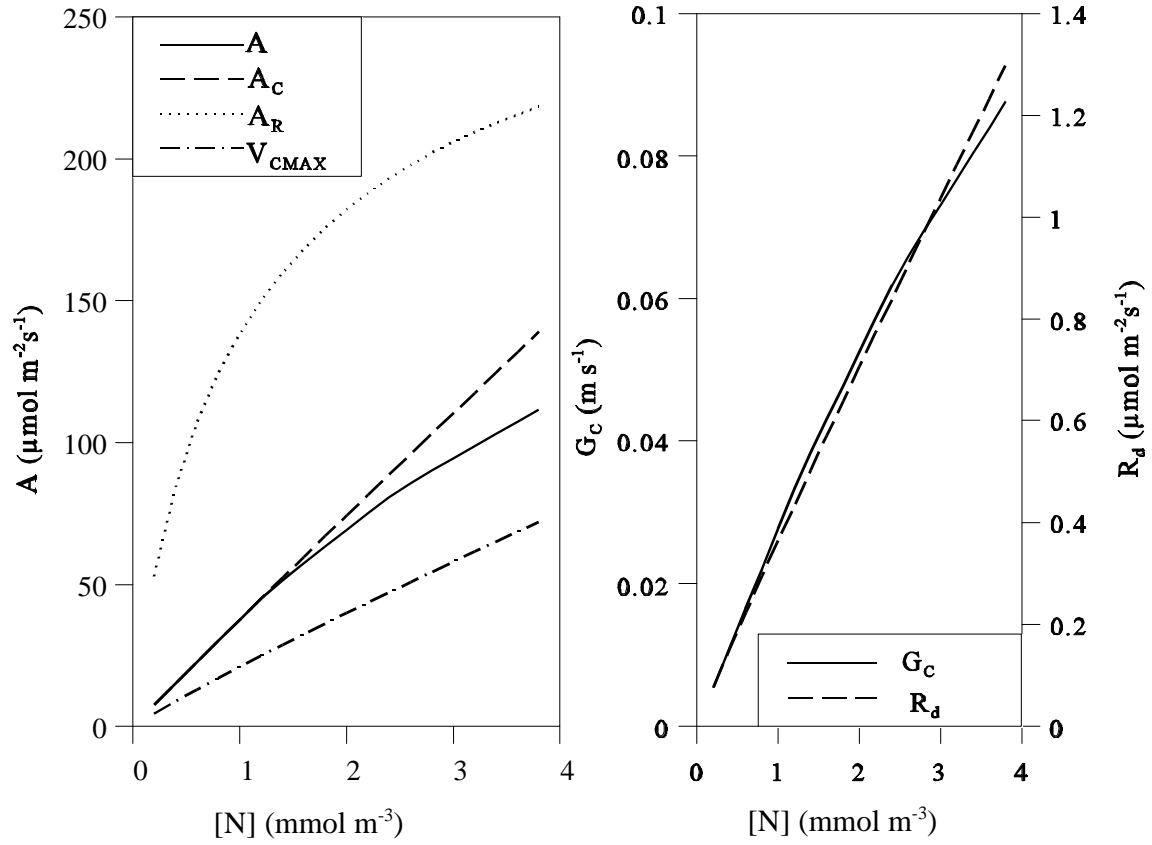


Figure 4.2. Assimilation rate (A), canopy conductance (G_c) and respiration rate (R_d) vs. nitrogen content of the leaf.

Caemmerer (1982):

$$J = \frac{J_{\max} PAR_{\alpha}}{PAR_{\alpha} + 2.1 J_{\max}} \quad (4.38)$$

The value of 2.1 is the amount of mol quanta absorbed, to deliver the necessary energy. This value depends on the way the additional ATP for the NADPH production is generated.

J_{\max} depends on the leaf chlorophyll content. The chlorophyll content is again calculated from the nitrogen content of the leaf, so J_{\max} is given by:

$$J_{\max} = \frac{j_{\max} f_{N,chl} N}{0.056} \quad (4.39)$$

where j_{\max} is the temperature dependent, irradiance-saturated potential electron transport

per mole of chlorophyll, and $f_{N,chl}$ the fraction of nitrogen, bound in chlorophyll. The value of 0.056 is calculated as the result of the molar mass of nitrogen ($0.014 \text{ kg mol}^{-1}$) and the number of moles N per mole of chlorophyll.

Temperature dependency of assimilation parameters

K_c and K_o are the Michaelis constants of Rubisco for CO_2 and O_2 respectively. K is temperature dependent in contrast to K_o (Jordan and Ogren, 1984).

k_o , k_c , R_{dt} and j_{max} also are temperature dependent. The temperature dependency of the first three parameters and that of K_c is calculated from (Thornley & Johnson, 1990):

$$p = a \cdot e^{\left(-\frac{E_a}{RT_L}\right)} \quad (4.40)$$

where p is K_c , k_o , k_c or R_{dt} respectively, a is a parameter-specific constant, E is the activation energy and R is the gas constant. The relation between p and T_L is given in figure 4.3A.

The temperature dependency of j_{max} is given by:

$$j_{max} = \frac{a \cdot \exp(-E_d/RT_L)}{1 + \exp((\Delta ST_L - E_d)/RT_L)} \quad (4.41)$$

Equation 4.41 shows a maximum of J_{max} around 30°C (see figure 4.3B).

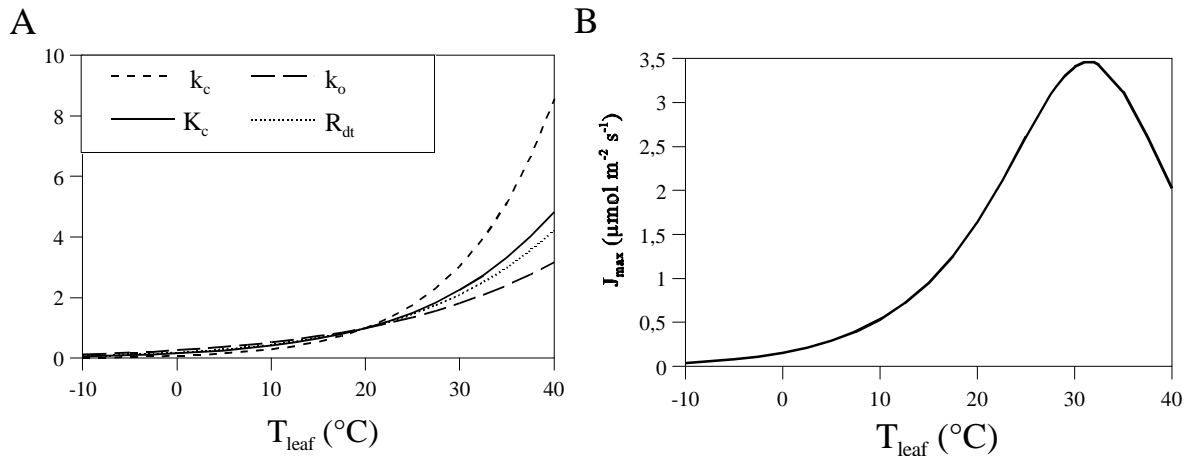


Figure 4.3. Temperature dependency of K_c , k_o , k_c and R_{dt} (A) and of J_{max} (B). The values of the parameters shown in figure A are relative to the value of the parameters at 20°C.

The values of K_c and K are corrected for the influence of solubility of CO_2 and O respectively, according to Friend (1995).

4.6 Discussion

A physiological $A-G_s$ type model was included in the forest water balance model to include the direct effect of atmospheric CO_2 on stomatal conductance. The $A-G_s$ model still uses a certain degree of empiricism, but the physiological processes, determining stomatal functioning, are realistically simulated. Advantages of the physiological description are (i) a smaller sensitivity on fitted (and thus 'black box') parameters and (ii) the possibility of extending the model to studies on simulation of growth, and of physiological and ecosystem processes. The model shows a realistic response of the stomata to environmental changes, especially to the air humidity (Dewar, 1995).

An indirect response of g to D follows from the (almost) linear empirical relation between g and E_v , as observed by Monteith (1995a), who re-analysed 52 sets of published measurements on humidity responses of the stomata of 16 species. Monteith showed, that the relationship in terms of the maximum stomatal conductance g_{max} (when $D \rightarrow 0$) and maximum transpiration rate E_{max} (when D was large) was constant. Dewar (1995) showed the consistency of the model by Leuning, by explaining both g_{max} and E_{max} , taking into account the osmotic gradient between the leaf cells and the hydraulic conductivity of the

cells. These characteristics can be related to the value of the empirical constants a_l and $D_{s,0}$ in the model of Leuning.

The results of the model also are, according to Dewar, in agreement with the stomatal response to the internal CO_2 concentration (Mott, 1988) and the sensing of the transpiration rate, E , by the stomata (Mott and Parkhurst, 1991).

Based on several assumptions the model might be improved. The sensitivity of the model to the N -content of the leaf makes the N concentration in the leaf probably a most crucial parameter in the simulation model. A small change in the N -content does strongly change A and g_s . Incorporation of a realistic simulation of the N -content in the leaf and its implication to assimilation and stomatal conductance is urgently needed.

Soil moisture deficit has no effect on the surface conductance until it reaches a certain value, see e.g. equation 3.11 (Hendriks *et al.*, 1990). Based on this conclusion, the relation of Stewart (1988) is used as a first approach to describe the relation between the stomatal conductance and soil water content in this model version. Monteith (1995a) found that the maximum stomatal conductance, g_m , shows no response to decreasing soil water availability, except down to very low values of 8% of the available soil water. Dewar (1995) linked this response of the plants to the ABA production in the roots under low water availability and by subsequent transport of ABA to the leaves and the consequent response of the stomata. The relationship of g_{max} to soil water content is similar to the relation, used by Stewart (1988), between $G_{s,max}$ and soil water deficit and it supports the use of the equation to describe the response of stomata to soil water deficit. As a first approach it is acceptable, although both the change in the sensitivity of the stomata to the CO_2 concentration, found when ABA is produced, and the sensitivity of E_{max} to leaf water potential, are not taken into account. The model might be improved using the mechanistic description (Dewar, 1995) of the response of stomatal conductance to soil water availability, leaf water and osmotic potential status.

Species differ in their sensitivity of the stomata to ambient CO_2 concentration. For example, many coniferous trees show little or no reaction to high atmospheric CO_2 concentration. This sensitivity difference is likely to be related to a_l or $D_{s,0}$, and leaf hydraulic conductivity, but also to genetic characteristics, expressed in anatomical adjustments (stomata density, pore size and leaf thickening) during leaf development (Kürschner, 1996). The topic of stomata sensitivity to atmospheric CO_2 , together with the response to soil water, needs further research.

The assumption of a similar roughness length for latent and sensible heat in the simulation

of the interception, is questionable. Direct measurements of $z_{0,v}$ for a wet canopy are rarely performed. Lindroth's (1993) measurements showed a similar roughness length for momentum and latent heat. However, a lower value for $z_{0,v}$ is possible, because Lindroth's selection of 'wet canopy-conditions' was more strictly applied than needed in simulation of interception (Lindroth, 1995 pers. comm.) and probably the canopy is seldom completely wet.

In the study by Lankreijer *et al.* (1993), the average evaporation rate (\bar{E}) for the Les Landes location was even smaller by mistake, due to an error in the use of equation 4.9. In the published study, the simulation results showed even better agreement with the measurements when the aerodynamic resistance was larger, than described by the equations. This implicates that - assuming no errors occurred in the measurements - $z_{0,v}$ might be even smaller than $z_{0,H}$. The measurements by Lindroth suggest a $\bar{z}_{0,v}$ close to $\bar{z}_{0,M}$. It is unclear, which value $z_{0,v}$ is realistic. The derivation of a correct $\bar{z}_{0,v}$ strongly depends on correct measurements of humidity deficit, which is difficult under wet circumstances, when humidity is often close to saturation. Therefore, measurement of humidity during and shortly after rainfall, needs more attention.

The interception of precipitation influences transpiration via the water availability in the soil compartment. Changes in interception through changes in canopy (e.g. LAI) will alter the soil water availability and transpiration, if soil water content is low. Lower interception and increase in throughfall will change the interception of the topsoil and soil evaporation. The change in leaf litter interception, soil evaporation and the relation between the descriptive parameters of the canopy S and p and the LAI and canopy are unclear and they need further research. To determine the canopy parameters from an exponential saturation of the canopy seems a right step in this direction (Klaassen *et al.*, 1996b), instead of the often used Leyton analysis.

Forest floor evaporation is explicitly not simulated by the model. Implicitly the floor evaporation is incorporated into the model by the fact that the transpiration model is fitted to total evaporation measurements, without distinction of leaf transpiration and soil evaporation. Although forests with a LAI larger than 4 will show a low value of floor evaporation, the model will give an underestimation for periods with low LAI during spring and fall. It is assumed that by incorporation of the soil evaporation into the transpiration model, the underestimation is small over long periods, compared to the total water balance.

The simulation of the water balance with a one-dimensional model is appropriate for large scale forests (Veen and Dolman, 1989). However, with small scale forests, the effect of advection of energy might be important. Only 25% of the Dutch forests is larger than 5 hectare, and 70% is smaller than 1.5 hectare (Braks, 1984). The water use of a forest edge is on an average larger than in the middle of an extensive forest. Harding *et al.* (1992) state, that the recharge of soil water of a one hectare forest area is only 68% of the value of a hectare forest without an edge effect. The difference is attributed to a higher transpiration, a higher leaf area index (LAI) and a higher radiation at the edge. Another explanation for the enhanced water use of forest edges is the increased evaporation rate, due to stronger turbulence (Klaassen *et al.*, 1996a). They also found, that the total amount of interception is not larger at the edge, but that the canopy dries more quickly after a storm, and thus, transpiration after the storm starts sooner. Both effects of increased LAI and increased evaporation rate increase the water use at forest edges. Forest edges are therefore important in the water balance of Dutch forests (Kruijt, 1994). Considering the regional water balance, no indication has yet been found, that the edge effect might be significantly enhanced or reduced by climate change.

4.7 Conclusion

To simulate the effect of increasing atmospheric CO₂ on the hydrology of forests, the dependency of the surface conductance on assimilation rate and on CO₂ is incorporated into the model, using the model of Leuning (1995). Confirmed by the results of Dewar (1995), the model realistically simulates the stomatal responses to environmental changes.

In an independent simulation study the interception model already showed good results (Lankreijer *et al.*, 1993), but estimation of the value for $z_{0,v}$ needs further research. The possible effects of a change in the canopy might be estimated more realistically by simulation of the canopy characteristics S and p in relation to the LAI and canopy structure.

This first version of the model uses several simplifications. However, the $A-g_s$ sub-model makes it possible to analyse the effects of changes in physiological processes on the water balance of trees.