

Technical manual for ForestFlux

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1 Overview

ForestFlux is a multi-layer canopy assimilation model operating at an hourly time-step. It is written in Fortran code, and was developed as the process-based canopy gas exchange model for input to the long-term forest growth model, GroMIT (Growth Model of Individual Trees), which operates at an annual timestep. GroMIT has been superseded by the development of ForestGrowth. The overview given here positions ForestFlux within the wider framework of GroMIT, but only deals with the technical specifications of ForestFlux.

The model is not structured as a single formulation, but is tailored to specific requirements, including the use of alternative sub-models. ‘Add-ons’ have been developed for specific purposes. In this description, only brief details of such add-ons are given, but where a function is integral to the model, it is described more fully.

The objective of the canopy assimilation module (ForestFlux) is to calculate carbon uptake for a given leaf area index (LAI). The well characterised biochemical formulation of photosynthesis developed by Farquhar and co-workers (Farquhar and von Caemmerer, 1982; von Caemmerer *et al.*, 1994) are used, together with a stomatal conductance model after Jarvis (1976). Dates representing bud-burst and end of season (senescence in broadleaf trees) are also modelled. This module has been used for some basic flux simulations, although it does not make any claims to be a full flux model as it includes no representation of canopy CO₂ storage. Its primary objective, within the framework of the growth model, is to define the relationship between LAI and assimilated carbon. The time-steps of calculation are necessarily short (usually hourly), although once basic relationships for a given site have been defined, then this intensive modelling approach may not be necessary.

The growth module uses the relationship derived between LAI and assimilated carbon, and allocates the carbon to compartments within the trees. The compartments consist of foliage, branches, stem, coarse (transport) roots and fine roots. Allocation between compartments follows the pipe model theory of Shinozaki *et al.* (1964). Each tree has a physical X-Y co-ordinate, and the space available to the tree is based on a polygon taking account of the size and location of its neighbours. The growth module uses annual time steps at present, although there is potential to simulate shorter periods.

2 Meteorological inputs and the weather generator

The simulation of carbon balance begins with the input of meteorological data. Typically, hourly data are used with inputs of solar radiation, air temperature, humidity (or wet-bulb temperature), wind-speed and precipitation, together with ambient carbon dioxide concentration. Such detailed datasets are often not available, especially for historical records and future predictions. In these cases, hourly data are derived from daily data using the following routines:

2.1 Temperature and Radiation Where daily values of temperature and radiation are available, sine curves are fitted with peaks at 14:00 hours and 12:00 hours respectively. A methodology has been developed to allow the derivation of hourly radiation estimates from historical data recorded as sunshine duration (Randle, 1997).

2.2 Relative Humidity If humidity is not available, it is calculated from wet-bulb and dry-bulb temperatures. Where daily values are given, it is assumed that vapour pressure remains constant throughout the day and relative humidity changes with temperature. For temperatures above freezing, the saturated vapour pressure (Svp) is given by:

$$Svp = 6.1708 \exp^{(17.269 T_k)/(237.3+T_k)} \quad 1$$

where, T_k is the temperature in kelvin, and the vapour pressure (Vp) is

$$Vp = Svp_{wet} - 0.66 (T_{dry} - T_{wet}) \quad 2$$

with T_{dry} and T_{wet} , the dry-bulb and wet-bulb temperatures.

Relative humidity, Rh , is calculated from the vapour pressure and the saturated vapour pressure (at T_{dry} ; Vp_{dry}) at the relevant time:

$$Rh = \frac{Vp}{Vp_{dry}} 100 \quad 3$$

2.3 Windspeed and Precipitation If hourly data are not available, a function must be developed which describes hour to hour variation. This function will be site specific.

2.4 Ambient Carbon dioxide Concentration If measured data are not available a simple function is used, with maximum and minimum concentrations at dawn and two hours after dawn, respectively. The concentration decreases linearly between the maximum and minimum values, remains at the minimum value until two hours prior to dusk, and then increases linearly up to the maximum value at dawn.

3 Canopy structure

The most appropriate way to envisage how the model considers the structure of the canopy of a tree is as a series of concentric shells (an analogy is a ‘Russian doll’). For ease of reference, the term ‘zone’ is used to represent each shell. Each ‘zone’ has a number of layers of foliage (definable), and each layer has a proportion of foliage that is either sun-lit or shaded. The physiological characteristics (R_d , V_{max} , J_{max} , g_{smax} etc.) are constant within each ‘zone’, but may vary between ‘zones’. To this end, there are many input and parameters that are required to define the canopy.

4 Light interception

Previously published formulations of the model have simulated CO₂ assimilation as light interception using the Beer-Lambert Law (Randle and Ludlow, 1998; Ludlow et al., 1990). The model now incorporates a biochemical photosynthesis routine, based on the model of Farquhar and co-workers (see Medlyn et al., 1999).

The canopy is divided into several ‘zones’ and each ‘zone’ has a maximum photosynthetic capacity explicitly defined in the parameterisation. Photosynthetically active radiation (PAR) falling on each layer of foliage is attenuated by the canopy leaf area extinction coefficient, such that the total PAR absorbed is given by

$$I_{abs} = I_0 (1 - \exp(-K_{ext} LAI)) \quad 4$$

where, I_{abs} is absorbed PAR, I_0 the PAR above the canopy, and K_{ext} the light extinction coefficient of the canopy.

ForestFlux treats light interception by shaded and sunlit foliage separately (Spitters, 1986b) and integrates these processes with a biochemical CO₂ assimilation model following Meng and Arp (1994). Their approach has been further developed, through assigning each ‘zone’ specific physiological characteristics, with the total number of zones limited to twelve. Each zone has a defined number of foliage layers (leaf area index, LAI), with each layer of foliage (irrespective of the number of layers in a ‘zone’) considered in turn, and calculated incident PAR falling on shaded and sunlit leaves used to drive the biochemical model. If a layer spans two ‘zones’, weighted averages of parameters are input into the biochemical model.

4.1 Partitioning of diffuse and direct light above the canopy

In order to treat sun-lit and shaded foliage separately, it is necessary to partition incoming radiation into diffuse and direct light.

The amount of cloud cover has a large effect on the proportion of direct and diffuse radiation. All irradiation is diffuse under an overcast sky but 23% is diffuse (with 77% of global irradiation direct) under a clear sky, (Spitters, 1986a). Historical meteorological records have consisted of daily measurements of sunshine duration, which have been used to derive the diffuse and direct components of PAR using functions dependent on zenith angle, atmospheric pressure and potential solar radiation. (Weiss and Norman, 1985). More recently, following the development of electronic sensors and data logging capabilities, PAR or global radiation is measured directly. These data, at a sub-daily timestep are used in many carbon flux and process-based models of forest growth such as GROMIT (Ludlow *et al.*, 1990), MAESTRO (Wang and Jarvis, 1990) and Biomass (McMurtrie *et al.*, 1990).

In order to provide these estimates of direct and diffuse radiation input, ForestFlux uses the approach of Spitters (1986a). In this approach, the total extra-terrestrial radiation at a plane parallel to the surface of the earth is given by:

$$S_0 = S_c (1 + 0.033 \cos(360 d/365)) \cos \theta_z \quad 5$$

Where d is the day of year, S_c is the solar constant (1370 W/m^2), and θ_z is the azimuth angle of the sun.

A four-part function describes the ratio of diffuse radiation (S_{df}) to total radiation at the earth surface (S_g), as a function of radiation at the earth surface and the extra-terrestrial radiance (S_0) (de Jong, 1980). Both daily and hourly values can be derived (Spitters, 1986a; de Jong, 1980). The relationships are notably constant over a range of climates and latitudes (Collares-Pereira and Rabl, 1979; Erbs *et al.*, 1982) and are appropriate to a wide range of conditions. Since ForestFlux usually calculates photosynthesis at an hourly time-step, the most appropriate function is:

$$\begin{aligned} S_{\text{df}}/S_g &= 1 & \text{for } S_g/S_0 &\leq 0.22 \\ S_{\text{df}}/S_g &= 1 - 6.4 (S_g/S_0 - 0.22)^2 & \text{for } 0.22 < S_g/S_0 &\leq 0.35 \\ S_{\text{df}}/S_g &= 1.47 - 1.66 (S_g/S_0) & \text{for } 0.35 < S_g/S_0 &\leq K \\ S_{\text{df}}/S_g &= R & \text{for } K < S_g/S_0 & \end{aligned} \quad 6$$

where $R = 0.847 - 1.61 \cos \theta_z + 1.04 \cos^2 \theta_z$ and $K = (1.47 - R) / 1.66$.

4.2 Calculation of sunlit and shade light intensities

Only photosynthetically active radiation (PAR) is considered, and it is assumed that reflection is negligible, although scattering of direct light is taken into account. The separation of PAR into diffuse and direct components is explained in the previous section. Following Neumann *et al.* (1989) and Meng and Arp (1994), PAR on sunlit leaves in the i th layer is calculated as:

$$\text{PAR}_{\text{sun}}(i) = \text{PAR}_{\text{dir0}} (\cos \Psi_{\text{orient}} / \sin \theta_z) + \text{PAR}_{\text{shade}}(i) \quad 7$$

where, PAR_{dir0} is the amount of direct PAR above the canopy, Ψ_{orient} is the orientation angle of the leaf in relation to the sun, and θ_z is the azimuth angle. In most circumstances, PAR_{sun} will be less than the incoming radiation as the surface of the canopy is not a plane surface.

The calculation of PAR incident shaded leaves is more complex, as they receive diffuse light, attenuated direct light and scattered direct light. Since each layer of leaves is treated separately, the average light within the layer is not calculated, although incident light above each layer is a necessary intermediate; for shaded leaves

$$\begin{aligned} \text{PAR}_{\text{shade}} = & \text{PAR}_{\text{diff0}} \exp(-K_{\text{df}} \sum \text{LAI}(i) - 1) + \\ & \text{PAR}_{\text{dir0}} \{ \exp[-(1 - \sigma_c)^{0.5} K_{\text{bl}} \sum \text{LAI}(i) - 1] - \\ & \exp(-K_{\text{bl}} \sum \text{LAI}(i) - 1) \} \end{aligned} \quad 8$$

where $\text{PAR}_{\text{diff0}}$ is diffuse PAR above the canopy, K_{df} the canopy extinction coefficient for diffuse light, and σ_c is the scattering coefficient of single leaves. K_{bl} is the black body canopy extinction coefficient (Spitters, 1986b, Meng and Arp, 1994) such that

$$K_{\text{bl}} = \frac{K_{\text{df}}}{1.6(1 - \sigma_c)^{0.5} \sin \theta_z} \quad 9$$

If light extinction is constant throughout the canopy, then equations (7) and (8) apply. In circumstances where extinction is not constant, an approximation is made, where for sequential layers of leaves, K_{df} becomes an average of the layers above, and K_{bl} is calculated (equation 2.9) using this value of K_{df} .

4.3 Calculation of sunlit foliage

In any layer, the foliage is either sunlit or shaded. The proportion of sunlit foliage in each layer is variable, and based on a Markov gap-frequency model, following Neumann *et al.*, (1989) and Meng and Arp (1994). A clumped foliage distribution is assumed, with leaf distribution in one layer dependent on the distribution in previous layers. For each layer of foliage, the proportion which is sunlit in layer, i , is defined as

$$P_{\text{sun}} = \exp \left(\frac{-\Omega_0 G \sum_{n=1}^i \text{LAI}(n)}{\cos \theta_z} \right) \quad 10$$

Where G is the leaf orientation function and Ω_0 is the degree of leaf dispersal. For the first layer (top of canopy), $i=1$, and $i=2,3$, etc., for subsequent layers.

5 Photosynthesis

The evaluation of incident PAR on shaded and sunlit foliage in each layer enables the calculation of carbon assimilation. The photosynthetic rate is limited by either the regeneration of ribulose 1,5-biphosphate (RuBP), (A_c) or by electron transport (A_j). The formulation follows von Caemmerer *et al.* (1994) and Medlyn *et al.* (1999).

$$A_{\text{net}} = \min(A_j, A_c) - R_d \quad 11$$

Where R_d is the dark respiration. A_c and A_j are given as:

$$A_c = \frac{V_{\text{max}}(C_i - \Gamma^*)}{C_i + K_m} \quad \text{and} \quad A_j = \frac{J(C_i - \Gamma^*)}{4(C_i + 2\Gamma^*)} \quad 12$$

K_m is the Michalis-Menton coefficient for the reaction ($K_m = K_c(1 + O_i / K_o)$), with O_i , the internal oxygen concentration; K_c and K_o temperature dependent Arrhenius (exponential) functions:

$$K_c = 404 \exp\left(\frac{59400(T - 298)}{(298 R T)}\right) \quad \text{and} \quad K_o = 248 \exp\left(\frac{36000(T - 298)}{(298 R T)}\right) \quad 13$$

where R is the universal gas constant.

Γ^* is the CO₂ compensation point, a function of temperature (in kelvin):

$$\Gamma^* = 36.9 + 1.88(T - 298) + 0.036(T - 298)^2 \quad 14$$

and J is a function of light, light absorption and quantum yield (α) such that:

$$\theta J^2 - (I\alpha + J_{\max})J + I\alpha J_{\max} = 0 \quad 15$$

where internal CO₂ concentration (C_i), is a function of ambient CO₂ concentration (C_a), net assimilation (A_{net}) and stomatal conductance to water vapour (g_s) such that

$$C_i = \frac{C_a - A_{net}}{1.6g_s} \quad 16$$

The values V_{\max} and R_d are temperature dependent Arrhenius (exponential) functions:

$$\text{Arrhenius:} \quad \exp\left(\frac{H_a (T - T_{ref})}{T_{ref} R T}\right) \quad 17$$

J_{\max} may take the form of either an Arrhenius function, or a Lloyd (humped) function:

$$\text{Lloyd:} \quad \frac{\exp\left(\frac{H_a (T - T_{ref})}{T_{ref} R T}\right) \left(1 + \exp\left(\frac{D_s T_{ref} - H_d}{R T_{ref}}\right)\right)}{\left(1 + \exp\left(\frac{D_s T - H_d}{R T}\right)\right)} \quad 18$$

The Arrhenius function requires an input parameter of the activation energy of the relevant process, H_a , together with Temperature, T (in kelvin), and the reference temperature for the value, T_{ref} , (also in kelvin). In addition to the parameters of the Arrhenius function, the Lloyd function requires additional parameter values for the de-activation energy (H_d), and an entropy term (D_s).

Calculations are performed layer by layer for both the sunlit and shaded foliage. The product of A_{net} and the proportion of foliage that is either sunlit or shaded gives carbon assimilation in that layer. The summation of successive layers gives the cumulative assimilation for an increasing number of layers of foliage.

6 Stomatal conductance

Calculation of stomatal conductance is made on a layer by layer basis following Jarvis (1976). Response functions to environmental variables (varying between 0 and 1), are imposed on the maximum value for stomatal conductance ($g_{s\max}$), which is variable between 'zones'.

$$g_s = g_{s\max} f(Q) f(T) f(\psi) f(\phi) f(C) \quad 19$$

where $f(x)$ is the response function to light, temperature, humidity, soil-moisture and ambient carbon dioxide concentration.

The light response function is defined as:

$$f(Q) = \frac{S_0(Q+q)}{g_{s\max} + S_0(Q+q)} \quad 20$$

where S_0 is the slope of the light response function at low light levels, Q is incident PAR and $q = g_{\text{dark}}/g_{\text{smax}}$, with g_{dark} defined as stomatal conductance in the dark.

The temperature response function is defined as:

$$f(T) = \frac{T - T_{\text{opt}}}{T_{\text{opt}} - T_{\text{min}}} \left(\frac{T_{\text{max}} - T}{T_{\text{max}} - T_{\text{opt}}} \right)^{\left(\frac{T_{\text{max}} - T_{\text{opt}}}{T_{\text{opt}} - T_{\text{min}}} \right)} \quad 21$$

where T (°C) is temperature, and T_{max} , T_{opt} and, T_{min} are the maximum, optimum and minimum temperatures for stomatal conductance.

The response function to vapour pressure deficit (humidity function) is defined as:

$$f(\psi) = \left\{ \begin{array}{ll} 0, & V_{pd} > V_2 \\ 1 - \frac{V_{pd} - V_1}{V_2 - V_1}, & V_2 \geq V_{pd} \geq V_1 \\ 1, & V_1 > V_{pd} \end{array} \right\} \quad 22$$

where V_1 and V_2 are the values of vapour pressure deficit at which g_{smax} is at a maximum and minimum, respectively, and $V_{pd} = (1 - (Rh/100))V$

The response to soil-moisture deficit (S_{md}) is defined as:

$$f(\varphi) = \max(1 - \exp^{S_{m1}(S_{md} - S_{m2})}, 0.0) \quad 23$$

where S_{m1} is a constant and S_{m2} is the soil moisture deficit at which stomatal closure is complete. The ground is assumed to be frozen (and thus $f(\varphi)=0$) when the air temperature is less than -1°C .

The response of stomata to ambient carbon dioxide concentrations is not well defined in literature. However, an empirical function has been derived for oak (Broadmeadow *et al.*, 1999):

$$f(C) = \max((1 - C_1(C_a - 350)), 0.2) \quad 24$$

where C_a is ambient carbon dioxide concentration, and C_l is a response function parameter.

7 Water Balance

ForestFlux assumes three water holding zones in the soil. The number of zones can be extended, but in practice three have been sufficient. Each of the zones is defined by a physical depth (which thus gives rise to a volume under the projected area of the crown), and a saturated (holding) capacity. The three zones are defined as:

Rooting zone: This is the only layer from which the tree draws water. Water movement by diffusion from or to storage zone 1 is dependent on the difference in water content (or potential) between the two zones.

Storage zone 1: water may flow by diffusion from or to the rooting zone as well as from and to storage zone 2.

Storage zone 2: water may only flow between this zone and the storage zone 1.

In reality, the flow (diffusion) of water between zones will be continuous. However, for ease of implementation, a time-step (or iterative) approach is used. The time step for evaluation (eg 1 hour) is divided into 12 smaller units, termed mini-steps, and calculations of water-balance (transpiration, precipitation and diffusion) are made over these shorter time-steps. This is repeated for each of the remaining mini-steps, thus simulating equilibrium and reducing oscillations.

7.1 Diffusion

The transfer of water (W_t), from one zone into another, in time, t , (mini-step) is based upon the difference in the water content between the zones ($W_{c1} - W_{c2}$) and a diffusion constant, D_c :

$$W_t = t(W_{c1} - W_{c2})D_c \quad 225$$

7.2 Rainfall

The proportion of precipitation falling as throughfall depends on the quantity of water intercepted and held within the canopy (leaf-water). If the water holding capacity of a layer is exceeded, then subsequent rainfall is intercepted by the next layer. When all foliage layers in the canopy are at capacity, additional precipitation falling within the time step is defined as throughfall.

The throughfall initially enters the rooting zone. The capacity of this zone depends on the current water content and the maximum holding capacity of the zone. Any additional throughfall enters storage zone 1 and finally storage zone 2. When all the soil water storage zones are full to capacity, additional precipitation are lost from the system as runoff. Throughfall is assumed to fall evenly over the main time-step, and is added within the mini-steps of water movement.

7.3 Transpiration

Water demand for transpiration is dependent on the soil moisture content of the rooting zone - if a deficit has developed, then stomatal closure will be initiated (see above). Uptake is also calculated on a mini-step basis.

Transpiration is reduced if foliage water is present, which must be lost through evaporation before transpiration can occur. The function weights transpiration of a layer by the proportion of time that the layer is 'dry'.

$$E_t = \min(L_w, P_e) + \max(0, \frac{L_w}{P_e}) \Phi \quad 26$$

Where E_t is evapo-transpiration, L_w , leaf-water, P_e , potential evaporation of a wet surface and Φ , the transpiration from a dry surface. Transpiration is also governed by boundary layer conductance (g_a), which is dependent on humidity, temperature, and wind-speed. Aerodynamic and boundary layer conductances are modelled as in MAESTRO (Wang and Jarvis, 1990; Jarvis *et al.*, 1976).

8 Respiration

Since the assimilation module generally operates at an hourly timestep, calculations of respiration are made within this module. Maintenance respiration of each of the main living tissue compartments (foliage, branch-wood, stem sapwood, transport roots and fine roots) is calculated using equation 2.27 and expressed on an annual basis as a proportion of tissue dry weight (i.e. kg C respired per kg carbon in living tissue).

$$R_t = R_b \exp^{Q_{10}(t-t_b)} \quad 27$$

where R_t is the respiration rate at temperature, t , Q_{10} is the respiratory quotient (default 2.0), and R_b is the maintenance respiration rate at reference temperature t_b .

9 Phenology

For deciduous trees, the growing season is defined as the period during which there is green foliage present on the tree. There is well-documented evidence of growth, elongation, thickening etc of various organs of the tree at various times of the year (e.g. McWilliam, 1972; Mitrukov, 1976; Pietarinen *et al.*, 1982). In ForestFlux, these phases are grouped together as the ‘growing season’. For evergreen species, the definition of growing season is less precise, although there is a period of defined bud-burst in spring, and in many cases, a dormant period during winter.

9.1 Bud-burst

Several types of models of bud-burst were evaluated, including a simple three parameter thermal time model (Cannell and Smith, 1983), and sequential, alternate and four-phase models which have been reviewed by Kramer (1994). The most suitable approach, given the limited data available for validation, is the synthesis model of Hänninen (1990). This is a four-phase model which has been extended to include the photosensitivity response of Kramer (1994). Unrealistic outputs have been produced for future climate scenarios, although these problems may be a result of poor input data. However, it does indicate that without sufficient parameterisation and validation, extrapolation using the ‘modified synthesis’ model is unwise. In this case, a modified thermal time model, provided more realistic output, although the model is less sensitive. Either of the models described below can be used, but care should be taken with parameterisation; this is particularly important for the more complex synthesis model which can easily be over-parameterised, requiring some of the less sensitive parameters to be fixed.

Both models have a state of chilling (S_{chl}) and forcing (S_{fre}):

$$S_{chl} = \sum_{t_1}^t R_{chl} \quad \text{and} \quad S_{fre} = \sum_{t_2}^t R_{fre} \quad 28$$

Bud-burst occurs as a function of S_{chl} and S_{fre} which are determined by model specific rates of chilling (R_{chl}) and forcing (R_{fre}). The thermal-time model used in ForestFlux predicts bud-burst occurs when $S_{fre} \geq S_{chl}$ and is expressed as:

$$R_{fre} = \begin{cases} 0, & T \leq T_{b1} \\ k(T - T_b), & T > T_{b2} \end{cases}, \quad k = \begin{cases} 0, & t < t_1 \\ 1, & t \geq t_2 \end{cases}, \quad \text{and} \quad R_{chl} = 1 \quad 29$$

The parameters t_1 and t_2 represent the date of the onset of rest and quiescence (namely November 1 and January 1), with t , the day of year. The parameters, T_{b1} and T_{b2} are the base temperatures at which chilling or forcing occurs. In the original thermal time model, $T_{b1}=T_{b2}=2^\circ\text{C}$.

The synthesis four-phase model is more complex. The chilling sum, S_{chl} , uses the rate of chilling with an additional modifier, daylength (D) and is calculated from November 1.

$$R_{chl} = \partial D_l \left\{ \begin{array}{ll} 0, & T \leq T_{\min} \\ \frac{T - T_{\min}}{T_{\text{opt}} - T_{\min}}, & T_{\min} < T \leq T_{\text{opt}} \\ \frac{T - T_{\max}}{T_{\text{opt}} - T_{\max}}, & T_{\text{opt}} < T \leq T_{\max} \\ 0, & T \geq T_{\max} \end{array} \right\} \quad 30$$

Modifiers to the chilling and forcing requirements (Δ_{chl} , Δ_{frc}) are also calculated from November 1:

$$\Delta_{chl} = \left\{ \begin{array}{ll} 0, & T < T_{low} \\ \frac{\Delta_{c \max}}{T_{high} - T_{low}} (T - T_{low}), & T_{low} \leq T < T_{high} \\ \Delta_{c \max}, & T \geq T_{high} \end{array} \right\} \quad 31$$

Similarly,

$$\Delta_{frc} = \left\{ \begin{array}{ll} 0 & T < T_{low} \\ \frac{\Delta_{f \max}}{T_{high} - T_{low}} (T - T_{low}) & T_{low} \leq T < T_{high} \\ \Delta_{f \max} & T \geq T_{high} \end{array} \right\} \quad 32$$

The chilling and forcing modifiers are used to calculate a competence function, $f(C)$:

$$f(C) = \left\{ \begin{array}{ll} 0, & R_{chl} < C_{\text{abs}} \\ \frac{1 - C_{\min} - \Delta_{frc}}{C_{\text{crit}} - \Delta_{chl} - C_{\text{abs}}} (R_{chl} - C_{\text{abs}}) + C_{\min} + \Delta_{frc}, & C_{\text{abs}} \leq R_{chl} < (C_{\text{crit}} - \Delta_{chl}) \\ 1, & R_{chl} \geq (C_{\text{crit}} - \Delta_{chl}) \end{array} \right\} \quad 33$$

The rate of forcing is calculated from the competence function:

$$R_{frc} = f(C) \left\{ \begin{array}{ll} 0, & T \leq 0 \\ \frac{a}{1 + \exp^{b(T+c)}}, & T > 0 \end{array} \right\} \quad 34$$

In this model, bud-burst occurs when the state of forcing, (S_{frc}), exceeds a critical threshold, (F_{crit}). For the modified synthesis model, the parameters required are listed in Table 1:

Parameter	
T_{\min}	Minimum temperature for chilling
T_{opt}	Optimal temperature for chilling
T_{\max}	Maximum temperature for chilling
δ	Constant for daylength effect
$\Delta_{c\max}$	Maximum decrease in chilling requirement for full growth competence.
$\Delta_{f\max}$	Maximum increase in growth competence from forcing temperature
T_{low}	Lower temperature value for effect on growth competence
T_{high}	Highest temperature value for effect on growth competence
C_{\min}	Minimum growth competence value
C_{crit}	Chilling requirement of rest completion
C_{abs}	Absolute chilling requirement
a	Constant for forcing rate
b	Constant for forcing rate
c	Constant for forcing rate
F_{crit}	Critical value of the state of forcing to achieve bud-burst

Table 1 Parameter nomenclature for the bud-burst model based on the modified synthesis model of Hänninen (1990), with photosensitivity of Kramer (1994). See equations 30–34.

9.2 Seasonal Development

Although the development of foliage is assumed to be instantaneous on the date of bud-burst, the physiological characteristics are assumed to develop as a function of time. The function Dv returns a value between 0.1 and 1.0 dependent on the number of days since bud-burst, with the maximum (1.0) occurring 28 days after bud-burst. The function is used as a scalar for the photosynthetic parameters of J_{\max} , V_{\max} and R_d , together with the maximum stomatal conductance, g_{smax} . The occurrence of a spring frost retards Dv by seven days. Where no instances of frost occur, the function is linear.

$$Dv = \min\left(\left(0.1 + \frac{0.9}{28} \sum d_i\right), 1.0\right) \quad 35$$

where d_i is the cumulative number of days since bud-burst (reduced by a maximum of 7 if a spring frost occurs).

Values of J_{\max} and V_{\max} may be determined by an empirical relationship based on nitrogen content of the foliage. There is no change in photosynthetic capacity associated with the withdrawal of nutrients in autumn, although all physiological parameters including those describing respiration can be input at specific time points.

9.3 Determination of the end of the growing season

For coniferous trees, the end of growing season is less marked, and in reality, limited photosynthesis may occur all year round. However, the amount of assimilation during the ‘winter months’ is small because of low light intensity and temperature, and short day-length.

For deciduous trees, the end of the growing season is defined by the senescence of foliage. There is a period that precedes this when nutrients are withdrawn from the foliage (leaf yellowing). No

attempt in the model is made to simulate this ‘nutrient withdrawal’. The errors in the calculation of the overall annual assimilation by this omission are small, as the low-light and temperature result in minimal photosynthetic CO₂ assimilation during this period. Models which attempt to account for the timing of senescence and the translocation of nutrients usually use a thermal chill function, which is sometimes coupled with a photo-period function (Pietarinen *et al.*, 1982; Koski and Sievänen, 1985).

ForestFlux defines leaf longevity as a function of carbon balance (between respiration and photosynthesis). The modelling of leaf longevity as a function of carbon gain was proposed by Charbot and Hicks (1982), who expressed it as the difference between photosynthetic rate during the favourable period of the year and maintenance costs during the unfavourable period, together with construction costs, and other costs including defence, transport and storage. This approach was further refined by Kikuzwa (1991, 1995). The assimilation module of ForestFlux contains no information on tree structure, and thus whole tree carbon balance cannot be used to assess the longevity of the growing season. An alternative approach has been adopted in which the carbon balance of the outer-most layer of foliage is assessed, and is defined as:

$$\sum_{i=1}^{14} \frac{A_i}{R_i} \geq \lambda \quad 36$$

Where A_i and R_i are the daily carbon assimilation totals and respiration costs of the outermost layer of foliage in the canopy, and λ is a threshold value. A 14-day moving average is used to smooth anomalies and prevent the premature prediction of leaf senescence. The end of the growing season is defined as the day when this 14 day moving average falls below λ . Low temperatures over-ride this senescence function, with the occurrence of n_5 days ($T > 5^\circ\text{C}$) or n_4 days ($T < 4^\circ\text{C}$) also defining the end of the growing season. The threshold value, λ , also responds to frost immediately after budburst.

10 Initialisation

Most of the input requirements for the assimilation model described above are entered via a single input file. These inputs use the FORTRAN feature of ‘namelist’. The ‘namelist’ feature allows the order of inputs (within any list) to be unimportant. The structure of the various lists groups relevant inputs together; for example, stomatal conductance, soil conditions etc. The input file is in common with the files used for the growth model, although the growth model parameters need not be set.

11 Model Validation

Individual modules have been validated using data from a variety of sources. The phenology sub-module was calibrated using data from the IPG (International Phenology Garden) project from 1970-1981, for which there was a site at Headley Park in Hampshire, 2 km from the Alice Holt forest plot. The meteorological data input is for the long-term Alice Holt climatological station, whilst the budburst data are for Ashted in Middlesex, UK, courtesy of the Institute of Terrestrial Ecology, Abbots Wood Research station (Fig. 1a). The correlation between observed and modelled data is good, although there is a nine day offset which is likely to represent the difference in temperature between the two sites, which are 50 km apart. In addition, Ashstead is within the conurbation of Greater London, and consequently subject to an urban heat sink effect.

The carbon and water exchange modules (ie photosynthesis and transpiration) have been validated using eddy correlation flux data (Figs. 2 and 3). The data shown are for June and July 1998, and represent fluxes measured at 30 minute intervals. The relationship between measured and modelled CO₂ flux is very good, with a slope of close to unity. However, the modelled flux saturates at approximately 23 $\mu\text{mol m}^{-2} \text{s}^{-1}$, which is lower than the maximum observed flux. This may represent error in the flux measurement system, or a limitation of the model in terms of canopy structure.

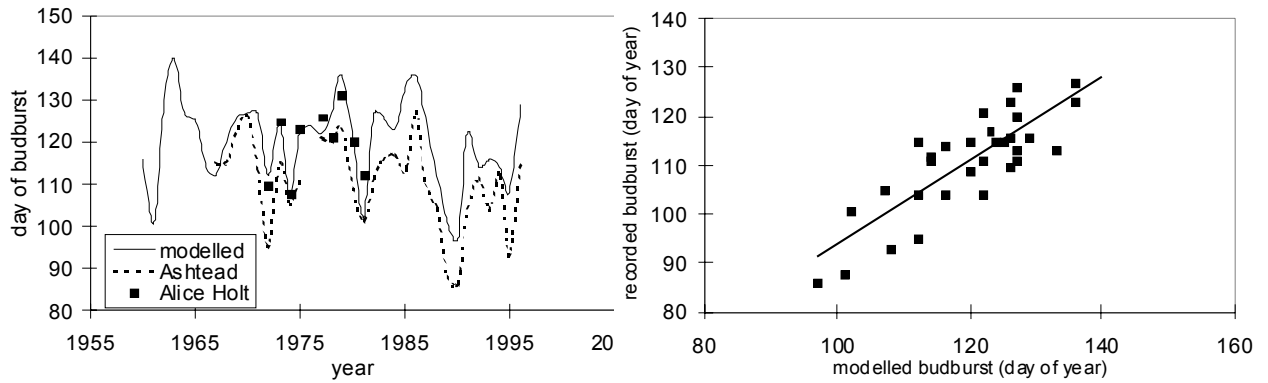


Figure 1. a) Variation in modelled and observed date of budburst at Alice Holt (1972-1981) and Ashtead (1960-1996). b) linear regression of observed on modelled date of budburst for Ashtead Surrey. ($Y=0.85x + 9.2$; $r^2=0.68$). Data for Ashtead courtesy of T. Sparks, Institute of Terrestrial Ecology, Huntingdon, UK).

The relationship between measured and modelled water flux is not as good as that for CO_2 . An offset of approximately $1 \text{ mmol m}^{-2} \text{ s}^{-1}$ on the modelled axis is apparent and may indicate the inability of the eddy correlation system to evaluate water fluxes at low saturation deficits, particularly from a wet canopy. Interception may therefore be underestimated from the measured flux data. However, in general terms, the magnitude of the transpiration fluxes agrees well with modelled estimates.

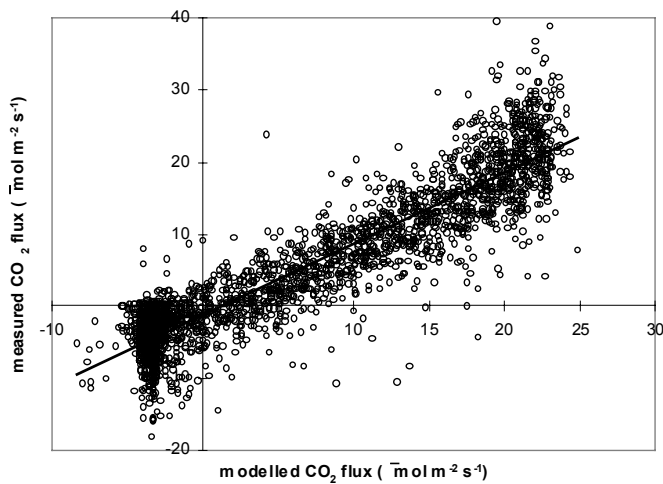


Figure 2. Comparison of measured and modelled CO_2 fluxes at Alice Holt during June and July 1998 ($y=0.989x-1.25$; $r^2=0.85$).

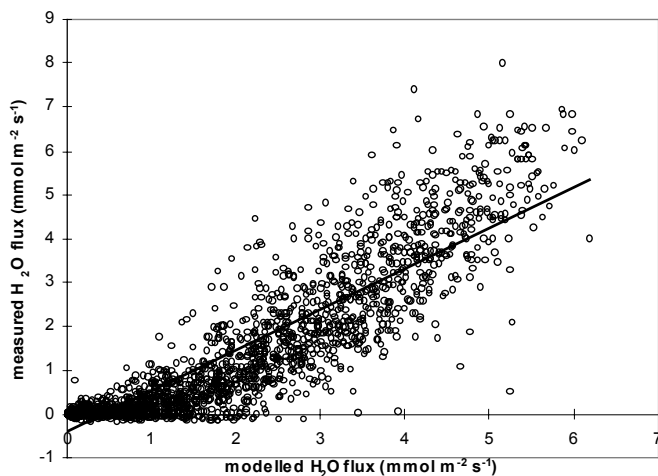


Figure 3. Comparison of measured and modelled water vapour fluxes for June and July 1998 at Alice Holt. $y=0.927x-0.38$; $r^2=0.81$.

Further validation of water and CO₂ fluxes has been carried out for Norway spruce in Sweden and beech in Italy (ECOCRAFT, 1999), whilst long-term model simulations have been carried out through coupling to the growth component of the model, including long term growth of the oak stand at Alice Holt, Sitka spruce in southern Scotland (Broadmeadow, 2000) and beech in Italy.

12 References

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