

DETAILED DESCRIPTION OF CENW 3.1

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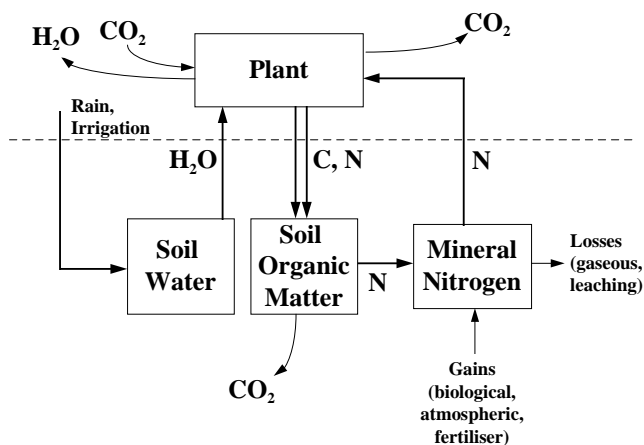
INTRODUCTION

The following gives a detailed description of the equations used in CenW. The basic equations have been published in Kirschbaum (1999, 2000b), then described as version 1.0.5. A number of more recent additions to the model have been described by Kirschbaum and Paul (2002). These latter modifications have been incorporated into CenW version 1.0.7. Further modifications have been described by Kirschbaum et al. (2003), Kirschbaum (2004, 2005) and Kirschbaum et al. (2007a, 2007b). The latest version of the model is designated as version 3.1.

MODELLING OVERVIEW

The model takes its name from the letters **C**arbon, **E**nergy, **N**utrients and **W**ater. Figure 1 gives the basic outline of the model. The model combines and links the important fluxes of carbon and nutrients, on the one hand, and CO₂ and water, on the other.

Figure 1: The basic structure of CenW, showing the key pools and fluxes of carbon, nitrogen and water between the system and the external environment.



Plants grow by fixing CO₂ from the atmosphere. However, the need to open a diffusion path for CO₂ uptake inevitably leads to water loss in the diffusive exchange of CO₂ and water through stomatal pores. Water can be replenished from the soil provided adequate soil water is available. Otherwise, further water loss must be prevented by stomatal closure, which also prevents CO₂ fixation. Water use is calculated with the Penman-Monteith equation, with canopy resistance given by stomatal conductance, which, in turn, is linked to calculated carbon gain. Water loss by transpiration and soil evaporation and water gain by rainfall or

irrigation then determine the soil water status for the following day.

The model runs on a daily time step. Photosynthetic carbon gain is calculated based on light absorption, temperature, soil water status, foliar nitrogen concentration and any foliage damage due to frost or scorching temperatures during preceding days. Some carbon is lost in respiration and the remainder utilised for growth, with allocation to different plant organs determined by plant nutrient status, tree height and species-specific allocation factors.

Nitrogen can be taken up from the mineral nitrogen pool. Nitrogen can be supplied by external sources or from the decomposition of organic matter. The nutrient cycle is closed through litter production by the death of trees, or by shedding of plant parts, such as roots, bark, branches and, most importantly, foliage. This transfers carbon and nitrogen to the soil to form organic matter. Organic matter is eventually decomposed, thereby releasing CO₂ to the atmosphere. Any nitrogen in excess of microbial requirements can enter the pool of mineral nitrogen from where it can be taken up by plants. Decomposition rate is determined by temperature, soil water status and soil organic matter quality in a modified formulation based on the CENTURY model.

DETAILED MODEL DESCRIPTION

1. Carbon Gain

Net photosynthesis is calculated based on the equations given by Sands (1995). Sands used a widely-used simple leaf-level photosynthesis model by which assimilation rate, A^1 , can be calculated as:

$$\theta A^2 - (\alpha I_a + A_{\max}) A + \alpha I_a A_{\max} = 0 \quad (1.1)$$

where θ is a curvature term, α the quantum yield of photosynthetic carbon gain, I_a absorbed photosynthetically active radiation and A_{\max} the maximum photosynthetic rate without radiation limitation. Sands (1995) assumed that the canopy is horizontally homogeneous, but vertically heterogeneous, that radiation is absorbed exponentially within the canopy in accordance with Beer's law, that A_{\max} within the canopy decreases in proportion to absorbed radiation, that α and θ are constant throughout the canopy, that radiation varies sinusoidally and that all photosynthetic parameters are constant throughout the day.

Using these constraining assumptions, Sands was able to develop a set of equations with which it is possible to calculate the daily photosynthesis based on incident radiation and single-leaf photosynthetic parameters (Sands, 1995). Radiation is normalised as:

$$q = \pi k_1 \alpha Q_a k_2 / [2 h (1 - m) A_{\max}] \quad (1.2)$$

where q is normalised radiation, k_1 is the light extinction coefficient, α the quantum yield (mol mol⁻¹), Q_a absorbed radiation (MJ m⁻² d⁻¹), k_2 a conversion term that converts from total solar radiation to photosynthetically active photon flux density, h day length in seconds and m is leaf transmissivity. The conversion term, k_2 was taken as 2.0 μmol quanta J⁻¹ after Sands (1995). The light extinction coefficient can optionally be modified through consideration of foliage clumping in young stands as calculated below.

Daily photosynthetic carbon gain, A_d , can then be calculated as:

¹ A full set of all abbreviations is given in the Appendix.

$$A_d = A_{\max} h g(q, \theta) [1 - \exp(-k_1 L)] / k_1 \quad (1.3)$$

where L is leaf area index. The complex function $g(q, \theta)$ is given by Sands (1995).

Total absorbed radiation, Q_a , is calculated as:

$$Q_a = Q_i (1 - r) \{1 - \exp[-k_1 L (1 - m)]\} \quad (1.4)$$

where Q_i is incident radiation and r is the fraction of radiation that is reflected (albedo).

Leaf area index, L , is calculated as:

$$L = S_l W_f \quad (1.5)$$

where S_l is specific leaf area and W_f foliage weight per unit area.

For C_3 plants, the terms α and A_{\max} are affected by temperature and CO_2 concentration. Simulations for C_4 photosynthesis are given below. For C_3 photosynthesis, the temperature dependence of α can be incorporated as (Kirschbaum and Farquhar, 1987):

$$\alpha = f_d \alpha_{vj} (c_i - \Gamma^*) / (c_i + 2 \Gamma^*) \quad (1.6)$$

where f_d describes damage to the canopy during experience of frost or scorching temperature on the same or during preceding days (see eqns 1.15 to 1.19), α_{vj} is the quantum yield of RuBP regeneration, with a theoretical maximum of around 0.09, depending to some extent on light quality (Kirschbaum and Farquhar, 1987), c_i is the intercellular CO_2 concentration and Γ^* the CO_2 compensation point in the absence of non-photorespiratory respiration.

Following Bernacchi et al. (2001), Γ^* is calculated from version CenW 3.1 onwards as:

$$\Gamma^* = 4.275 \exp[15.261 (T_{\text{day}} - 25) / (T_{\text{day}} + 273.15)] \quad (1.7)$$

where T_{day} is average daytime temperature.

In earlier versions (up to CenW 3.0), Γ^* was calculated, following McMurtrie et al. (1992) as:

$$\Gamma^* = 4.2 \exp[9.46 (T_{\text{day}} - 25) / (T_{\text{day}} + 273.2)] \quad (1.8)$$

With these newer parameters, the CO_2 dependence of photosynthesis is significantly more temperature dependence than it had been with the earlier parameters (see Kirschbaum, 2004).

The temperature dependence of the quantum yield is only due to the changing ratio of carboxylations to oxygenations, whereas in the case of A_{\max} , temperature affects the changing ratio of carboxylations to oxygenation as well as the maximum rate at which reactions can be carried out. The temperature dependence of A_{\max} is therefore calculated, following Kirschbaum (1994), in two stages as:

$$A_{\max} = A_{vj} (c_i - \Gamma^*) / (c_i + 2 \Gamma^*) \quad (1.9)$$

where A_{vj} is the potential RuBP regeneration rate at a given temperature. This assumes that assimilation rate is limited by RuBP regeneration rather than Rubisco activity, which seems reasonable for most conditions (see Kirschbaum, 1994, for further discussion of this point).

The temperature dependence of A_{vj} is calculated with a simple hump function as:

$$A_{vj} = 0 \quad \text{if } T_{\text{mean}} \leq T_n \quad (1.10a)$$

$$A_{vj} = A_{\text{opt}} (T_{\text{mean}} - T_n) / (T_{\text{opt1}} - T_n) \quad \text{if } T_n < T_{\text{mean}} < T_{\text{opt1}} \quad (1.10b)$$

$$A_{vj} = A_{\text{opt}} \quad \text{if } T_{\text{opt1}} \leq T_{\text{mean}} \leq T_{\text{opt2}} \quad (1.10c)$$

$$A_{vj} = A_{\text{opt}} (T_x - T_{\text{mean}}) / (T_x - T_{\text{opt2}}) \quad \text{if } T_{\text{opt2}} < T_{\text{mean}} < T_x \quad (1.10d)$$

$$A_{vj} = 0 \quad \text{if } T_{\text{mean}} \geq T_x \quad (1.10e)$$

where T_n and T_x are the minimum and maximum temperatures that allow any photosynthesis, T_{opt1} and T_{opt2} are lower and upper temperature bounds that allow optimum photosynthetic rates and T_{mean} is mean daily temperature.

It is linked here to the daily mean (rather than mean daytime) temperature because it is considered that photosynthesis is affected not only by the temperature during the day but also by feed-back processes of the plant as a whole, especially at low temperature. Hence, the assumption is that whole-plant performance is affected by daily mean temperature, and that this then exerts a controlling feed-back effect on photosynthesis.

A_{opt} is calculated as a multiplicative function of foliar nitrogen concentration and a range of limitation terms as:

$$A_{opt} = (1 - k_{p,3}) f_d f_{age} f_{size} A_x N_{lim} W_{lim} \quad (1.11)$$

where $k_{p,3}$ is a term that described the reduction of photosynthetic capacity by insect pests, f_d is a temperature damage term, f_{age} an age-limitation term, f_{size} a similar limitation term linked to stand size rather than age, A_x is the highest photosynthetic rate for that species under optimum temperature and non-limiting CO_2 and foliar nitrogen concentrations and without any other limitations, W_{lim} is a water-stress limitation parameter and N_{lim} is a nitrogen limitation parameter. All these terms are described in further detail below.

N_{lim} is defined as:

$$N_{lim} = 0 \quad \text{if } n_f \leq n_{min} \quad (1.12a)$$

$$N_{lim} = (n_f - n_{min}) / (n_{opt} - n_{min}) \quad \text{if } n_{min} < n_f < n_{opt} \quad (1.12b)$$

$$N_{lim} = 1 \quad \text{if } n_f \geq n_{opt} \quad (1.12c)$$

where n_f is foliar nitrogen concentration at the top layer of the canopy, n_{min} is the minimum nitrogen concentration that allows any photosynthesis and n_{opt} is the foliar nitrogen concentration at which photosynthesis reaches its optimum.

Nitrogen concentration at the top of the canopy is calculated as:

$$n_f = (N_f / C_f) / n_{grad} \quad (1.13)$$

where N_f and C_f are the amounts of nitrogen and carbon in the foliage pool and n_{grad} is an empirical plant-specific term that describes the nitrogen gradient within the canopy.

Stomatal conductance

To calculate the intercellular CO_2 concentration, c_i , the Ball/Berry relationship is used (Ball et al., 1987) according to which stomatal conductance can be calculated as:

$$g_s = k_3 A r_h / c_a \quad (1.14)$$

Given that $A = g_s (c_a - c_i) / 1.6$, eqn. 1.14 can be rearranged to give:

$$c_i = c_a [1 - 1.6 / (k_3 r_h)] \quad (1.15)$$

where g_s is stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$), A is assimilation rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$), r_h is relative humidity (dimensionless), c_a is atmospheric CO_2 concentration (Pa) and k_3 a species-specific constant. As water stressed plants typically operate at lower intercellular CO_2 concentration (Korol et al., 1999), not a single value for k_3 is used, but it is variable depending on plant water status so that:

$$k_3 = k_{3,d} + W_{lim} (k_{3,w} - k_{3,d}) \quad (1.16)$$

where $k_{3,d}$ are stomatal factors for (notionally) completely dry stands, $k_{3,w}$ for stands not limited by water availability and W_{lim} a water limitation factor calculated below (eqn. 2.18).

Temperature damage

It is assumed that plants can be damaged by either cold (frost) if minimum temperatures fall below a threshold value or by heat (scorch) if maximum temperatures increase above a threshold, and that this damage can be repaired over some period of time. It is also assumed to equally affect both maximum photosynthetic capacity and quantum yield. More complex interactions with pre-conditioning or irradiance have not been included.

The frost and scorch damage multiplier, f_d , is, thus, calculated as:

$$f_d = 1 \quad \text{if } (D_f + D_s) = 0 \quad (1.17a)$$

$$f_d = 1 - (D_f S_c + D_s S_h) \quad \text{if } (D_f S_c + D_s S_h) < 1 \quad (1.17b)$$

$$f_d = 0 \quad \text{if } (D_f S_c + D_s S_h) \geq 1 \quad (1.17c)$$

where D_f and D_s are cumulative units of temperature damage by frost and scorching heat, respectively, and S_c and S_h are empirically determined temperature sensitivity terms for cold (frost) and heat (scorch) damage. They determine the extent to which photosynthesis is inhibited for each degree by which temperatures exceed threshold temperatures for frost or scorch damage. The change in cumulative temperature damage units is then calculated as:

$$dD_f/dt = (F_0 - T_{\min}) - R_f \quad \text{if } T_{\min} < F_0 \quad (1.18a)$$

$$dD_f/dt = -R_f \quad \text{if } T_{\min} \geq F_0 \quad (1.18b)$$

$$dD_s/dt = (T_{\max} - S_0) - R_s \quad \text{if } T_{\max} > S_0 \quad (1.19a)$$

$$dD_s/dt = -R_s \quad \text{if } T_{\max} \geq S_0 \quad (1.19b)$$

where F_0 and S_0 are threshold temperatures for frost and scorch damage, T_{\min} and T_{\max} are overnight minimum and daytime maximum temperatures, and R_f and R_s are empirically determined rates of repair, which give the number of damage units that can be repaired per day.

It is also assumed that there is a maximum extent of damage that can occur so that:

$$0 \leq D_f \leq D_{f, \max} \quad (1.20)$$

$$0 \leq D_s \leq D_{s, \max} \quad (1.21)$$

where $D_{f, \max}$ and $D_{s, \max}$ are the maximum extent of repairable damage due to frost or scorch damage, respectively. The maximum extent of damage is calculated by reference to the maximum length of time it can take for a maximally damaged plant to be fully repaired (if no further damage occurs) so that

$$D_{f, \max} = R_f R_{f, \max} \quad (1.22)$$

$$D_{s, \max} = R_s R_{s, \max} \quad (1.23)$$

where $R_{f, \max}$ and $R_{s, \max}$ are the maximum number of days needed for complete repair from frost and scorch damage, respectively. For example, plants subject to severe winters might be assumed to be maximally damaged at the end of the winter. If they were not subject to any further frost damage, the maximum length to repair would give the time to when they are fully functional again.

Emission of volatile organic compounds

A small fraction of carbon fixed in photosynthesis can be lost from the ecosystem in the emission of volatile organic compounds, especially isoprene. This carbon loss, V_e , is calculated here simply as:

$$V_e = v A_d \quad (1.24)$$

where v is a simple proportionality term that links photosynthesis and the emission rate of volatile organic compounds. Available photosynthate is then calculated by subtracting V_e from A_d .

Insect damage

Sap sucking insects cause a diversion of photosynthate from trees to insects. For specified dates, this extra respiratory loss, R_p , (via insect respiration) is simply calculated as:

$$R_p = k_{p,1} \quad (1.25)$$

where $k_{p,1}$ is a user defined constant for specified dates. This extra respiratory carbon loss is added to other carbon losses and the amount of available carbohydrate for subsequent growth is reduced by the amount diverted to insect respiration.

Carbohydrate loss is accompanied by a loss of soluble nitrogen, N_{pest} , calculated as:

$$N_{pest} = k_{p,1} N_s / C_s \quad (1.26)$$

where N_s and C_s are the amounts of carbon and nitrogen in the plant-internal soluble pools, respectively. It is assumed, however, that nitrogen extracted from the plant pool is not lost from the system but added to surface litter (which means that time delays due to the death of insects are ignored).

Insect pests can also cause additional leaf senescence, S_p , also defined simply as:

$$S_p = k_{p,2} \quad (1.27)$$

where $k_{p,2}$ is a user defined constant applied over specified dates that gives the additional amount of foliage shed on each day as a result of the insect damage. This foliage loss reduces leaf area and adds senesced foliage to the surface litter pool. It is assumed that no nitrogen retranslocation takes place before leaves are shed due to insect damage so that carbon and nitrogen losses in this form of senescence correspond to the ratio of carbon and nitrogen in live foliage.

Pests can also reduce photosynthetic carbon gain, which is implemented here through an effect on maximum photosynthetic capacity. Hence, maximum photosynthesis can be reduced by insect damage by the term $(1 - k_{p,3})$ where $k_{p,3}$ is the reduction in photosynthetic capacity by insect damage. The term has the value of 0 if there is no damage. This term is then used in equation 1.11.

C₄ photosynthesis

C_4 photosynthesis was modelled in a simplified routine based on the work of Collatz et al. (1992) and G. Simioni (unpublished). Assimilation rate with non-limiting light, A_{max} , is calculated using a quadratic equation as:

$$\beta_c A^2 - A_{max} (V_t + k_p c_i) + V_t k_p c_i = 0 \quad (1.28)$$

where V_t is the maximum Rubisco limited rate, k_p is the Phosphoenolpyruvate (PEP)-carboxylase activity (or the initial slope of the relationship of A as a function of intercellular CO_2), c_i is the intercellular CO_2 concentration and β_c is a curvature term in the transition from CO_2 limited to maximum-capacity limited rate.

Both V_t and k_p are calculated as functions of temperature so that

$$V_t = V_{t(25)} \frac{Q_v^{(T_{day}-25)/10}}{(1 + e^{0.3(13-T_{day})})(1 + e^{0.3(T_{day}-36)})} \quad (1.29)$$

$$k_p = k_{p(25)} Q_k^{(T_{day}-25)/10} \quad (1.30)$$

where $V_{t(25)}$ and $k_{p(25)}$ are the Rubisco-limited rate and PEP-carboxylase activity at 25°C, Q_v and Q_k are Q_{10} functions, both set to 2 and T_{day} is average daytime temperature.

The terms $V_{t(25)}$ and $k_{p(25)}$ are linked in the present model to retain a constant proportionality irrespective of changes in nitrogen or water status or any damage by insects or extreme temperatures that are assumed to inhibit both processes equally.

Hence,

$$k_{p(25)} = r_{kV} V_{t(25)} \quad (1.31)$$

where r_{kV} is the proportionality ratio of PEP-carboxylase activity and the Rubisco limited rate.

The maximum rate, defined according to eqn. 1.28, together with the quantum yield, typically set to 0.06 for C_4 plants (Ehleringer and Pearcy 1984), and a curvature term, θ , then feed into the sward simulation model given in eqn. 1.3. Both quantum yield and curvature terms can be adjusted for different species.

Foliage Clumping

Young stands typically have a non-uniform distribution of foliage across a site because their branches are simply not long enough to evenly distribute their foliage for optimal light interception across a site. This was calculated based on work in ??? and implemented by G. Simioni (unpublished).

The light extinction coefficient, k_1 , is then calculated as:

$$k_1 = k_{1,max} [(1 - k_{1,r}) C_c + k_{1,r}] \quad (1.32)$$

where $k_{1,max}$ is the maximum extinction coefficient with uniform foliage distribution (and the extinction coefficient determined on by an average leaf-angle distribution), $k_{1,r}$ is the relative range of variation in the extinction coefficient (in the range of 0..1) and C_c is the percentage of canopy cover. This is calculated as:

$$C_c = [\pi (C_w / 2)^2] s / 10000 \quad (1.33)$$

where C_w is an average canopy width and s is stand stocking in stems per hectare.

Percentage canopy cover is restricted to a maximum value of 1.

Average canopy width, C_w , is empirically determined, following Leech (1984) as:

$$C_w = 0.7544 + 0.2073 d \quad (1.34)$$

where d is diameter at breast height.

These parameters have been developed for *Pinus radiata* and at this stage cannot be modified by users. Only the maximum extinction coefficient and its range can be modified. This routine thus provides an initial partial adjustment for the incomplete light interception of young stands. It should be more appropriate than the assumption of constant light interception capacity irrespective of the clumping effect in young stands that inevitably leads to less efficient light interception.

2. Soil Water Balance

The soil water balance routine used in CenW 3.1 uses a more detailed treatment of the litter layer than had been used in the earlier versions of CenW. In this new formulation, the 'soil' is divided into a litter layer and a user-specified number of soil layers of variable depth and specific water holding capacity. Effective additional rain water is added to the litter layer. If the water content of the litter layer with the added water input exceeds its water holding capacity, excess water is transferred to the upper-most soil layer.

For each soil layer it is then checked whether its water contents exceeds its water-holding capacity and, if it does, any excess water is transferred to the layer below. The same check is conducted for the next soil layer, and if its water content exceeds its water holding capacity, water is transferred further down. This procedure is repeated through to the lowest soil layer. Any excess water in the bottom layer is lost as deep drainage. Horizontal or any upward movement of water are not modelled.

Formally, the input of water into the litter layer and n soil layers is calculated as:

$$dW_L/dt = R_{\text{eff}} + W_i - W_{d,L} \quad (2.1a)$$

$$dW_1/dt = W_{d,L} - W_{d,1} \quad (2.1b)$$

$$dW_j/dt = W_{d,j-1} - W_{d,j} \quad (2.1c)$$

$$dW_n/dt = W_{d,n-1} - W_d \quad (2.1d)$$

where j refers to all soil layers other than the top and bottom layers, R_{eff} is effectively received rainfall, W_i is irrigation water, $W_{d,L}$ is drainage out of the litter layer, $W_{d,j}$ is drainage out of layer j, and W_d is deep drainage out of the root zone. Drainage at any layer is calculated as the excess of water in that layer over the maximum that can be held by the soil. Effective rainfall is calculated as total rainfall minus that which is intercepted by the canopy or the litter layer so that:

$$R_{\text{eff}} = R - I_c \quad (2.2)$$

where R is total daily rainfall and I_c is the amount of rain intercepted by the canopy.

Myers and Talsma (1992) observed that at most half of rainfall received in light rainfall events could be intercepted by the canopy. Canopy interception is thus calculated as:

$$I_c = f_c L \quad (2.3)$$

The litter layer is explicitly included as both a contributor to evaporation, and in preventing evaporation from the underlying soil. It is assumed that roots could not access water from the litter layer so that water from the litter layer can only be lost as a result of evaporation.

where f_c is an empirical term and L is leaf area index.

Evapotranspiration

Transpiration rate, T_p , is calculated with the Penman-Monteith equation (Monteith, 1965, Martin et al., 1989) as:

$$T_p = h \frac{\sigma Q_a + \Delta p_a C_p / r_a}{\sigma + \gamma(r_a + r_c) / r_a} / L_h \quad (2.4)$$

where σ (Pa K^{-1}) is the derivative of the saturation vapour pressure with respect to temperature, Q_a ($\text{J m}^{-2} \text{d}^{-1}$) is daily radiation absorbed by the canopy, p_a (kg m^{-3}) the density of air, C_p ($\text{J kg}^{-1} \text{K}^{-1}$) the specific heat of air, Δ (Pa) the vapour pressure saturation deficit of the air, r_a (s m^{-1}) is aerodynamic resistance, r_c (s m^{-1}) the canopy resistance, γ (Pa K^{-1}) the psychrometric constant, h is day length in seconds and L_h (J kg^{-1}) the latent heat of vaporisation. This assumes that transpiration is confined to daylight hours.

There is an inherent difficulty in calculating daily transpiration rate when all driving variables, radiation, temperature and humidity deficit, as well as the plant-dependent modifier, r_c , are varying throughout the day. Calculating daily transpiration rate from average daily values for these variables must therefore be treated with caution.

However, at this stage, there appears to be no alternative approach to the use of these existing formulations.

The vapour pressure deficit, Δ , is calculated as:

$$\Delta = e(T_{\text{day}}) - e(T_{\text{min}}) \quad (2.5)$$

where $e(T)$ is the saturation vapour pressure at temperature T , T_{day} is average daytime temperature and T_{min} the overnight minimum temperature. Average daytime temperature is calculated by eqn. 7.1 below. Saturated vapour pressure (in Pa) is calculated as:

$$e(T) = 610.78e^{\left[\frac{17.269T}{T+237.3}\right]} \quad (2.6)$$

Aerodynamic resistance is an empirical user-input term that can be adjusted to suit different forest types. Canopy conductance is taken to equal stomatal conductance of the total canopy and is calculated from the Ball/Berry relationship (eqn. 1.11) after daily canopy photosynthesis has been calculated. This ensures that a clear and explicit linkage between carbon gain and water use is maintained in the model.

The psychrometric constant, γ , scales linearly with atmospheric pressure. The other terms in eqn. 2.4 are treated as constants and small temperature dependencies (see Martin et al., 1989) are ignored.

$$\gamma = 65 \quad (\text{Pa K}^{-1}) \quad \{\text{at atmospheric pressure} = 10^5 \text{ Pa}\} \quad (2.7)$$

$$L_h = 2.5 \cdot 10^6 \quad (\text{J kg}^{-1}) \quad (2.8)$$

$$p_a = 1.204 \quad (\text{kg m}^{-3}) \quad (2.9)$$

$$C_p = 1010 \quad (\text{J kg}^{-1} \text{ K}^{-1}) \quad (2.10)$$

Evaporation from the litter, E_{lit} , and soil, E_{soil} , are calculated with the Penman-Monteith equation as:

$$E_{\text{lit}} = h f_{\text{lit}} \frac{\sigma R_u + \Delta p_a C_p / r_u}{\sigma + \gamma(r_u + r_{\text{lit}}) / r_u} / L_h \quad (2.11)$$

$$E_{\text{soil}} = h(1 - f_{\text{lit}}) \frac{\sigma R_u + \Delta p_a C_p / r_u}{\sigma + \gamma(r_u + r_{\text{soil}}) / r_u} / L_h \quad (2.12)$$

where f_{lit} is the fraction of ground covered by litter, R_u ($\text{J m}^{-2} \text{ d}^{-1}$) is net radiation that passes through the canopy and reaches the ground, r_u (s m^{-1}) is aerodynamic resistance underneath the canopy and r_{lit} and r_{soil} (s m^{-1}) the diffusion resistances out of the litter and upper soil layers, respectively. Aerodynamic resistance in these calculations, r_u , was taken to be five times as large as the user-input aerodynamic resistance, r_a , for transpiration from the canopy (Massman, 1992; Kelliher et al., 1993).

The fraction of the surface of mineral soil covered by litter, f_{lit} , is calculated as:

$$f_{\text{lit}} = 1 - \exp(-f_{\text{mulch}} L_s) \quad (2.13)$$

where L_s is the amount of non-woody surface litter including partly decomposed material, and f_{mulch} an empirical parameter that describes the surface coverage by different litter types.

Diffusion resistances from the litter, r_{lit} , and soil layers, r_{soil} , were calculated, loosely following Camillo and Gurney (1986), as:

$$r_{\text{lit}} = 800 W_{\text{lit, max}} / W_{\text{lit}} \quad (2.14a)$$

$$r_{\text{soil}} = 800 W_{\text{soil(1), max}} / W_{\text{soil(1)}} \quad (2.14b)$$

where W_{lit} and $W_{\text{soil(1)}}$ are the amounts of water held in the litter and upper-most soil layers, respectively, and $W_{\text{lit, max}}$ and $W_{\text{soil(1), max}}$ are their maximum water-holding capacities, respectively.

In the case of the upper soil layer, those values were user-specified, whereas for the litter layer, maximum water-holding capacity was calculated as:

$$W_{lit. \max} = L_s f_{hold} \quad (2.15)$$

where f_{hold} is a user-input parameter that gives the water holding capacity per unit of litter dry weight.

Water Limitation

To calculate the extent to which plant function is impaired by water shortage, W_{lim} , two options are provided. In the first option, the total amount of water available in the whole profile is taken as the basis of calculating water limitation so that:

$$W_{lim} = (W / W_{hold}) / W_{crit} \quad \text{if } (W / W_{hold}) < W_{crit} \quad (2.16a)$$

$$W_{lim} = 1 \quad \text{if } (W / W_{hold}) \geq W_{crit} \quad (2.16b)$$

where W is the total amount of water held in the entire profile, W_{hold} is the water holding capacity of the entire profile and W_{crit} is an empirical term that determines the relative water content when water stress begins to impair plant function. This implies that even if some parts of the soil dry out completely, plants do not experience that as a stress provided other layers in the soil still contain adequate amounts of water.

This leads to different soil layers drying out at different rates, with the top layer generally drying out fastest because of the combined effect of higher root activity and additional water loss by soil evaporation. On the other hand, when rainfall is received, it starts to re-wet the profile from the top layer, and lower layers receive water only when the water content of upper layers exceeds their water-holding capacity. This differential drying has some minor implications for water loss from soil evaporation and the extent to which decomposition rates are inhibited by soil drying.

For most work, it was found that this formulation, indeed, appeared to give the best calculated stress values as judged, for example, by observed gas exchange rates measured with continuous eddy-covariance measurements (Kirschbaum et al. 2007b). However, there are root environments where that is not likely to be applicable. These are particularly environments, such as in south-western Australia, that may have very deep soils with excess to water but where only a small amount of roots grow to those depths to access water. In these circumstances, it seems reasonable to model plant access to extend to a large pool but that stress is primarily determined by the availability of water in the upper soil layers with a greater concentration of roots.

Simioni et al. (2007) therefore assumed water-stress experience to differ between layers. Each soil layer can then be given a parameter that determines the layer's relative contribution to plant water stress. The water limitation is then calculated for each layer as:

$$W_{lim,j} = (W_j / W_{hold,j}) / W_{crit} \quad \text{if } (W_j / W_{hold,j}) < W_{crit} \quad (2.17a)$$

$$W_{lim,j} = 1 \quad \text{if } (W_j / W_{hold,j}) \geq W_{crit} \quad (2.17b)$$

where each term has the same meaning as in eq. 2.16, but is restricted to each specified soil layer and 'j' is a counter for each individual layer. These values for individual layers are then combined for an overall limitation calculation as:

$$W_{lim} = \sum w_j W_{lim,j} \quad (2.18)$$

where w_j is the relative contribution of each soil layer towards determining the overall water-stress sensitivity. The sum of all relative contribution terms for all soil layers must be 1 by definition.

3. Age Effects

Net primary productivity can be reduced through a number of processes, such as increasing respiration, increasing senescence and mortality losses, immobilisation of nutrients and unfavourable shifts in biomass allocation. However, there is evidence that these processes are sometimes not sufficient to account for the full magnitude of observed reductions in age-related decline in productivity.

An additional empirical term, f_{age} , is therefore provided to account for additional age related decrease in productivity that is not yet accounted for through the other processes listed above. It is calculated, following Landsberg and Waring (1997), as:

$$f_{age} = \frac{1}{1 + (A_{act} / A_{mat})^{x_{age}}} \quad (3.1)$$

where A_{act} is the age of the stand, A_{mat} is the species-specific typical age of maturity (where productivity is halved) and x_{age} is a power term that described the steepness of the age effect (Kirschbaum 2005). Alternatively, the age effect can be described as:

$$f_{size} = \frac{1}{1 + (D_{act} / D_{mat})^{x_{size}}} \quad (3.2)$$

where D_{act} is the total dry weight of the stand, D_{mat} is the species-specific typical size of maturity (where productivity is halved) and x_{size} is a power term that described the steepness of the age effect (Kirschbaum 2005).

The program can be run with the age effect omitted, expressed as a function of age (according to eq. 3.1), as a function of size (according to eq. 3.2), or as a function of both size and age together.

4. Carbon Loss

Carbon can be lost through plant respiration, through senescence of plant organs or through death of individual trees. There may also the selective removal of trees (harvesting/ thinning) or branches (pruning).

Plant Respiration

Respiration is calculated as growth respiration, R_g , plus maintenance respiration, R_m . Growth respiration is calculated as:

$$R_g = f_{growth} \sum G_i \quad (4.1)$$

where f_{growth} is an empirical term that quantifies the amount of carbon lost in growth respiration per unit of new growth, and $\sum G_i$ is the sum of new carbon growth of all plant organs. Maintenance respiration, R_m , is calculated as:

$$R_m = f_{maint} f_{T, resp} R_b \sum N_i \quad (4.2)$$

where f_{maint} is an empirical term that gives the daily respiration rate per unit of nitrogen at 25°C, R_b is a base rate of respiration and $\sum N_i$ is the sum of nitrogen contained in all plant pools except foliage. Foliage respiration is calculated only for the night time period, and respiration during the day is included as part of net photosynthetic carbon gain calculations. The temperature response of respiration is based on the recognition that there is a strong short-term response of respiration rate to temperature, but that acclimation tends to occur which causes longer-term respiration rates to be almost invariant with temperature (Gifford 1995, Körner, 1996; Atkin et al. 2000). Hence, modification of the base rate of

respiration, together with a short-term temperature-response function gives adequate description of both short- and long-term respiration responses to temperature.

The base rate is thus adjusted as:

$$dR_b / dt = [(1 / f_{T, resp}) - R_b] / \tau_r \quad (4.3)$$

where τ_r is the time constant for the respiratory acclimation response.

The short-term temperature response is calculated as:

$$f_{T, resp} = \exp[a + b T_{mean} (2 T_{m, r} - T_{mean})] \quad (A20)$$

where T_{mean} is daily mean temperature in °C, and $T_{m, r}$ is the temperature of maximum respiration rate and b is a user-input parameter. $T_{m, r}$ and b together determine the temperature dependence of respiration rate. The term a determines the absolute rate of the function which is set to a value so that the function is normalised to '1' at 25 °C.

Mortality

Tree death is modelled as a simple daily fractional mortality rate. Loss of tree biomass is calculated as:

$$D_b = D_n f_m \quad (4.5)$$

where D_b is the daily fraction of stem biomass lost due to mortality per day, D_n is the daily fraction of stems lost and f_m is the ratio of the biomass of dieing relative to average sized trees in the stand. Loss of above-ground biomass is assumed to lead to the same relative loss of root biomass. The daily death rate can be either input as a constant, or it can be calculated based on the self-thinning rule (Pretzsch 2002), which states that for any stand density, there is a critical average tree biomass. If tree biomass increases beyond that critical mean biomass, mortality of individual trees occurs until stand density is sufficiently reduced for the relationship to be satisfied again. For these simulations, a critical individual-tree stem biomass, B_{crit} , is calculated as:

$$B_{crit} = k_{thin} s^{-3/2} \quad (4.6)$$

where s is stocking in stems per hectare and k_{thin} is a constant. When the size of average trees exceeds B_{crit} , stem mortality ensues which reduces stand density to that allowed by the critical stem biomass for average trees. For these calculations, only stem wood biomass is included as the basis of calculating a critical biomass.

Senescence

Senescence of plant organs other than foliage and fine roots is calculated as a simple daily fractional loss, with different empirical loss fractions for different organs. For foliage and fine root senescence, a more complex approach is used. It is assumed that foliage and fine root senescence may be accelerated by drought. For foliage, it further includes the consideration that over a wide range of productivities, leaf area indices are often observed to be relatively conservative (see below). This is simulated by assuming that foliage at the bottom layer of the canopy senesces when it receives less than a specified minimum amount of radiation.

Hence, daily foliage senescence rate, S_f , is calculated as:

$$S_f = S_b + S_{low} + S_{dry} + S_p \quad (4.7)$$

where S_b is a constant minimum foliage senescence rate, S_{low} is senescence due to low radiation experienced at the bottom of the canopy, S_{dry} is drought induced senescence and

S_p is pest-induced senescence (as described above). Root senescence is modelled in a similar way but without including the low-radiation senescence term. Daily low-radiation senescence is calculated as:

$$S_{\text{low}} = S_{l, \text{max}} \quad \text{if } Q_c < Q_{\text{crit}} \quad (4.8a)$$

$$S_{\text{low}} = 0 \quad \text{if } Q_c \geq Q_{\text{crit}} \quad (4.8b)$$

where Q_c is the daily amount of radiation transmitted through to the bottom of the canopy and Q_{crit} is a critical radiation level for low-radiation senescence. This essentially defines the maximum density of the canopy that can be supported before foliage at the bottom of the canopy senesces. Radiation transmitted through to the bottom of the canopy, Q_c , is calculated as:

$$Q_c = Q_i e^{[-k_i L(1-m)]} \quad (4.9)$$

Drought senescence is calculated as:

$$S_{\text{dry}} = S_{d, \text{max}} (1 - W_{\text{lim}}) \quad (4.10)$$

where $S_{d, \text{max}}$ is a maximal daily drought senescence rate and W_{lim} is the water limitation term calculated above.

Senesced plant material is transferred to the litter pools defined in the original CENTURY model (Parton et al. 1987). In addition three further litter pools were introduced: senesced or pruned branches are added to the surface pool of fine woody litter, dead stems to the surface pool of coarse woody litter and dead coarse roots to the soil pool of coarse woody litter, with decomposition characteristics similar to that of structural litter.

For foliage, a fraction of nitrogen is assumed to be retranslocated prior to senescence. The flux of nitrogen from senescing foliage to the foliage litter pool, F_n , is calculated as:

$$F_n = S_f N_f r_f \quad (4.11)$$

where S_f is the daily foliage senescence rate, N_f is the amount of nitrogen in the foliage pool and r_f is a retranslocation factor that gives the ratio of nitrogen in senescing and live foliage. Retranslocated nitrogen is added to the plant pool of soluble nitrogen. For other plant tissues, litter is assumed to have the same nitrogen concentration as live tissue.

5. Allocation

Newly fixed carbon and nitrogen from the soil are initially taken up into plant soluble pools. Carbon for respiration is subtracted from the soluble carbon pool. The remaining carbon in the soluble pool can then be utilised for growth with a Michaelis-Menten type dependence on the amount of carbon in the soluble pool relative to the total of all existing pools. Hence, new growth, G , is calculated as:

$$G = W_{\text{lim}} C_s^2 / (C_s + K_c \Sigma C_i) \quad (5.1)$$

where C_s is the amount of carbon in the soluble pool, K_c is an empirical Michaelis-Menten constant and ΣC_i is the sum of all carbon pools in the plant (other than the soluble carbon pool). Equivalent calculations are done for nitrogen, but for nitrogen there is the further restriction that at most as much nitrogen can be turned into new growth as corresponds to the new foliage growth rate at maximum foliar nitrogen concentration. This limits the extent and rapidity with which plant pools can take up large amounts of nitrogen if it suddenly becomes available through fertilisation.

New growth is then allocated to the different biomass pools based on a number of different considerations. Allocation of carbon is dealt with first. A constant fraction is allocated to reproductive organs once trees have reached the age of sexual maturity. Allocation to other biomass components is based on the assumption that allocation ratios between certain biomass components, such as stem wood and bark, are constant, whereas allocation ratios between other biomass components, such as fine roots and foliage, are variable depending on plant height and nutritional status.

The allocation ratio between foliage and fine roots is based on the consideration that allocation to foliage is favoured when stands have ready access to nutrients, and root allocation is favoured when nutrients are limiting. Water limitations are not considered in these allocation shifts based on observation at the BFG experimental site that fine root allocation was affected by nutrient but not by water status. Hence, the ratio of fine root to foliage allocation, r_{rf} , is given by:

$$r_{rf} = r_{\max} - N_{\text{lim}} (r_{\max} - r_{\min}) \quad (5.2)$$

where r_{\max} is the maximal root-foliage allocation ratio when nutrition is maximally limiting, r_{\min} is the minimum allocation ratio when nutrients are non-limiting and N_{lim} is a nitrogen limitation parameter defined above.

The allocation ratio between the woody components, stems and branches, on the one hand, and foliage, on the other, is assumed to be linearly related to average tree height. Formally, it is the ratio of foliage to branch allocation, r_{fb} , that is assumed to be inversely related to tree height so that:

$$r_{fb} = 10 r_{fb(10)} / H \quad (5.3)$$

where $r_{fb(10)}$ is the notional allocation ratio between foliage and branches for a ten-meter high tree and H is tree height. This is essentially a variant of the pipe model theory of allocation to stem wood (Mäkelä, 1997; Valentine et al., 1997).

This is further modified by optionally setting a minimum carbon allocation for allocation to stem wood which is applicable for small trees where the tree-height based proportional allocation would result in too little wood allocation. So, a minimum wood allocation may be set to 10% or 20% so that wood growth ensues in even very small trees.

The allocation ratios branch : stem wood, stem wood : bark and stem wood : coarse roots are all taken as constants. These allocation ratios together completely constrain the allocation to each individual plant biomass pool for a given age, height and foliar nitrogen concentration.

The stem wood allocation only relates to the allocation to sapwood. Sapwood is assumed to turn into heartwood at a species-specific wood age. All sapwood that has been formed in one year is assumed to turn into heartwood a specified number of years later.

Height and Diameter

Initial tree height and diameter at breast height (1.3 m) must be input as initial values for trees with a diameter at breast height greater than a specified minimum diameter.

If the simulation starts with trees with a stem diameter less than the specified minimum, d_{\min} , then initial height and diameter are calculated based on stem weight, wood density, stocking and a tree-form factor. First, the volume of an average tree, V , is calculated as:

$$V = W_s / (\rho s) \quad (5.4)$$

where W_s is stem wood weight (kg ha^{-1}), ρ is wood density (kg m^{-3}) and s is stocking rate (trees ha^{-1}). Since the volume of a cone can be calculated as

$$V = \frac{1}{3} \pi r^2 H \quad \text{or} \quad V = \frac{\pi d_g^2 H}{3 \cdot 4} \quad (5.5)$$

where H is height, d_g the diameter at ground level and r the corresponding radius at ground level. This can be inverted and a stem form factor, f_t , included so that tree height can be calculated as:

$$H = \sqrt[3]{4 h_d^2 \frac{V}{\pi f_t}} \quad (5.6)$$

where h_d is the ratio of tree height and diameter at ground level and f_t is a form factor related to stem taper. If trees were perfect cones then f_t would be $1/3$, but in practice, trees tend to be wider in their middle section so that factors like 0.4 tend to give better descriptions for trees like *Pinus radiata*.

From the calculated height and the ratio of height to diameter, the diameter at ground level, d_g , is calculated as:

$$d_g = 100 H / h_d \quad (5.6)$$

and the diameter at breast height, d , as:

$$d = 0 \quad \text{if } H \leq 1.3 \text{ m (5.7a)}$$

$$d = d_g (H - 1.3) / H \quad \text{if } H > 1.3 \text{ m (5.7b)}$$

Trees of less than 1.3 metres in height have no diameters at 1.3 m (by definition). For trees taller than 1.3 m, a diameter at 1.3 is calculated based on treating trees as perfect cones so that the diameter at 1.3 m can be calculated based on the diameter at ground level.

Height can also be calculated as:

$$H = \exp[a_1 + a_2 \ln(d_{\min})] \quad (5.8)$$

where a_1 is the intercept and a_2 the slope parameters in the allometric relationship between height and diameter at breast height and d_{\min} is the minimum diameter at which the relationship is applicable.

Again treating trees as perfect cones, the diameter at ground level can then be calculated as:

$$d_g = d_{\min} H / (H - 1.3) \quad (5.9)$$

and the ratio of height to diameter, h_d , can then be calculated simply as:

$$h_d = 100 H / d_g \quad (5.10)$$

These calculations assume that height and diameter increase proportionately in very small trees until they reach a defined minimum diameter. As trees grow even taller, the calculations ensure that they grow in accordance with the defined allometric relationships. This ensures internally consistency at all growth stages.

To calculate the further increase in height and diameter for taller trees, the approach of Korol et al. (1995) is used. That approach makes use of the allometric relationship between height and diameter (eqn. 5.11a) and between stem weight, diameter and height:

$$\ln(H) = a_1 + a_2 \ln(d) \quad (5.11a)$$

$$\ln(W) = a_3 + a_4 \ln(d) + a_5 \ln(H) \quad (5.11b)$$

where W is total stem dry weight and a_1 , a_2 , a_3 , a_4 and a_5 are constants. These equations can be combined to yield the expressions:

$$d_{i+1} = d_i (W_{s,i+1} / W_{s,i})^{[1 / (a_2 a_5 + a_4)]} \quad (5.12)$$

$$H_{i+1} = H_i (W_{s,i+1} / W_{s,i})^{[1/(a_5 + a_4 / a_2)]} \quad (5.13)$$

where d_{i+1} , H_{i+1} and $W_{s,i+1}$ refer to the new diameter, height and total wood weight, and d_i , H_i and $W_{s,i}$ refer to the corresponding values at the previous time step. These equations are expressed differently and differ slightly in their expression from those developed by Korol et al. (1995), as retracing of the mathematical transformations resulted in the expression of eqn. 5.13 rather than the slightly different one obtained by Korol et al. (1995).

Basal area is calculated from mean diameter as:

$$B = 1.05 s \pi (d / 2)^2 \quad (5.14)$$

where B is stand basal area and s is stocking in stems per hectare. The factor 1.05 makes allowance for variation in the diameters of individual trees. As basal area is calculated from the square of the diameters of trees, larger trees make a disproportionately larger distribution to stand basal area than to mean stand diameter. The factor 1.05 translates to a standard deviation of tree diameters of about 23%.

Nitrogen Allocation

Nitrogen allocation is calculated on the basis of the same considerations that govern the allocation of carbon, but in addition, the nitrogen concentration in all plant organs is expressed relative to the nitrogen concentration in foliage, so that:

$$a_{n,i} = b_i a_{c,i} / \Sigma (b_i a_{c,i}) \quad (5.15)$$

where $a_{n,i}$ and $a_{c,i}$ are the allocation coefficients for nitrogen and carbon to biomass component, i, and b_i is an empirical nitrogen concentration ratio for plant component i relative to that in foliage. This means that the nitrogen concentration of all biomass components dynamically adjust with changes in foliar nitrogen concentration as is observed experimentally.

Nitrogen concentration in heartwood is assumed to be lower than in sapwood, and upon conversion of sapwood to heartwood, any excess nitrogen is retranslocated into the soluble nitrogen pool.

6. Soil Nitrogen Dynamics

Available nitrogen may come from atmospheric deposition, fertiliser application, biological nitrogen fixation or mineralisation of organic nitrogen during the decomposition of soil organic matter so that

$$N_{\min} = N_{\text{dep}} + N_{\text{fert}} + N_{\text{fix}} + N_{\text{act}} \quad (6.1)$$

where N_{\min} is the total amount of nitrogen becoming available in mineral form, N_{dep} is the amount deposited from the atmosphere, N_{fert} is the amount added as fertiliser, N_{fix} is the amount biologically fixed, and N_{act} is the amount mineralised from the active (decomposer) pool of organic matter. The rates N_{dep} and N_{fert} are user input, with atmospheric input taken to be the same for each day of the simulation and fertiliser being added at specified dates.

Biological nitrogen fixation is calculated as:

$$N_{\text{fix}} = f_{\text{Biol}} A_d \quad (6.2)$$

where f_{Biol} is an empirical fraction and A_d daily photosynthetic carbon gain. This formulation is based on the assumption that the same factors, light, temperature, water

availability that affect carbon gain have an equivalent effect on symbiotic nitrogen fixation. The factor f_{Biol} can be set to zero for system, such as pine forests, without symbiotic nitrogen fixation.

The amount of nitrogen mineralised is calculated with a variant of the CENTURY model (Parton et al., 1987). The key modifications are (Kirschbaum and Paul 2002):

- 1) nitrogen exchange is assumed to occur only between the active organic matter and the mineral nitrogen pool.;
- 2) the C:N ratio of all pools are allowed to vary depending on the C:N ratios of the pools from where organic matter is received;
- 3) Additional pools are included for coarse woody surface litter (from dead stems), fine woody surface litter (from dead branches) and coarse woody soil litter (from dead structural roots).

These changes have been introduced into the model to more realistically simulate the time course of mineralisation/ immobilisation following litter addition, and to make it possible for soil carbon and nitrogen dynamics to respond realistically to changes in litter quality, such as during the transition between woody and non-woody vegetation.

The temperature dependence of soil organic matter decomposition, $T_{d, \text{lim}}$, is described by the equation developed by Kirschbaum (2000a):

$$T_{d, \text{lim}} = e^{[3.36(T_{\text{soil}} - 40)/(T_{\text{soil}} - 31.79)]} \quad (6.3)$$

This is further multiplied by a soil moisture modifier, $W_{d, \text{lim}}$, described for each soil layer as:

$$W_{d, \text{lim}} = d_{\text{min}} + (1 - d_{\text{min}}) \left(\frac{W / W_{\text{hold}}}{W_{\text{crit}}} \right)^{x_d} \quad \text{if } (W / W_{\text{hold}}) < W_{\text{crit}} \quad (6.4a)$$

$$W_{d, \text{lim}} = 1 \quad \text{if } (W / W_{\text{hold}}) \geq W_{\text{crit}} \quad (6.4b)$$

where d_{min} is a minimum decomposition activity that occurs in even apparently dry soil due, for example, to photo-oxidation, W is the volumetric water content of each soil layer, W_{hold} the water-holding capacity for each layer, W_{crit} an empirical term that determines at what water content stress-induced reductions in plant and decomposition activity commence and x_d is an empirical term that describes the shape response of decomposition limitation to the volumetric water content.

The C:N ratios of both structural and metabolic litter pools were allowed to vary, but maintaining a constant proportionality between those ratios. Hence, variations in N concentration of fresh litter were reflected in variation in the C:N ratio of both structural and metabolic litter, but proportionality of the C:N ratios in those two pools was kept constant so that:

$$N_{\text{metab}} = \frac{N_{\text{tot}}}{\left(1 + \frac{C_{\text{struct}}}{r_{\text{sm}} C_{\text{metab}}} \right)} \quad (6.5a)$$

$$N_{\text{struct}} = N_{\text{tot}} - N_{\text{metab}} \quad (6.5b)$$

where N_{metab} is the flux of litter N to the metabolic litter pool, N_{struct} is the flux of litter N to the structural litter pool, N_{tot} is total N flux to litter, C_{metab} and C_{struct} are corresponding C fluxes and r_{sm} is the ratio of the C:N ratios of the structural and metabolic pools.

For mineralisation and immobilisation of N, it was assumed that essentially only the active SOM pool contributed to exchange of N between soil organic matter and the mineral

N pool. Hence, the amount of N mineralised (N_{\min}) and immobilised (N_{imm}) in one time step were calculated as:

$$N_{\min} = P_{a,n} - P_{a,c} / R_{\text{CN}} \quad \text{if } P_{a,n} > P_{a,c} / R_{\text{CN}} \quad (6.6a)$$

$$N_{\text{imm}} = P_{a,c} / R_{\text{CN}} - P_{a,n} \quad \text{if } P_{a,n} < P_{a,c} / R_{\text{CN}} \quad (6.6b)$$

where $P_{a,n}$ and $P_{a,c}$ are the amounts of N and C in the active SOM pool, respectively, and R_{CN} is the critical C:N ratio of the active pool for N mineralisation. The N_{\min} flux is the flux of N entering the mineral N pool, while the N_{imm} flux is the flux of N from the mineral N pool to SOM. The amount of N in the mineral N pool provided a constraint on the maximum amount of N that could be immobilised.

It was also assumed that there is a minor flux of N, N_r , from the pool of mineral N to the resistant SOM pool:

$$N_r = k_{\text{imm}} P_{\min} \quad (6.7)$$

where P_{\min} is the pool of mineral nitrogen and k_{imm} is the proportion of mineral N that can be immobilised into the resistant pool.

In contrast to most grassland soils, mycorrhizal uptake of N is an important process in many forest soils (Chapin et al., 1993; Nasholm et al., 1998). It allows continued relatively high rates of N uptake even after the addition of large amounts of C-rich litter, such as after thinning, pruning or clearfelling operations that might prevent any net N mineralisation.

An additional plant uptake of N from the active SOM pool by mycorrhizal uptake, N_y , was included as:

$$N_y = f_y T_{d,\text{lim}} P_{a,n} \quad (6.8)$$

where f_y is a proportionality term that relates the size of the total active N pool to the mycorrhizal uptake of N, and $P_{a,n}$ is the pool of active N.

Nitrogen Uptake Dynamics

For moderate amounts of nitrogen being mineralised, it is assumed that all nitrogen is taken up by plants at each time step (minus fractions volatilised, leached or sequestered in slow organic matter).

However, it is assumed that only a maximum amount of nitrogen can be taken up by plants during each day. When nitrogen is taken up, it is initially added to a soluble plant pool which can be utilised for subsequent growth. The maximum amount that can be taken up into the soluble plant pool, U_{\max} , is given by:

$$U_{\max} = X_n \sum N_{\max,i} - \sum N_i \quad (6.9)$$

where X_n is an empirical excess nitrogen storage ratio, $\sum N_{\max,i}$ is the sum over all plant organs of the maximum amount of nitrogen that could be taken up in growth by each pool if that pool had the maximum permissible nitrogen concentration and $\sum N_i$ is the sum of the amounts actually contained in each pool. Calculations for the maximal amount that can be contained in each pool are given as:

$$N_{\max,i} = C_i n_{\max} b_i \quad (6.10)$$

where C_i is the amount of carbon in organ 'i', n_{\max} is maximum foliar nitrogen concentration and b_i is the nitrogen concentration ratio of organ 'i' relative to that of foliage.

7. Climatic Information

The model can be run with either constant, observed or simulated climate. For sites where climate data are available, observed data should normally be used. If observed data are not available, it is possible to generate artificial sequences based on observed mean climatic parameters. It is also possible to run the model with constant climatic data. This is principally useful as an analytical tool to investigate the model response to some other perturbation which is easier to identify in the absence of climatic variability.

The minimum climatic data set consists of daily minimum and maximum temperature, radiation and rainfall. Humidity may be input as either absolute or relative humidity. If relative humidity is supplied it is taken to be the relative humidity at the time of day when mean daytime temperature is reached. When information about humidity cannot be supplied, it is calculated based on the assumption that air is saturated with water vapour at the overnight minimum temperature.

Daily mean temperature is calculated as the mean of minimum and maximum temperatures. Daytime temperature, T_{day} , is calculated, following Running et al. (1987), as:

$$T_{\text{day}} = 0.606 T_{\text{max}} + 0.394 T_{\text{min}} \quad (7.1)$$

where T_{max} is daily maximum temperature and T_{min} overnight minimum temperature.

For simulated climate runs, daily maximum temperature is calculated as:

$$T_{\text{max}} = \bar{T}_{\text{max}} + T_{\text{amp}} \sin[\pi (d_j - d_w + 91.25)/182.5] \quad (7.2)$$

where \bar{T}_{max} is the annual mean maximum temperature, T_{amp} is a temperature amplitude term, d_j the Julian day and d_w the warmest day of the year. The warmest day is taken as day 19 (19 January) for the southern hemisphere and day 201 (20 July) for the northern hemisphere. The same equation is used for T_{min} , with \bar{T}_{max} being replaced by a corresponding \bar{T}_{min} . Annual temperature amplitude and the warmest day of the year are assumed to be identical for calculations of T_{max} and T_{min} .

Absolute humidity, e_{abs} , can either be calculated from the minimum temperature as the saturated vapour pressure at the overnight minimum temperature, or it can be calculated separately as:

$$e_{\text{abs}} = \bar{e}_{\text{abs}} + e_{\text{amp}} \sin[\pi (d_j - d_w + 91.25)/182.5] \quad (7.3)$$

where \bar{e}_{abs} is the annual mean absolute humidity and e_{amp} is a humidity amplitude term.

Incident radiation, Q_i , is similarly calculated as:

$$Q_i = \bar{Q}_i + Q_{\text{amp}} \sin[\pi (d_j - d_q + 91.25)/182.5] \quad (7.4)$$

where \bar{Q}_i is the mean daily incident radiation for the whole year, Q_{amp} is the amplitude of daily incident radiation throughout the year and d_q is the day with highest radiation. That day is primarily determined by the location of the sun, but cloudiness can also play a role. Day 356 (22 December) is taken as the day with highest radiation for the southern hemisphere and day 173 (22 June) for the northern hemisphere.

For constant-climate runs, rainfall is added as a constant daily rate. For simulated climate, a more sophisticated procedure is used. It essentially assumes that the probability of a particular rainfall event occurring is inversely proportional to the size of the daily rainfall total. Stochastic daily rainfall, R , for a particular day is then calculated as:

$$R = -\ln(1 - j) \bar{R} / P_r \quad (7.5)$$

where \ln is the natural log, j is a random number in the range (0..1), \bar{R} is daily average rainfall and P_r is the probability that rain will fall on a particular day. This equation is

based on analysis of rainfall patterns at the BFG site over 15 years which showed that this simple equation could adequately describe the observed probability distribution of rainfall amounts (M.U.F. Kirschbaum, unpublished). Rainfall seasonality is not included in this procedure.

Incident daily net radiation, Q_i , is calculated as (Kirschbaum et al., 2007b):

$$Q_i = Q_0 \{0.147 + 0.796 \cdot [1 - \exp(-0.080 \Delta T)]\} [0.657 + 0.343 \exp(-0.293 P)] \quad (7.6)$$
 where ΔT is the diurnal temperature range, P is precipitation and Q_0 is the radiation that would be received if there were no atmospheric turbidity absorbing part of incoming radiation.

The diurnal temperature range was calculated as:

$$\Delta T = T_{\max} - T_{\min(-1)} \quad (7.7)$$

where T_{\max} is daily maximum, $T_{\min(-1)}$ the minimum temperatures of the preceding night. Incident radiation can be reduced by cloud cover. Clouds also reduce the diurnal temperature range and may bring precipitation. Information about precipitation and the diurnal temperature range can thus be used to infer the presence of clouds and their effect on reducing incident radiation. It was found that the minimum temperature of the night preceding the day of interest provided a stronger constraint on atmospheric turbidity than the minimum temperature of the following night.

The numeric parameters in Equation A1 were fitted to data from the Tumbarumba site in order to minimise the residual sums of squares of modelled minus observed data (Kirschbaum et al. 2007b).

Q_0 was calculated as:

$$Q_0 = 86400 Q_x d_{\text{sol}}^2 \sin(\pi L_t / 180) \sin(\delta) [d_{\text{rel}} - \tan(d_{\text{rel}})] / \pi \quad (7.8)$$

where Q_x is the incident daily radiation outside the Earth's atmosphere ($1360 \text{ MJ m}^{-2} \text{ d}^{-1}$), 86,400 the number of seconds in a day, d_{sol} is the relative distance between the sun and the Earth, d_{rel} is relative daylength in radians, L_t is latitude and δ is the solar declination.

The variation in the mean distance between sun and Earth is calculated based on information in Gates (1980) as:

$$d_{\text{sol}} = 1 + 0.01705 \cos[2 \pi (d_j - 3) / 365.24] \quad (7.9)$$

where d_j is the day of the year.

Solar declination, δ , is calculated as (Collares-Pereira and Rabl 1979):

$$\delta = \arcsin[0.3979 \sin(\varepsilon)] \quad (7.10)$$

with ε calculated as:

$$\varepsilon = 2 \pi (d_j + 284) / 365.24 \quad (7.11)$$

Relative daylength (in radians), d_{rel} , is calculated as:

$$d_{\text{rel}} = 0 \quad \text{if } d_L \leq -1 \quad (7.12a)$$

$$d_{\text{rel}} = \pi \quad \text{if } d_L \geq 1 \quad (7.12b)$$

$$d_{\text{rel}} = \pi - \arccos(d_L) \quad \text{if } -1 < d_L < 1 \quad (7.12c)$$

with d_L calculated as:

$$d_L = \tan(0.0174533 L_t) \tan(\delta) \quad (7.13)$$

Precipitation is assumed to fall as snow, S , when daily mean temperature is below 0°C (Kirschbaum 2004):

$$dS/dt = P \quad \text{if } T_{\text{mean}} < 0 \quad (7.14)$$

where T_{mean} is mean air temperature.

Snow is assumed to melt due to the combined effects of sensible and radiative heat transfer as:

$$dS/dt = -(m_T T_{day} + m_Q Q_i) \quad \text{if } (m_T T_d + m_Q Q_i) > 0 \quad (7.15)$$

where T_{day} is mean daytime temperature and m_T and m_Q are empirical parameters that describes the dependence of the rate of snow melt on daytime temperature and incident radiation, respectively.

Without snow, soil temperature follows mean air temperature, with some characteristic delay term so that

$$dT_{soil}/dt = (T_0 - T_{soil}) / r_T \quad (7.16)$$

where T_0 is the temperature at the top of the soil, T_{soil} is soil temperature and r_T is the soil resistance to temperature change. When there is snow cover and the temperature in below 0°C, snow acts as an additional resistance to temperature change so that:

$$dT_s/dt = (T_0 - T_{soil}) / (r_T + r_s S) \quad (7.17)$$

When snow is melting, the temperature at the top of the soil cannot be greater than 0°C. Hence, the rate of soil warming in spring is given by the lesser of heat transfer through the insulating snow layer and the heat transfer from the top of the soil at 0°C. Hence, when air temperature is above 0°C:

$$dT_{soil}/dt = (T_0 - T_{soil}) / (r_T + r_s S) \quad \text{if } -T_{soil} / r_T < (T_0 - T_{soil}) / (r_T + r_s S) \quad (7.18a)$$

$$dT_{soil}/dt = -T_{soil} / r_T \quad \text{if } -T_{soil} / r_T \geq (T_0 - T_{soil}) / (r_T + r_s S) \quad (7.18b)$$

where r_s gives the additional resistance to soil temperature change per mm (water equivalent) in the snow layer. This is an obvious simplification as snow in reality compacts over time and its thermal properties thereby change. It also omits the consideration of the latent heat of freezing and melting. However, the current formulation was regarded as adequate for the present purposes, and predicted soil temperatures agreed closely with observed soil temperatures at the sample site of Flakaliden (Kirschbaum, 2004).

The temperature at the top of the soil had originally been taken as just equal to daily mean temperature. Following Paul et al. (2004), the effective surface temperature, T_0 , is now modulated by leaf area so that:

$$T_0 = T_{mean} (1 + p_L e^{-L t_L}) \quad (7.19)$$

where T_{mean} is daily mean temperature, p_L is the proportional extent by which mean soil temperature can be elevated above mean air temperature in the absence of a protective canopy, L is leaf area index and t_L is a term describing the sensitivity of soil temperature cooling by leaf area.

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APPENDIX: ABBREVIATIONS USED

$a_{c,i}$ = carbon allocation coefficient to plant biomass component, i	-
$a_{n,i}$ = nitrogen allocation coefficient to plant biomass component, i	-
$a_{1..a_5}$ = allometric constants for stand dimensions	-
A = instantaneous CO ₂ assimilation rate	$\mu\text{mol m}^{-2} \text{s}^{-1}$
A_{act} = the age of the stand	yr
A_{d} = CO ₂ assimilation rate over one day	$\text{kgC ha}^{-1} \text{d}^{-1}$
A_{mat} = age of maturity	yr
A_{max} = maximum photosynthetic rate without light limitation	$\mu\text{mol m}^{-2} \text{s}^{-1}$
A_{opt} = RuBP regeneration capacity at optimum temperature	$\mu\text{mol m}^{-2} \text{s}^{-1}$
A_{Vj} = RuBP regeneration capacity at a given temperature	$\mu\text{mol m}^{-2} \text{s}^{-1}$
A_{x} = potential RuBP regeneration rate under optimum temperature and non-limiting CO ₂ and foliar nitrogen concentrations	$\mu\text{mol m}^{-2} \text{s}^{-1}$
b_i = nitrogen concentration ratio of biomass component i relative to foliage	-
B = stand basal area	$\text{m}^2 \text{ha}^{-1}$
B_{crit} = Critical biomass of individual trees for the self-thinning rule	kgC tree^{-1}
c_a = atmospheric CO ₂ concentration	Pa
c_i = intercellular CO ₂ concentration	Pa
C_c = fractional canopy cover of the site	-
C_f = carbon in foliage	kgC ha^{-1}
C_i = carbon pools in the plant	kgC ha^{-1}
C_{metab} = flux of litter C to the metabolic litter pool	$\text{kgC ha}^{-1} \text{d}^{-1}$
C_p = specific heat of air	$\text{J kg}^{-1} \text{K}^{-1}$
C_s = the amount of carbon in the soluble pool	kgC ha^{-1}
C_{struct} = flux of litter C to the structural litter pool	$\text{kgC ha}^{-1} \text{d}^{-1}$
C_w = average canopy width (mainly of young trees)	m
d = average tree diameter at breast height	cm
d_g = tree diameter at ground level	cm
d_j = day of the year	-
d_{min} = minimum decomposition activity in even apparently dry soil	-
d_q = day with highest radiation.	-
d_{rel} = relative daylength	radians
d_{sol} = the relative distance between the sun and the Earth	radians
d_w = warmest day of the year	-
D_{act} = total dry weight of the stand	kgC ha^{-1}
D_b = daily fraction of stem biomass lost due to tree death	-
D_f = units of frost damage	-
$D_{f, \text{max}}$ = maximum number of frost damage units	-
D_{mat} = size of maturity of a stand	kgC ha^{-1}
D_n = daily fraction of stems lost due to mortality	-
D_s = units of scorch damage	-
$D_{s, \text{max}}$ = maximum number of scorch damage units	-
$e(T)$ = saturation vapour pressure at temperature T	Pa

e_{abs} = absolute humidity	Pa
\bar{e}_{abs} = annual mean absolute humidity	Pa
e_{amp} = humidity amplitude term	Pa
E_{lit} = litter evaporation rate	mm d ⁻¹
E_{soil} = soil evaporation rate	mm d ⁻¹
f_{age} = a limitation term that describes how carbon gain decreases with stand age	-
f_{Biol} = empirical term that relates N fixation to carbon assimilation	kgN kgC ⁻¹
f_c = empirical term that relates rainfall interception to leaf area index	-
f_d = fractional canopy damage by frost or scorching temperature	-
f_{growth} = empirical term that quantifies the amount of carbon lost in growth respiration per unit of new growth	-
f_{hold} = water holding capacity per unit of litter	mm (kgC ha ⁻¹) ⁻¹
f_m = ratio of stem size of dieing to average sized trees	-
f_{maint} = daily respiration rate per unit of nitrogen at 25°C	kg C (kg N) ⁻¹
f_{lit} = the fraction of ground covered by litter	-
f_{mulch} = litter-surface coverage parameter	ha kgC ⁻¹
f_{soil} = fraction of light passing through to the litter layer	-
f_{size} = reduction term for growth due to size-related downturn in productivity	-
f_t = form factor of stem dimensions	-
$f_{T, \text{resp}}$ = temperature response function of maintenance respiration	-
f_y = a proportionality term that relates the size of the total active N pool to the rate of mycorrhizal N uptake	-
F_0 = is a threshold temperature for frost damage	°C
F_n = loss of nitrogen from the live foliage pool	kgN ha ⁻¹ d ⁻¹
g_s = stomatal conductance	mol m ⁻² s ⁻¹
G = new carbon growth	kgC ha ⁻¹ d ⁻¹
h = day length	s
H = tree height	m
I_a = absorbed photosynthetically active radiation	μmol m ⁻² s ⁻¹
I_c = rain intercepted by the canopy	mm d ⁻¹
k_1 = light extinction coefficient	-
$k_{1, \text{max}}$ = maximum light extinction coefficient with uniform foliage distribution	-
$k_{1, r}$ = relative range in the light extinction coefficient with foliage clumping	-
k_2 = conversion term of radiation to photosynthetic photon flux	μmol quanta J ⁻¹
k_3 = a constant for stomatal conductance relative to photosynthetic carbon gain	-
$k_{3, d}$ = stomatal factors for (notionally) completely dry stands	-
$k_{3, w}$ = stomatal factors for stands with adequate water	-
k_{imm} = the proportion of mineral nitrogen immobilised daily into the resistant pool	d ⁻¹
k_p = Phosphoenolpyruvate (PEP)-carboxylase activity (or the initial slope of the relationship of A as a function of intercellular CO ₂)	μmol m ⁻² s ⁻¹
$k_{p(25)} = k_p$ at 25°C	μmol m ⁻² s ⁻¹
$k_{p,1}$ = extra respiration by pests	kgC ha ⁻¹ d ⁻¹
$k_{p,2}$ = extra foliage loss due to pests	kgC ha ⁻¹ d ⁻¹
$k_{p,3}$ = proportional suppression of photosynthesis by pests	-
k_{thin} = constant in the self-thinning rule	-

K_c = an empirical Michaelis-Menten constant that describes the dependence of growth on the relative amount of soluble carbon in the plant	-
L = leaf area index	-
L_s = non-woody surface litter including partly decomposed material	kgC ha ⁻¹
L_t = latitude	°
L_h = latent heat of vaporisation	J kg ⁻¹
m = leaf transmissivity	-
m_Q = empirical parameter that describes the dependence of the rate of snow melt on incident radiation MJ m ⁻² d ⁻¹	mm m ² d MJ ⁻¹
m_T = empirical parameter that describes the dependence of the rate of snow melt on daytime temperature	mm (°C) ⁻¹
n_{grad} = ratio of nitrogen between foliage at the top and the bulk canopy	-
n_f = foliar nitrogen concentration at the top of the canopy	kgN (kgC) ⁻¹
n_{max} = maximum foliar nitrogen concentration	kgN (kgC) ⁻¹
n_{min} = minimum nitrogen concentration that allows any photosynthesis	kgN (kgC) ⁻¹
n_{opt} = foliar N concentration for optimum photosynthesis	kgN (kgC) ⁻¹
N_{act} = N mineralised from the active (decomposer) organic matter pool	kgN ha ⁻¹ d ⁻¹
N_{dep} = the amount deposited from the atmosphere	kgN ha ⁻¹ d ⁻¹
N_f = the amount of nitrogen in the foliage pool	kgN ha ⁻¹
N_{fert} = the amount added as fertiliser	kgN ha ⁻¹ d ⁻¹
N_{fix} = the amount biologically fixed	kgN ha ⁻¹ d ⁻¹
N_i = amount of nitrogen in different plant pools	kgN ha ⁻¹
N_{lim} = nitrogen limitation parameter	-
N_{imm} = total amount of nitrogen being immobilised into organic matter	kgN ha ⁻¹ d ⁻¹
N_{min} = total amount of nitrogen being mineralised from organic matter	kgN ha ⁻¹ d ⁻¹
$N_{max, i}$ = maximum amount of nitrogen that could be taken up by plant pool, i, if that pool had the maximum permissible nitrogen concentration	kgN ha ⁻¹
N_{metab} = the flux of litter N to the metabolic litter pool	kgN ha ⁻¹ d ⁻¹
N_{min} = total amount of nitrogen becoming available in mineral form	kgN ha ⁻¹ d ⁻¹
N_{pest} = loss of soluble nitrogen due to pest damage	kgN ha ⁻¹ d ⁻¹
N_s = nitrogen in a soluble plant pool	kgN ha ⁻¹
N_{struct} = the flux of litter N to the structural litter pool	kgN ha ⁻¹ d ⁻¹
N_{tot} = total flux of litter N to both metabolic and structural litter pools	kgN ha ⁻¹ d ⁻¹
N_y = the rate of mycorrhizal N uptake	kgN ha ⁻¹ d ⁻¹
p_a = the density of air	kg m ⁻³
p_L = proportional soil heating if the ground is not covered by vegetation	-
P = precipitation	mm d ⁻¹
P_{min} = the amount of nitrogen in the pool of mineral nitrogen	kg ha ⁻¹
$P_{a, c}$ = the amount of C in the active SOM pool	kg ha ⁻¹
$P_{a, n}$ = the amount of N in the active SOM pool	kg ha ⁻¹
P_r = daily rainfall probability	-
q = normalised radiation	-
Q_0 = the radiation that would be received if there were no atmospheric turbidity absorbing part of incoming radiation	MJ m ⁻² d ⁻¹
Q_a = absorbed total radiation	MJ m ⁻² d ⁻¹
Q_{amp} = the amplitude of daily radiation	MJ m ⁻² d ⁻¹

Q_c = light transmitted through to the bottom of the canopy	$\text{MJ m}^{-2} \text{d}^{-1}$
Q_{crit} = critical light level for low-light senescence	$\text{MJ m}^{-2} \text{d}^{-1}$
Q_i = daily incident radiation	$\text{MJ m}^{-2} \text{d}^{-1}$
\bar{Q}_i = mean daily incident radiation	$\text{MJ m}^{-2} \text{d}^{-1}$
Q_k = temperature response coefficient for PEP-carboxylase-limited rate in C_4 phs	-
Q_s = net radiation absorbed by the forest floor	$\text{MJ m}^{-2} \text{d}^{-1}$
Q_v = temperature response coefficient for Rubisco-limited rate in C_4 phs	-
Q_x = incident daily radiation outside the Earth's atmosphere	$1360 \text{ MJ m}^{-2} \text{d}^{-1}$
r = the fraction of radiation that is reflected (albedo)	-
r_a = aerodynamic resistance	s m^{-1}
r_c = canopy resistance	s m^{-1}
r_f = retranslocation factor that gives the ratio of nitrogen in senescing and live foliage	-
r_{fb} = allocation ratio between foliage and branches	-
$r_{fb(10)}$ = notional r_{fb} for a ten-meter high tree	-
r_h = relative humidity	-
r_{kV} = proportionality ratio of PEP-carboxylase activity and the Rubisco limited rate	-
r_{lit} = water vapour diffusion resistance out of the litter layer	s m^{-1}
r_{max} = maximal ratio of root to foliage allocation	-
r_{min} = minimal ratio of root to foliage allocation	-
r_{rf} = ratio of root to foliage allocation	-
r_{sm} = the ratio of the C:N ratios of the structural and metabolic litter pools	-
r_{soil} = water vapour diffusion resistance out of the soil	s m^{-1}
r_S = additional resistance to soil temperature change caused by a snow layer	mm^{-1}
r_T = soil resistance to temperature change	-
r_u = aerodynamic resistance underneath the canopy	s m^{-1}
\bar{R} = total daily rainfall	mm d^{-1}
\bar{R} = daily average rainfall	mm d^{-1}
R_b = base rate of respiration (compensates for short-term response to T)	-
R_{eff} = effectively received rainfall	mm
R_{CN} = the critical C:N ratio of the active pool for N mineralisation	-
R_f = repair rate of frost damage to foliage	-
$R_{f, \text{max}}$ = maximum number of days for complete repair from frost damage	d
R_g = growth respiration	$\text{kgC ha}^{-1} \text{d}^{-1}$
R_m = maintenance respiration	$\text{kgC ha}^{-1} \text{d}^{-1}$
R_p = respiration rate by insects or other pests	$\text{kgC ha}^{-1} \text{d}^{-1}$
R_s = repair rate of scorch damage to foliage	-
$R_{s, \text{max}}$ = maximum number of days for complete repair from scorch damage	d
R_u = net radiation that passes through the canopy and reaches the ground	$\text{MJ m}^{-2} \text{d}^{-1}$
s = stocking	trees ha^{-1}
S = snow pack	mm (water equiv.)
S_0 = threshold temperature for scorch damage	$^{\circ}\text{C}$
S_b = minimum proportional daily foliage senescence rate	kg kg^{-1}
S_c = sensitivity to cold (frost) damage	-
$S_{d, \text{max}}$ = maximal daily drought senescence rate	$\text{kg ha}^{-1} \text{d}^{-1}$
S_{dry} = senescence due to drought	$\text{kg ha}^{-1} \text{d}^{-1}$
S_f = daily foliage senescence rate	$\text{kg ha}^{-1} \text{d}^{-1}$

S_h = sensitivity to heat (scorch) damage	-
S_l = specific leaf area	$m^2 kg^{-1}$
$S_{l, max}$ = maximum daily foliage senescence rate caused by low light	$kg kg^{-1}$
S_{low} = senescence due to low light experienced at the bottom of the canopy	$kg kg^{-1}$
S_p = daily foliage senescence due to pest damage	-
t_L = term in the exponential relationship to describe the temperature shielding effect of a vegetation cover	-
T = temperature	$^{\circ}C$
T_0 = temperature at the top of the soil	$^{\circ}C$
T_{amp} = temperature amplitude term	$^{\circ}C$
T_{day} = average daytime temperature	$^{\circ}C$
$T_{d, lim}$ = temperature limitation for soil organic matter decomposition	-
$T_{m, r}$ = temperature for maximum respiration rate	$^{\circ}C$
T_{max} = daytime maximum temperature	$^{\circ}C$
\bar{T}_{max} = annual mean maximum temperature	$^{\circ}C$
T_{mean} = daily mean temperature	$^{\circ}C$
T_{min} = overnight minimum temperature	$^{\circ}C$
\bar{T}_{min} = annual mean minimum temperature	$^{\circ}C$
T_n = minimum mean daily temperature that allows any photosynthesis	$^{\circ}C$
T_{opt1} = lower optimum temperature for maximum photosynthesis	$^{\circ}C$
T_{opt2} = upper optimum temperature for maximum photosynthesis	$^{\circ}C$
T_p = transpiration rate	$mm d^{-1}$
T_{soil} = soil temperature	$^{\circ}C$
T_x = maximum mean daily temperature that allows any photosynthesis	$^{\circ}C$
v = proportionality term between photosynthesis and emission of volatile organics	-
V_e = rate of emission of volatile organics	$kgC ha^{-1} d^{-1}$
V = average tree stem volume	$m^3 tree^{-1}$
V_t = maximum Rubisco limited rate in C_4 photosynthesis	$\mu mol m^{-2} s^{-1}$
$V_{t(25)} = V_t$ at $25^{\circ}C$	$\mu mol m^{-2} s^{-1}$
U_{max} = maximum amount of nitrogen that can be taken up by plants	$kgN ha^{-1} d^{-1}$
w_i = relative contribution of a soil layer to determining overall water stress	-
$w_{d, j}$ = drainage of water out of a specified soil layer	$mm d^{-1}$
$w_{d, L}$ = drainage of water out of the litter layer	$mm d^{-1}$
W = amount of water held in the soil	mm
W_{crit} = empirical term that determines at what relative water content plants begin to experience water stress limitations	-
W_d = deep drainage	mm
$W_{d, lim}$ = moisture limitation term for organic matter decomposition	-
W_f = foliage weight	$kgC ha^{-1}$
W_{hold} = water holding capacity of the soil	mm
$W_{hold, j}$ = water holding capacity of a specified soil layer	mm
W_i = irrigation water	mm
W_j = water held in a specific soil layer	mm
W_{lim} = water limitation factor	-
$W_{lim, j}$ = water limitation factor of a specified soil layer	-

W_{lit} = the amounts of water held in the litter layer	mm
$W_{lit, max}$ = the maximum amounts of water held in the litter layer	mm
W_L = water held in the litter layer	mm
W_s = stem wood weight	kgC ha ⁻¹
$W_{soil(1), max}$ = the maximum amounts of water held in the upper-most soil layer	mm
$W_{soil(1)}$ = the amounts of water held in the upper-most soil layer	mm
x_{age} = a power term that described the steepness of the age effect on productivity	-
x_d = a power term to determine the shape response of decomposition activity to water limitations	-
x_{size} = a power term that described the steepness of the size effect on productivity	-
X_n = an empirical excess nitrogen storage ratio	-
α = quantum yield of CO ₂ assimilation rate	mol mol ⁻¹
α_{vj} = quantum yield of RuBP regeneration rate	mol mol ⁻¹
β_c = curvature term in the transition from CO ₂ limited to maximum-capacity limited rate in C ₄ photosynthesis	-
δ = solar declination	radians
Δ = vapour saturation deficit of the air	Pa
ΔT = diurnal temperature range	°C
γ = psychrometric constant	Pa K ⁻¹
Γ^* = CO ₂ compensation point in the absence of non-photorespiratory respiration	Pa
θ = curvature term in photosynthetic light response curve	-
τ_r = time constant for the acclimation response in respiration	d
ρ = wood density	kg m ⁻³
σ = derivative of saturation vapour pressure with respect to temperature	Pa K ⁻¹

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