

SUPPORTING INFORMATION FOR:

“PLANT: A PACKAGE FOR MODELLING FOREST TRAIT ECOLOGY & EVOLUTION”

DESCRIPTION OF THE FF16 PHYSIOLOGICAL MODEL

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1 INTRODUCTION

This document outlines the core physiological model used in the `PLANT` package. This model has primarily been developed elsewhere, in particular in Falster *et al.* (2011). The model’s

equations are presented here not as original findings, but rather so that users can understand the full system of equations being solved within `PLANT`.

The purpose of the physiological model in `PLANT` is to take a plant's current size, light environment, and physiological parameters as inputs, and return its growth, mortality, and fecundity rates. In the default physiological model within `PLANT`, these vital rates are all derived from the rate at which living biomass is produced by the plant, which in turn is calculated based on well-understood physiology (Fig. 1). Various physiological parameters influence demographic outcomes. Varying these parameters allows accounting for species differences, potentially via traits (see last section). Tables 1, 3, 4 summarize the units and definitions of all variables, parameters, and hyper-parameters used in the material below.

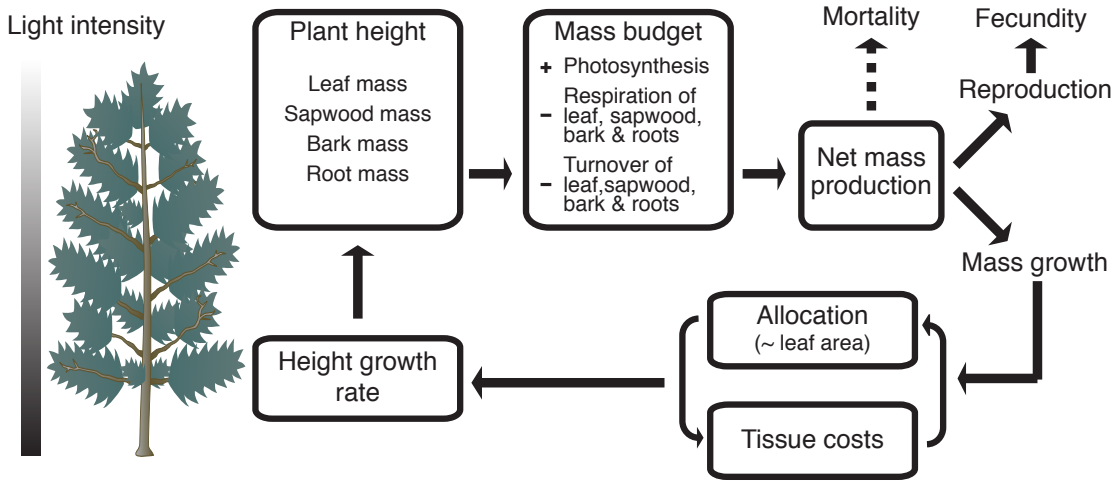


FIGURE 1: Physiological model in `PLANT`, giving demographic rates on the basis of its traits, size, and light environment, as functions of net mass production. The dashed arrow towards mortality indicates that, although the mortality rate is assumed to depend on mass production, no mass is actually allocated there. Figure adapted from Falster *et al.* (2011) and Falster *et al.* (2015).

2 LEAF PHOTOSYNTHESIS

We denote by $p(x, E)$ the gross rate of leaf photosynthesis per unit leaf area within the canopy of a plant with traits x at light level $E(z)$, where z is height within the canopy. We assume a relationship of the form

$$p(x, E(z)) = \frac{\alpha_{p1}}{E(z) + \alpha_{p2}}, \quad (1)$$

for the average of p across the year. The parameters α_{p1} and α_{p2} are derived from a detailed leaf-level model and measure the light levels, respectively, at maximum annual photosynthesis and at 50% of this maximum. The average rate of leaf photosynthesis across the plant is then

$$\bar{p}(x, H, E_a) = \int_0^H p(x, E_a(z)) q(z, H) dz, \quad (2)$$

where $q(z, H)$ is the density of leaf area at height z (Eq. 13).

3 MASS PRODUCTION

The amount of biomass available for growth, dB/dt , is given by the difference between income (total photosynthetic rate) and losses (respiration and turnover) within the plant (Mäkelä, 1997; Thornley & Cannell, 2000; Falster *et al.*, 2011),

$$\underbrace{\frac{dB}{dt}}_{\text{net biomass production}} = \underbrace{\alpha_{\text{bio}}}_{\text{mass per c}} \underbrace{\alpha_y}_{\text{yield}} \left(\underbrace{A_l \bar{p}}_{\text{photosynthesis}} - \underbrace{\sum_{i=l,b,s,r} M_i r_i}_{\text{respiration}} \right) - \underbrace{\sum_{i=l,b,s,r} M_i k_i}_{\text{turnover}}. \quad (3)$$

Here, M , r , and k refer to the mass, maintenance respiration rate, and turnover rate of different tissues, denoted by subscripts l = leaves, b = bark, s = sapwood, and r = roots. \bar{p} is the assimilation rate of CO_2 per leaf area, α_y is yield (i.e., the fraction of assimilated carbon fixed in biomass, with the remaining fraction being lost as growth respiration; this comes in addition to the costs of maintenance respiration), and α_{bio} is the amount of biomass per unit carbon fixed. Gross photosynthetic production is proportional to leaf area, $A_l = M_l/\phi$, where ϕ is leaf mass per area. The total mass of living tissues is $M_a = M_l + M_b + M_s + M_r$.

4 HEIGHT GROWTH

The key measure of growth required by the demographic model is the rate of height growth, $g(x, H, E_a)$. To model height growth requires that we translate mass production into height increment, accounting for the costs of building new tissues, allocation to reproduction, and architectural layout. Using the chain rule, height growth can be decomposed into a product of physiologically relevant terms (Falster *et al.*, 2011),

$$g(x, H, E_a) = \frac{dH}{dt} = \frac{dH}{dA_l} \times \frac{dA_l}{dM_a} \times \frac{dM_a}{dB} \times \frac{dB}{dt}. \quad (4)$$

The first factor, dH/dA_l , is the growth in plant height per unit growth in total leaf area – accounting for the architectural strategy of the plant. Some species tend to leaf out more than grow tall, while other species emphasise vertical extension.

The second factor, dA_l/dM_a , accounts for the marginal cost of deploying an additional unit of leaf area, including construction of the leaf itself and various support structures. As such, dA_l/dM_a can itself be expressed as a sum of construction costs per unit leaf area,

$$\frac{dA_l}{dM_a} = \left(\frac{dM_l}{dA_l} + \frac{dM_s}{dA_l} + \frac{dM_b}{dA_l} + \frac{dM_r}{dA_l} \right)^{-1}. \quad (5)$$

The third factor, dM_a/dM_b , is the fraction of net biomass production (Eq. 3) that is allocated to growth rather than reproduction or storage. In the default physiological model, we let this growth fraction decrease with height according to the function

$$\frac{dM_a}{dB}(H) = 1 - \frac{\alpha_{f1}}{1 + \exp(\alpha_{f2}(1 - H/H_{\text{mat}}))}, \quad (6)$$

where α_{f1} is the maximum possible allocation (0 – 1) and α_{f2} determines the sharpness of the transition (Falster *et al.*, 2011).

5 DIAMETER GROWTH

Analogously, the growth in basal area A_{st} can be expressed as the sum of growth in sapwood, bark, and heartwood areas (A_s , A_b , and A_h , respectively),

$$\frac{dA_{st}}{dt} = \frac{dA_b}{dt} + \frac{dA_s}{dt} + \frac{dA_h}{dt}.$$

Applying the chain rule, we derive an equation for basal area growth that contains many of the same elements as Eq. 4,

$$\frac{dA_{st}}{dt} = \left(\frac{dA_s}{dA_l} + \frac{dA_b}{dA_l} \right) \times \frac{dA_l}{dM_a} \times \frac{dM_a}{dB} \times \frac{dB}{dt} + \frac{dA_h}{dt}. \quad (7)$$

Diameter growth is then given by the geometric relationship between stem diameter D and A_{st} ,

$$\frac{dD}{dt} = \sqrt{\frac{\pi}{A_{st}}} \frac{dA_{st}}{dt}. \quad (8)$$

6 FUNCTIONAL-BALANCE MODEL FOR ALLOCATION

Here we describe an allometric model linking to a plant's height its various other size dimensions required by most ecologically realistic vegetation models (i.e., the masses of leaves, sapwood, bark, and fine roots). This approach allows us to track only the plant's height, while still accounting for the mass needs to build leaves, roots, and stems. The growth rates of various tissues can then also be derived (Table 2).

6.1 Leaf area

Based on empirically observed allometry, we assume an allometric power-law scaling relationship between the accumulated leaf area of a plant and its height,

$$A_l = \alpha_{11} H^{\alpha_{12}}. \quad (9)$$

Note that this scaling relationship is inverted relative to that in [Falster *et al.* \(2011\)](#).

6.2 Vertical distribution of leaf area

We follow the model of [Yokozawa & Hara \(1995\)](#) describing the vertical distribution of leaf area within the crowns of individual plants. This model can account for a variety of canopy profiles through a single parameter η . Setting $\eta = 1$ results in a conical canopy, as seen in many conifers, while higher values, e.g., $\eta = 12$, give a top-heavy canopy profile similar to those seen among angiosperms. We denote by $A_{s,z}$ the sapwood area at height z , by $q(z, H)$ the vertical distribution of leaf area of leaf area with respect to height z , and by $Q(z, H)$ the cumulative fraction of a plant's leaves above height z . As defined previously, A_s is the sapwood area at the base of the plant. Following [Yokozawa & Hara \(1995\)](#), we assume a relationship between $A_{s,z}$ and height such that

$$\frac{A_{s,z}}{A_s} = \left(1 - \left(\frac{z}{H} \right)^\eta \right)^2. \quad (10)$$

We also assume that each unit of leaf area is supported by a fixed area θ of sapwood (in agreement with the pipe model; [Shinozaki *et al.*, 1964](#)), so that the total canopy area of a plant

relates to its basal sapwood area A_s ,

$$A_s = \theta A_l. \quad (11)$$

The pipe model is assumed to hold within individual plants, as well as across plants of different size. It follows that

$$Q(z, H) = \left(1 - \left(\frac{z}{H}\right)^\eta\right)^2. \quad (12)$$

Differentiating with respect to z then yields a solution for the probability density of leaf area as a function of height,

$$q(z, H) = 2 \frac{\eta}{H} \left(1 - \left(\frac{z}{H}\right)^\eta\right) \left(\frac{z}{H}\right)^{\eta-1}. \quad (13)$$

6.3 Sapwood mass

Integrating $A_{s,z}$ yields the total mass of sapwood in a plant,

$$M_s = \rho \int_0^h A_{s,z} dz = \rho A_s H \eta_c, \quad (14)$$

where $\eta_c = 1 - \frac{2}{1+\eta} + \frac{1}{1+2\eta}$ (Yokozawa & Hara, 1995). Substituting from Eq. 11 into Eq. 14 then gives an expression for sapwood mass as a function of leaf area and height,

$$M_s = \rho \eta_c \theta A_l H. \quad (15)$$

6.4 Bark mass

Bark and phloem tissue are modelled using an analogue of the pipe model, leading to a similar equation as that for sapwood mass (Eq. 15). The cross-section area of bark per unit leaf area is assumed to be a constant fraction b of sapwood area per unit leaf area such that

$$M_b = \alpha_{b1} M_s. \quad (16)$$

6.5 Root mass

Also consistent with the pipe model, we assume a fixed ratio of root mass per unit leaf area,

$$M_r = \alpha_{r1} A_l. \quad (17)$$

Even though nitrogen and water uptake are not modelled explicitly, imposing a fixed ratio of root mass to leaf area ensures that approximate costs of root production are included in calculations of carbon budget.

7 SEED PRODUCTION

The rate of seed production, $f(x, H, E_a)$, is a direct function of the mass allocated to reproduction,

$$f(x, H, E_a) = \frac{\left(1 - \frac{dM_a}{dB}\right) \times \frac{dB}{dt}}{\omega + \alpha_{f3}}, \quad (18)$$

where ω is the mass of the seed and α_{f3} is the cost per seed of accessories, such as fruits, flowers, and dispersal structures. The function $\frac{dM_a}{dB}$ is the fraction of $\frac{dB}{dt}$ that is allocated to growth (from Eq. 6, while $1 - \frac{dM_a}{dB}$ gives the fraction allocated to reproduction).

8 MORTALITY

Instantaneous rates of plant mortality are given by the sum of a growth-independent and a growth-dependent rate (Falster *et al.*, 2011; Moorcroft, Hurtt & Pacala, 2001),

$$d(x, H, E_a) = d_I(x, H) + d_G(x, H, E_a). \quad (19)$$

The growth-independent rate is taken to be constant, independent of plant performance, but potentially varying with species traits. The growth-dependent rate is assumed to decline exponentially with the rate of mass production per unit leaf area,

$$d_G(x, H, E_a) = \alpha_{dG1} \exp(-\alpha_{dG3} X), \quad (20)$$

where $X = dB/dt/A_l$. This relationship allows for plants to increase in mortality as their growth rate approaches zero, while allowing for species to differ in the parameters α_{dG1} and α_{dG3} .

We also require a function $S_G(x', H_0, E_{a0})$ for plant survival through germination. For the demographic model to behave smoothly, $S_G(x', H_0, E_{a0})/g(x, H_0, E_{a0})$ should approach zero as $g(x, H_0, E_{a0})$ approaches zero. Following Falster *et al.* (2011), we use the function

$$S_G(x', H_0, E_{a0}) = \frac{1}{1 + X^2} \quad (21)$$

where $X = \alpha_{d0} \frac{A_l}{dB/dt}$ and α_{d0} is a constant. Eq. 21 is consistent with Eq. 20, as both cause survival to decline with mass production.

9 HYPER-PARAMETERISATION OF PHYSIOLOGICAL MODEL VIA TRAITS

The physiological model includes default values for all needed parameters (Table 3). Species are known to vary considerably in many of these parameters, such as ϕ , ρ , ν , and ω ; so by varying parameters one can account for species differences. When altering a parameter in the model, however, one must also consider whether there are trade-offs linking parameters.

PLANT allows for the hyper-parameterisation of the physiological model via plant functional traits: this enables simultaneous variation in multiple parameters in accordance with an assumed trade-off. In the default physiological model, we implement the relationships described below. For more details, see `make_FF16_hyperpar.R`.

9.1 Leaf mass per unit area

The trait leaf mass per unit area (LMA), denoted by ϕ , directly influences growth by changing dA_l/dM_a . In addition, we link ϕ to the rate of leaf turnover, based on a widely observed scaling relationship from Wright *et al.* (2004),

$$k_l = \beta_{kl1} \left(\frac{\phi}{\phi_0} \right)^{-\beta_{kl2}}.$$

This relationship is normalised around ϕ_0 , the global mean of ϕ . This allows us to vary β_{kl1} and β_{kl2} without displacing the relationship from the observed mean.

We also vary the mass-based leaf respiration rate so that it stays constant per unit leaf area and varies with LMA and NAREA, as empirically observed Wright *et al.* (2004),

$$r_l = \frac{\beta_{lf4} \nu}{\phi}.$$

9.2 Wood density

The trait wood density, denoted by ρ , directly influences growth by changing dA_I/dM_a . In addition, we link ρ to the rate of growth-independent mortality,

$$d_I = \beta_{dI1} \left(\frac{\rho}{\rho_0} \right)^{-\beta_{dI2}}.$$

In addition, ρ is assumed to influence the rate of sapwood turnover,

$$k_s = \beta_{ks1} \left(\frac{\rho}{\rho_0} \right)^{-\beta_{ks2}},$$

As for ϕ , these relationships are normalized around ρ_0 , the global mean of ρ .

The rate of sapwood respiration per unit volume is assumed to be constant, so sapwood respiration per unit mass varies as

$$r_r = \frac{\beta_{rs1}}{\rho}.$$

Similarly, the rate of bark respiration per unit mass varies as

$$r_b = \frac{\beta_{rb1}}{\rho},$$

with $\beta_{rb1} = 2\beta_{rs1}$.

9.3 Seed mass

Effects of the trait seed mass, denoted by ω , are naturally embedded in the equation determining fecundity (Eq. 18) and the initial height of seedlings. In addition, we let the accessory cost per seed be a linear function of seed size,

$$\alpha_{f3} = \beta_{f1}\omega,$$

as empirically observed (Henery & Westoby, 2001).

9.4 Nitrogen per leaf area

Photosynthesis per unit leaf area and respiration rates per unit leaf mass (or area) are assumed to vary with leaf nitrogen per unit area, ν . The calculation of respiration rates is already described above. To calculate the average annual photosynthesis for a leaf, we integrate the instantaneous rate per unit leaf area over the annual solar trajectory, using a rectangular-hyperbolic photosynthesis light response curve,

$$p(\nu, E) = \frac{1}{365d} \int_0^{365d} \frac{Y(t) + A_m - \sqrt{(Y(t) + A_m)^2 - 4\beta_{lf2}Y(t)A_m}}{2\beta_{lf2}} dt,$$

where

- $A_m = \nu \beta_{lf1}$ is the maximum photosynthetic capacity of the leaf,
- β_{lf2} is the curvature of the light response curve,
- $Y(t) = \beta_{lf3}I(t)$ is the initial yield of the light response curve, with β_{lf3} being the quantum yield parameter,

- $I(t) = k_1 I_0(t) E$ is the intensity of light on the leaf surface, and
- $I_0(t)$ is light incident on a surface perpendicular to the sun's rays directly above the canopy at time t .

The profile of $I_0(t)$ is given by a solar model adapted from [Ter Steege \(1997\)](#).

Values of $p(\nu, E)$ are calculated across a range of values of E , and then an expression of the form in Eq. 1 is fitted to extract the parameters α_{p1} and α_{p2} , such that these become functions of ν .

10 TABLES

TABLE 1: Key variables of the physiological model. For mass (M), respiration (r), and turnover (k) variables, subscripts refer to any of the following tissues : l = leaves, b = bark, s = sapwood, r = roots, a = all living tissue . For area A variables, subscripts refer to any of the following: l = leaves, st = total stem cross-section, ss = sapwood cross-section.

Symbol	Unit	Description
Plant construction		
x		Vector of traits for a species
H_0	m	Height of a seedling after germination
H	m	Height of a plant
B	kg	Biomass originating from parent plant
M_i	kg	Mass of tissue type i retained on plant
A_i	m ²	Surface area or area of cross-section of tissue type i
$q(z, H)$	m ⁻¹	Vertical distribution of leaf area for a plant with height H
$Q(z, H)$		Fraction of leaf area above height z for a plant with height H
Mass production		
p, \bar{p}	kg yr ⁻¹ m ⁻²	Photosynthetic rate per unit area
r_i	kg kg ⁻¹ yr ⁻¹	Respiration rate per unit mass of tissue type i
k_i	yr ⁻¹	Turnover rate for tissue type i
Environment		
a	yr ⁻¹	Patch age
E_a		Profile of canopy openness within a patch of age a
$E_a(z)$		Canopy openness at height z within a patch of age a
Demographic outcomes		
$g(x, H, E_a)$	m yr ⁻¹	Height growth rate of a plant with traits x and height H in the light environment E_a in a patch of age a
$f(x, H, E_a)$	yr ⁻¹	Seed production rate of a plant with traits x and height H in the light environment E_a in a patch of age a
$d(x, H, E_a)$	yr ⁻¹	Instantaneous mortality rate of a plant with traits x and height H in the light environment E_a in a patch of age a
$S_G(x, H_0, E_{a0})$		Probability that a seed germinates successfully

TABLE 2: Equations of an allometric growth model based on functional-balance assumptions. The key assumptions of the physiological model are listed in (a), under "Function". From these assumptions, allocation functions are derived for tissue areas and tissue masses (b). Also the growth rate of each tissue type can be expressed as a function of the growth rate of leaf area. For mass (M), respiration (r), and turnover (k) variables, subscripts denote different tissues: l = leaves, b = bark, s = sapwood, r = roots, a = all living tissue. For area A variables, subscripts denote: l = leaves, st = total stem cross-section, ss = sapwood cross-section.

Variable	Function	Allocation	Growth rate
(a) Assumed relationships with leaf area			
Height	$H = \alpha_{l1} A_l^{\alpha_{l2}}$	$\frac{dH}{dA_l} = \alpha_{l2} \alpha_{l1} A_l^{\alpha_{l2}-1}$	$\frac{dH}{dt} = \frac{dH}{dA_l} \frac{dA_l}{dt}$
Sapwood area	$A_s = \theta A_l$	$\frac{dA_s}{dA_l} = \theta$	$\frac{dA_s}{dt} = \frac{dA_s}{dA_l} \frac{dA_l}{dt}$
Bark area	$A_b = \alpha_{b1} \theta A_l$	$\frac{dA_b}{dA_l} = \alpha_{b1} \theta$	$\frac{dA_b}{dt} = \frac{dA_b}{dA_l} \frac{dA_l}{dt}$
(b) Derived equations for mass of tissue			
Leaf mass	$M_l = \phi A_l$	$\frac{dM_l}{dA_l} = \phi$	$\frac{dM_l}{dt} = \frac{dM_l}{dA_l} \frac{dA_l}{dt}$
Sapwood mass	$M_s = \rho \theta \eta_c A_l H$	$\frac{dM_s}{dA_l} = \rho \theta \eta_c (H + A_l \frac{dH}{dA_l})$	$\frac{dM_s}{dt} = \frac{dM_s}{dA_l} \frac{dA_l}{dt}$
Bark mass	$M_b = \alpha_{b1} \rho \theta \eta_c A_l H$	$\frac{dM_b}{dA_l} = \alpha_{b1} \rho \theta \eta_c (H + A_l \frac{dH}{dA_l})$	$\frac{dM_b}{dt} = \frac{dM_b}{dA_l} \frac{dA_l}{dt}$
Root mass	$M_r = \alpha_{r1} A_l$	$\frac{dM_r}{dA_l} = \alpha_{r1}$	$\frac{dM_r}{dt} = \frac{dM_r}{dA_l} \frac{dA_l}{dt}$

TABLE 3: Core model parameters

Description	Symbol	Units	Code	Value
Plant construction				
Crown-shape parameter	η	-	eta	12
Leaf mass per area	ϕ	kg m^{-2}	lma	0.1978791
Wood density	ρ	kg m^{-3}	rho	608
Sapwood area per leaf area	θ	-	theta	0.0002141786
Height-leaf area scaling, intercept	α_{l1}	m^{-1}	a_l1	5.44
Height-leaf area scaling, slope	α_{l2}	-	a_l2	0.306
Root mass per leaf area	α_{r1}	kg m^{-2}	a_r1	0.07
Ratio of bark area to sapwood area	α_{b1}	-	a_b1	0.17
Production				
Leaf photosynthesis per area	α_{p1}	$\text{mol yr}^{-1} \text{m}^{-2}$	a_p1	151.1778
Saturation of leaf photosynthesis per area	α_{p2}	-	a_p2	0.2047162
Yield, = fraction of carbon fixed converted into mass	α_y	-	a_y	0.7
Biomass per mol carbon	α_{bio}	kg mol^{-1}	a_bio	0.0245
Leaf respiration per mass	r_l	$\text{mol yr}^{-1} \text{kg}^{-1}$	r_l	198.4545
Fine-root respiration per mass	r_r	$\text{mol yr}^{-1} \text{kg}^{-1}$	r_r	217
Sapwood respiration per mass	r_s	$\text{mol yr}^{-1} \text{kg}^{-1}$	r_s	6.598684
Bark respiration per mass	r_b	$\text{mol yr}^{-1} \text{kg}^{-1}$	r_b	13.19737
Turnover rate for leaves	k_l	yr^{-1}	k_l	0.4565855
Turnover rate for sapwood	k_s	yr^{-1}	k_s	0.2
Turnover rate for bark	k_b	yr^{-1}	k_b	0.2
Turnover rate for fine roots	k_r	yr^{-1}	k_r	1
Fecundity				
Seed mass	ω	kg	omega	0.000038
Height at maturation	H_{mat}	m	hmat	16.59587
Maximum allocation to reproduction	α_{f1}	-	a_f1	1
Parameter determining rate of change in $r(x, m_l)$ around H_{mat}	α_{f2}	-	a_f2	50
Accessory cost per seed	α_{f3}	kg	a_f3	0.000114
Mortality				
Survival probability during dispersal	S_D	-	S_D	0.25
Parameter influencing survival through germination	α_{d0}	$\text{kg yr}^{-1} \text{m}^{-2}$	a_d0	0.1
Intrinsic or growth-independent mortality	d_l	yr^{-1}	d_I	0.01
Baseline rate for growth-related mortality	α_{dG1}	yr^{-1}	a_dG1	5.5
Risk coefficient for dry-mass production per unit leaf area in growth-related mortality	α_{dG2}	$\text{yr m}^2 \text{kg}^{-1}$	a_dG2	20

TABLE 4: Parameters for hyper-parameterisation

Description	Symbol	Units	Code	Value
Leaf turnover				
Average leaf mass per area	ϕ_0	kg m^{-2}	lma_0	0.1978791
Rate of leaf turnover at ϕ_0	β_{kl1}	yr^{-1}	B_kl1	0.4565855
Scaling slope for ϕ in leaf turnover	β_{kl2}	-	B_kl2	1.71
Sapwood turnover				
Average wood density	ρ_0	kg m^{-3}	rho_0	608
Rate of sapwood turnover at ρ_0	β_{ks1}	yr^{-1}	B_ks1	0.2
Scaling slope for ρ in sapwood turnover	β_{ks2}	-	B_ks2	0
Growth independent mortality				
Rate of instantaneous mortality at ρ_0	β_{dl1}	yr^{-1}	B_dI1	0.01
Scaling slope for wood density in intrinsic mortality	β_{dl2}	-	B_dI2	0
Photosynthesis				
Nitrogen per leaf area	ν_0	kg m^{-2}	narea_0	0.00187
Potential CO ₂ photosynthesis per unit nitrogen	β_{lf1}	$\text{mol kg}^{-1} \text{d}^{-1}$	B_lf1	442.4318
Curvature of light response curve	β_{lf2}	-	B_lf2	0.5
Quantum yield of leaf photosynthesis (CO ₂ per unit PAR)	β_{lf3}	-	B_lf3	0.04
Respiration				
CO ₂ respiration per unit leaf nitrogen	β_{lf4}	$\text{mol yr}^{-1} \text{m}^{-3}$	B_lf4	21000
CO ₂ respiration per unit sapwood volume	β_{rs1}	$\text{mol yr}^{-1} \text{m}^{-3}$	B_rs1	4012
CO ₂ respiration per unit bark volume	β_{rb1}	$\text{mol kg}^{-1} \text{yr}^{-1}$	B_rb1	8024
Reproduction				
Cost of seed accessories per unit seed mass	β_{f1}	-	B_f1	3

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