CASSIA Instruction Booklet

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Contents

1 What is the CASSIA model?

NOTE: ***A lot of this material is the same as in the documentation for the package, and this is updated simultaneously with the documentation. However there is a greater depth here on the theoretical side and no inclusion of the code for each function, after the initial use of the model section with more examples and the assumptions explained more clearly than could be possible in the small help functions of the package.***

1.1 Introduction

CASSIA model is an intra-annual growth model for an individual tree in boreal conditions. Seasonal organ level cell growth is modelled, as well as sugar and water when the appropriate settings are chosen. Further details for the individual functions can be found with the functions themselves.

The main mathematical structure and equations are found in Schiestl-Aalto et al. [2015] where the science behind this model as well as the basic principle and structure are clearly explained. The variable links in the papers and the model are written in the vignette section of this package. These equations will be added to this instruction booklet, but are currently reported in later publications listed below. This package also has newer developments not yet published in papers such as a sugar internal allocation model and more detailed xylogenesis.

The package is available from GitHub: https://github.com/josimms/CASSIA

1.1.1 Git and GitHub resources

https://docs.github.com/en
https://docs.github.com/en/get-started/quickstart/hello-world

1.2 Coding plan

The model is maintained both in R and in C++. The C++ model runs quicker, but R is an easier language to use.

Currently a C++ version of the code is under development, which is currently being calibrated. The C++ version of the model changes the running time of the model from 0.397 seconds to 0.006, so is useful for calibrations, but not all subfunctions have been translated. Currently the basic model and the sugar allocation model are the ones that are working. Xylogenesis and water functions will soon be added (email Joanna if needed quicker). In 2024 a soil, mycorrhizal growth and photosynthesis model are being integrated.

1.3 R and C++ resources

RStudio: https://education.rstudio.com/learn/beginner/
R: https://www.codecademy.com/learn/learn-r
C++: https://www.codecademy.com/learn/learn-c-plus-plus

2 CASSIA

2.1 Basic Model

Model Lowdown: CASSIA.

Model type: Carbon based growth model
Inputs: Temperature (air, soil), soil water content, photosynthesis
Scope: Tree level (with categorisation and cell level growth)
Timestep: Daily
Reference: Schiestl-Aalto et al. [2015, 2019]

NOTE: Please check the references to understand the full structure of the CASSIA model - equations will be added here when water dependencies are added (again email Joanna if these are needed sooner).

2.2 Sugar Model

CASSIA includes an organ level internal sugar model based on the logic from Sperling et al. [2019], which predicts the bloom dates of almond trees by considering that bloom happens when the sugar level drops beyond a certain threshold. The sugar level is controlled by enzymes that convert sugar to starch. The enzyme activity is affected by the amount of enzymes and temperature. Plant production of enzymes is also generated by the difference between current sugar level and the "expected" sugar level (equilibrium point).

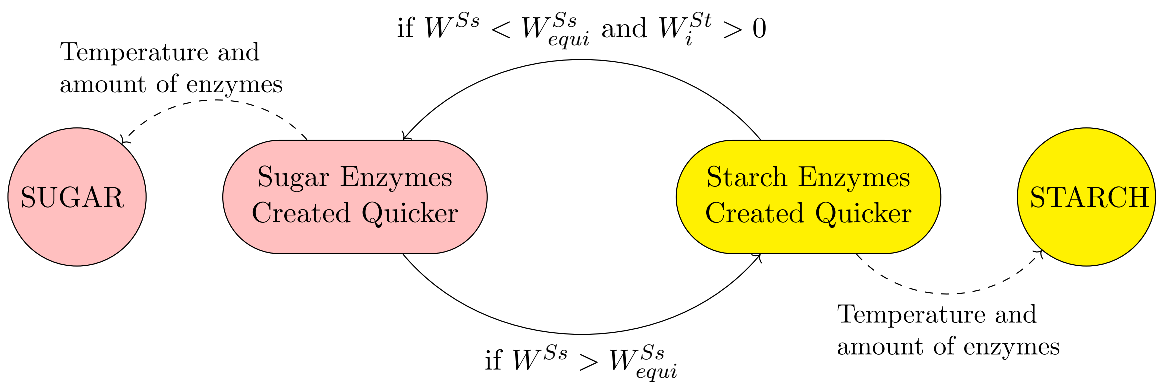

Figure 1: Figure to show the Sperling model process.

This is mathematically represented by;

$$
\begin{aligned}
&W_i^{Ss} > W_{equi,i}^{Ss}: \\
&\qquad \begin{cases} \frac{dD_i^{Ss}}{dt} = \lambda_i D_i^{Ss} + \delta_i \\ \frac{dD_i^{St}}{dt} = \lambda_i D_i^{St} \end{cases} \\
&W_i^{Ss} < W_{equi,i}^{Ss} \text{ and } W_i^{St} > 0: \\
&\qquad \begin{cases} \frac{dD_i^{Ss}}{dt} = \lambda_i D_i^{Ss} \\ \frac{dD_i^{Sd}}{dt} = \lambda_i D_i^{St} + \delta_i \end{cases}
\end{aligned} \tag{1}
$$

$$K_i^{St}(T, D^{St}) = D^{St} e^{F^{St} T} \tag{2}$$

$$K_i^{Ss}(T, D^{Ss}) = D^{Ss} e^{F^{Ss} T} \tag{3}$$

$$Q_i(W^{Ss}) = 0.004211 \rho_i (-K_i^{St}(T, A_i^{St}) + K_i^{Ss}(T, A_i^{Ss})) \tag{4}$$

Where W is the amount of sugar, Q is the transfer of sugar to starch, Ss is sugar and St is starch, K is the synthesis of of sugar or starch dependent on temperature and amount of relevant enzymes, D is the amount of enzymes, δ, λ, F are all parameters that control the enzymatic behaviour and amount, T is temperature and ρ is the organ density. i determines the organ.

Emergency supplies of sugar – when the organ's sugar concentration is less than a threshold L_i – is from the starch storage and is released by $E(W_i^{Ss}, W_i^{St})$ seen in (5).

$$E\left(W^{Ss}, W^{St}\right) = \begin{cases} \min\left[\max\left[\frac{L_i - W_i^{Ss}}{\tau}, 0\right], W_i^{St}\right] & W_i^{St} \geq 0 \\ 0 & \text{else} \end{cases} \tag{5}$$

2.2.1 Allocation Original

Sugar moves between the organs via a concentration-based model seen in Figure 1. Between each organ and the phloem, there is a diffusion-based relationship [Dietze et al., 2014] seen in Figure 2.

$$W_{i,j}^{\text{allocation}} = \frac{W_i^{\text{all}} B_j - W_j^{\text{all}} B_i}{q_{i,j} B_i B_j} \tag{6}$$

Where $q_{i,j}$ is a fitted parameter to represent both a resistance in the system as well as incorporating the normal concentration difference. This means the concentration is the driver as opposed to the magnitude difference. This is updated each iteration, where i is the sugar origin organ, and j, is the destination organ. $W^{\text{all}} = W^{\text{Ss}} + W^{\text{St}}$ is the amount of carbon (kg dw-1).

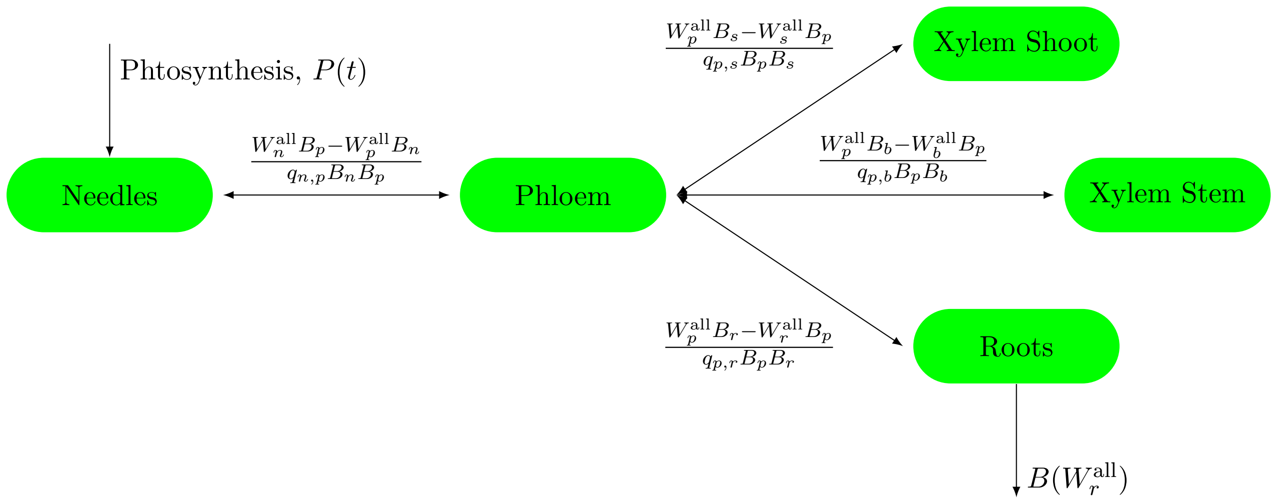

Figure 2: Figure to show the sugar transport of the model

$G(t)$ is growth associated with that organ and $R(t)$ is both growth and maintenance respiration associated with the organ. Growth and respiration are calculated to be the maximum possible growth [Schiestl-Aalto et al., 2015] and then multiplied by a scaling of the total storage of sugar and starch (f). α, W^{ala} and h are fitted parameters.

$$f(W_i^{all}) = \max\left[0, \min\left[1, h_i\left(1 - \frac{1}{e^{\alpha_i\left(W_i^{all} - W_i^{ala}\right)}}\right)\right]\right] \tag{7}$$

There are two organ-specific processes, one is photosynthesis, which is calculated in a different model and then used as an input to CASSIA. The other is belowground allocation. This is represented by

$$B(W_r^{all}) = \min(\max(W_r^{all} - \text{limit}, 0), W_r^{Ss}) \tag{8}$$

2.2.2 Allocation Alternatives

1. Observed: Allocation affected by tree nitrogen content. e.g. if the nitrogen in the tree pool is greater than $N_{\min}$ then allocation parameters are altered by a multiplier to make the allocation to roots greater to allow for more mycorrhiza. Although this affect should be present in the trading model (in terms of more carbon being transferred from the tree when there is a deficit of nitrogen), it adds another dynamic to have the carbon be in the form of biomass rather than exudes.

2. Fitness function: max Biomass, daily level would allow interaction with the mycorrhiza. As the seasonal uptake is already in the growth section, I don't think that taking an annual approach would change the results too much, although I can check.

3. Fitness function: max N Uptake, daily level. Yearly function could make a difference here, so would be interesting to see if there is a difference in the optimisation here! Daily would allow for the trading to have more of an impact on the type of N uptake as well.

2.2.3 Sugar and Starch complete process

Therefore, sugar and starch transfer is calculated via:

$$\frac{dW^{Ss}}{dt} = \begin{cases} P + Q + E - f\,[G + R] - W^{\text{allocation}}_{n,p} & & \text{Needles} \\ \quad Q + E - f\,[G + R] - W^{\text{allocation}}_{p,s,b,r} + W^{\text{allocation}}_{n,p} & & \text{Phloem} \\ \quad Q + E - f\,[G + R] & + W^{\text{allocation}}_{p,b} & \text{Xylem, Shoot} \\ \quad Q + E - f\,[G + R] & + W^{\text{allocation}}_{p,s} & \text{Xylem, Stem} \\ \quad Q + E - f\,[G + R] & + W^{\text{allocation}}_{p,r} - B(W^{all}_r) & \text{Roots} \end{cases}$$

$$\frac{dW^{St}_i}{dt} = -Q - E$$

The timing of bud burst is determined by a factor W^{Ss}_{bud} which is close to the minimum possible sugar, when the total storage of sugar goes below this threshold the first day of bud growth begins. The model is run twice for each year, the first run is to find the bud date, and then the model is run again using this value for the bud date to calculate growth. These second run results are the final results of the model. The fact that the equilibrium point and the bud burst have to be defined is an obvious assumption and mean that the system isn't fully dynamic - although the point when the system would reach these hard limits is.

The symbols are defined in Table 1. When the model is calibrared the actual parameter values will be added. Both from literature and from the Bayesian calibration. When the parameters are calibrated, the uniform distribution was chosen due to a lack of prior knowledge.

Table 1: Table to define all of the symbols in the sugar model. TODO: units and values

Symbol	Function	Units (day-1)	Meaning
			Variable
W	Variable	kg C	Amount of of carbon in the organ indicated by the superscript
D	Variable	mg g-1	Amount of enzyme
T	Variable	Degrees C	Temperature, input to the model timeseries
			Process in the model
K	Process	mg g-1	Creation of sugar or starch
Q	Process	kg C	The Sperling model process amalgamated
$E(W^{Ss}, W^{St})$	Process	kg C	Emergency transfer when the sugar concentration is too low if there is enough starch to send an emergency transfer of starch.
$f(W_i^{all})$	Multiplier	0-1	Function between 0 and 1 which scales growth based on the carbohydrate reserves.
$F(W_r^{all})$	Process	kg C	Allocation to mycorrhiza
$R(t)$	Process	kg C	Respiration is worked out as in other CASSIA papers and includes growth and maintenance [Schiestl-Aalto et al., 2019]
$G(t)$	Process	kg C	Growth is worked out as in other CASSIA papers [Schiestl-Aalto et al., 2019]
			Index
Ss	Index		Sugar
St	Index		Starch
all	Index		Both sugar and starch summed
equi	Index		Equilibrium point of relevant variable derived from measurements
n, p, s, b, r	Index		As subscripts these represent all of the organs respectively; needles, phloem, xylem shoot, xylem stem and roots.
			Parameter
λ	Parameter	1e-4	Decay rate of enzymes
δ	Parameter	25e-6	Emzymic parameter
F	Parameter		$= log(Q10)/10$, $Q10$ for sugar synthesis and 1.8 for starch.
0.004211	Parameter		Scale factor from sugar concentration in mg g^{-1} to kg C to match the CASSIA units.
ρ	Parameter		density of organ
L	Parameter		Threshold for appropriate processes
W^{ala}	Parameter		lower bound for storage effects on growth
h	Parameter		Control of the sugar storage effects on growth
α	Parameter		Control of the sugar storage effects on growth
L_r^M	Parameter	kg C	Threshold for allocation to roots
W_{bud}^{Ss}	Parameter	kg C	Threshold of sugar concentration for spring awaken / bud burst
			Other
$P(t)$	Timeseries	kg C tree-1	Photosynthesis, timeseries input, calculated by the external model or PRELES depeding on the version of the model. Therefore, there is no dynamic effect on the daily photosynthesis input [Susiluoto et al., 2010].

2.3 Photosynthesis

The original CASSIA model used SPP to calculate photosynthesis, although PRELES has been used more lately. As this version of the model needs to consider the nitrogen effect on photosynthesis PRELES is integrated into the model and an extra multiplier function is added into the PRELES model (structure explained below). Furthermore, PRELES is originally a canopy level model, so the output of PRELES has been divided by the amount of trees in Hyyitälä (1010) to give an 'average tree" value. As the amount of trees changes in Hyytiälä, this could also be a variable in the future for Hyyiälä comparisons.

Model Lowdown: PRELES.

Model type: Photosynthesis model with a water balance
Inputs: Climate data, fAPAR
Scope: Stand level
Timestep: Daily
Reference: Mäkelä et al. [2008], Peltoniemi et al. [2015], Minunno et al. [2016]

The current PRELES structure for GPP generation is;

$$\mathrm{P} = \beta \cdot \phi \cdot f_{\mathrm{APAR}} \cdot f_{\mathrm{L}} \cdot f_{\mathrm{S}} \cdot \min\left(f_{\mathrm{D}}, f_{\mathrm{W,P}}\right) \cdot f_{\mathrm{CO_2},P} \tag{9}$$

Where GPP is first defined as the maximum possible under light interception (first two terms) and then down-scaled with daily multipliers for other weather conditions such as light (L), temperature (T), VPD (D), water (W,P) and carbon dioxide (CO2). Therefore to have a nitrogen feedback effect PRELES should be modified to include a f_N multiplier. I suggest this function should be from McMURTRIE [1991]:

$$f_N(N) = \frac{\epsilon}{\epsilon_0} = \frac{\epsilon_0\left(1+\frac{N}{N_0}\right) - \sqrt{\left(\epsilon_0\left(1+\frac{N}{N_0}\right)\right)^2 - 4\theta\epsilon_0^2\frac{N}{N_0}}}{2\theta\epsilon_0} \tag{10}$$

Key factors:

- To get the function to be between 0 and 1 divide ϵ with ϵ_0 (the point at the asymptote). Currently N limits at the average needle N concentration (9.1).
- CASSIA used to generate the fAPAR as in Tian et al. [2021]
- When combining CASSIA and PRELES in this way, N is directly limiting photosynthesis, but there are no N controls in CASSIA so growth is only limited indirectly apart from diameter which directly uses GPP.

Calibration data:

- Peltoniemi

- Kainulainen and Holopainen [2002]

Table 2: McMurtrie: table of symbols

Symbol	Function in the system	Units	Meaning
			Variable
N	Variable	Day	Nitrogen
			Parameter
N_0	Parameter	mg g-1	Parameter characterising dependence of ϵ on $[N]$
e_0	Parameter	g MJ-1	Light utilisation coefficient at high $[N]$
θ	Parameter		Curvature parameter of relationship pf ϵ to $[N]$

3 Respiration

TODO: add the respiration function here from Ryhti! [Ryhti et al., 2021, 2022]

4 Soil Functions

The extended model structure is shown in Figure 3. The equations are then stated afterwords according to the figure's sections.

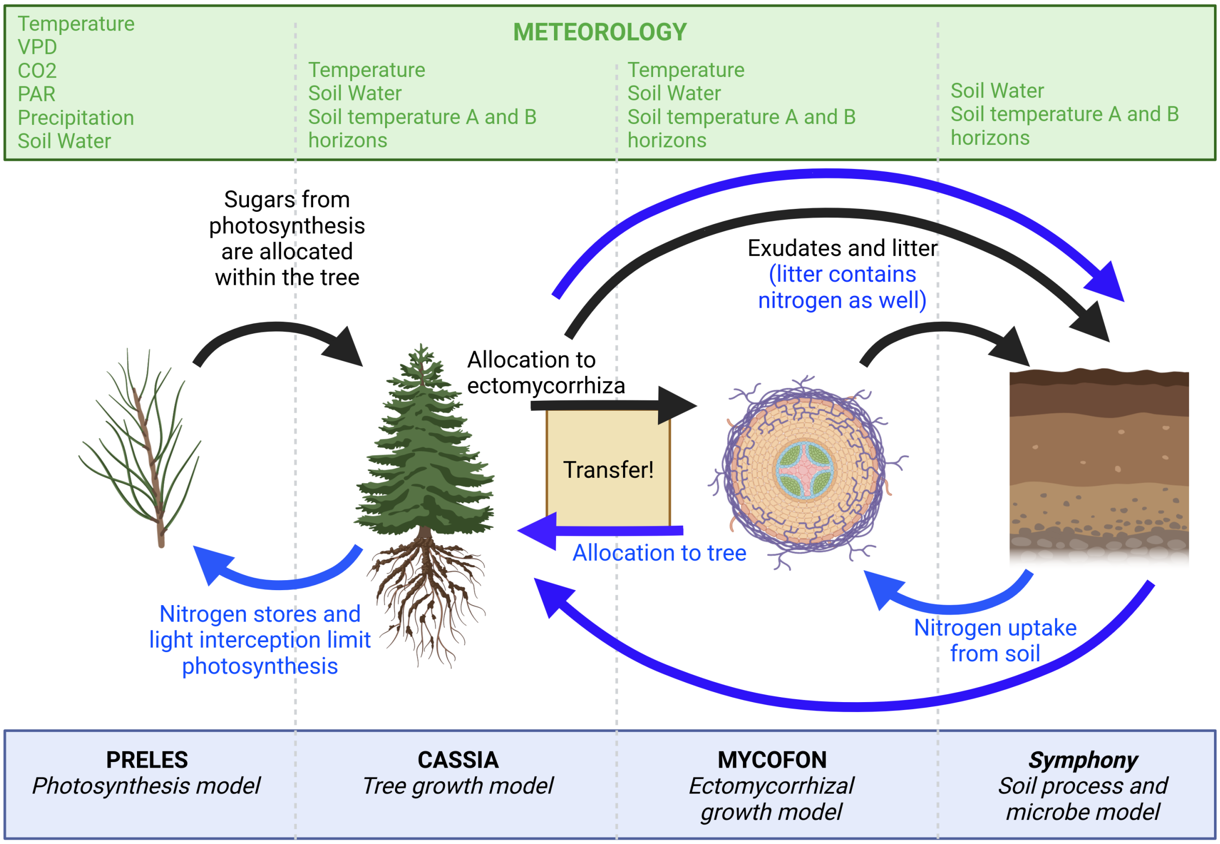

Figure 3: Figure to show the model process. Arrows show the most important inputs to the separate modules in terms of this question. Created with BioRender.com

Assumption:

- No root competition - big problem in a boreal forest! Hyyitälä (the main site in this calibration / model) specifically has been shown to have intense competition [Ryhti et al., 2022]
- As in Ekblad et al. [2013] assume that the seasonality effect is produced by different parts of the model (N, C inputs and growth)
- The mycorrhiza should be reflective of one tree as there is only C input from one tree - this should naturally limit the growth
- Although Symphony is based on grassland originally, I think the model is general enough for me to be able to apply it to forests (with careful parameterisation), although technically it is thinking about other mycorrhizal species [Adamczyk et al., 2019]

- One nitrogen pool for the whole plant - this nitrogen affects the photosynthetic effect, but is not specifically leaf nitrogen

- No spacial considerations in the nitrogen patches. As mycorrhiza and plant roots are observed to create "patches" [Brandes et al., 1998], we can assume that they detect and uptake the nitrogen that is closely available to them and thus they get an average uptake of high and low nitrogen patches. The problem comes when data collecting. The value for the N:C ratio needs to be taken from lots of different locations to make sure that the average is representative of the entire area.

- All nitrogen uptake should be considered - organic, nitrate and ammonium - as they form a significant part of nitrogen uptake in the plant [Wallenda and Read, 1999, Näsholm et al., 2009]

4.1 Uptake Functions

4.1.1 Nitrogen uptake

The organic uptake of N is currently controlled by considering the maximum possible uptake and then this is downscaled with environment dependent functions, taking a value between 0 and 1. These functions take the same logic, but not the same form as the PRELES equations.

$$u(N) = \frac{kN^8}{N_{limit}^8 + N^8} \tag{11}$$

$$f_T(T) = \begin{cases} \frac{T+20}{55} & T > 0 \\ 0 & T \leq 0 \end{cases} \tag{12}$$

$$f_{SWC}(SWC) = \frac{SWC^8}{0.3^8 + SWC^8} \tag{13}$$

$$u_{actual} = f_T(T) f_{SWC}(SWC) u(N) \tag{14}$$

Where fs are the environmental modification functions and $f \in [0, 1]$, $u()$ is the uptake. In equation 11, N is the concentration of a form of nitrogen, N_{limit} and k are parameters to control the uptake. Equation 12 controls the temperature response, where T is the temperature, 20 and 55 are parameters to control the uptake (non-fitted, will change with calibration). Finally the water effect is controlled by Equation 13, where SWC is soil water content and 0.3 is a parameter (will change with calibration). Equation 14 is the final nitrogen uptake effect. The parameters are dependant on the type of nitrogen.

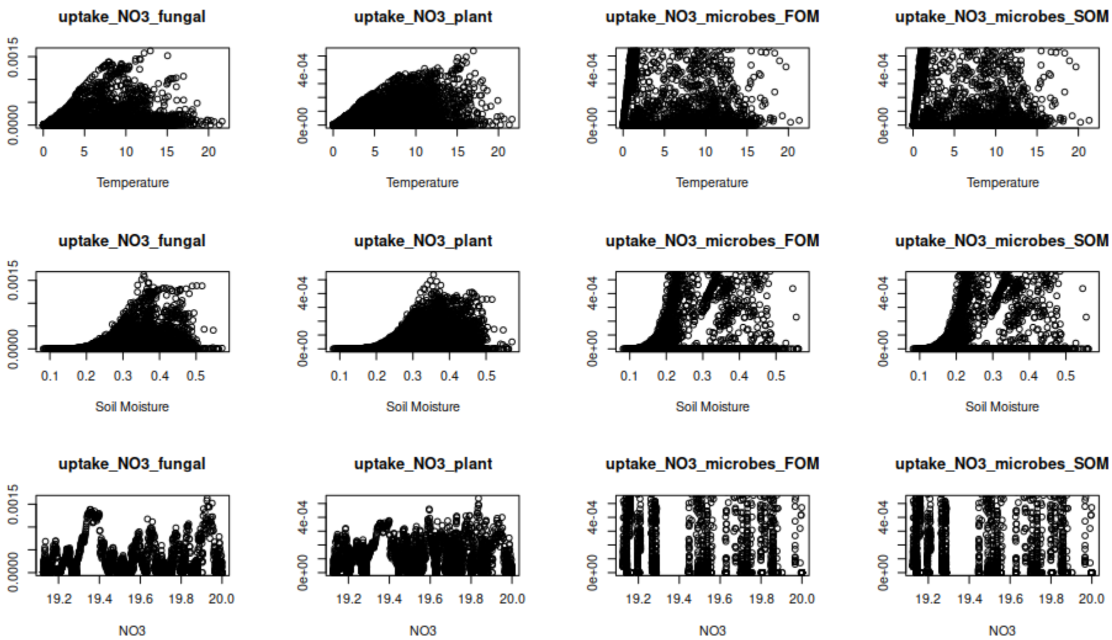

Figure 4: Figure to show the results of the uptake equation with respect to these environmental variables when the simulations are run for a few different years. Note the model is yet to be calibrated so the scales are not sensible.

4.1.2 Microbe Carbon Uptake

This is the carbon uptake of the mycorrhiza and other microbes in the soil. Current version of the model only has microbial uptake. This uptake is formed using the same logic as the nitrogen uptake. The carbon uptake is in the form of organic compounds, although considered in kg C in the model.

$$u(C) = \frac{kC^8}{C_{\text{limit}}^8 + C^8} \tag{15}$$

$$f_T(T) = \begin{cases} \frac{T+20}{55} & T > 0 \\ 0 & T \leq 0 \end{cases} \tag{16}$$

$$f_{SWC}(SWC) = \frac{SWC^8}{0.3^8 + SWC^8} \tag{17}$$

$$u_{actual} = f_T(T) f_{SWC}(SWC) u(C) \tag{18}$$

4.1.3 Plant N Uptake

This function is for the soil to root uptake only. This function uses the nitrogen uptake functions for each of the individual types of N compiled for the plant. The demand is calculated by the decision function, then used to scale the maximum uptake Section 4.2.1. Although demand is currently 1 for all decision functions included until the code works better and strategies have been chosen

that reflect the demand being 1 [Meyer et al., 2010, Franklin et al., 2014]. Eventually, the demand should be inversely proportional to the concentration of the desired nutrient in each organism. The nitrogen transferred to the root is a combination of all of the uptake functions, with the NO3 nitrogen uptake updated with a NH4 modifier. NH4, NO3 and FOM are the amounts in the soil. T is temperature in the soil B horizon and then SWC is the soil water content. For $f(NH4)$, a and b are fitted parameters and the function gives a value between 0 and 1. m is the ratio of mycorrhized roots.
Original formulation:

$$f(NH4) = \frac{aNH4^8}{NH4^8 + b^8} \tag{19}$$

$$\begin{aligned} \text{N to root} =& (1-m) \cdot \text{ demand (plant N amount)} \cdot [u_{organic}(FOM, T, SWC) \\ & + u_{NH4}(NH4, T, SWC) + f(NH4) u_{NO3}(NO3, T, SWC)] \end{aligned} \tag{20}$$

New formulation: (to be added to code)

$$\text{Allocation factor for roots} = \text{demand (plant N amount)} \tag{21}$$

$$\begin{aligned} \text{N to root} =& (1-m) \cdot [u_{organic}(FOM, T, SWC) \\ & + u_{NH4}(NH4, T, SWC) + f(NH4) u_{NO3}(NO3, T, SWC)] \end{aligned} \tag{22}$$

Table 3: Uptake functions

Symbol	Function in the system	Units	Meaning
			Variable
N	Variable	kg N	Nitrogen
$NH4$	Variable	kg N	NH4 pool in soil
$NO3$	Variable	kg N	NO3 pool in soil
FOM	Variable	kg N	FOM pool in soil
C	Variable	kg C	Carbon
T	Variable	degree C	Temperature
SWC	Variable	%	Soil water content
m	Variable	0-1	Amount of roots mycorrhized, will eventually by a moving value as in Equation 46
			Parameter
N_{limit}	Parameter	kg N	Parameter that controls when the switch in the uptake is in terms of the N limitations
k	Parameter		Parameter to control the nitrogen
0.3	Parameter	%	Parameter that controls when the switch in the uptake is in terms of SWC
20, 55	Parameter		Parameters controlling the uptake of nitrogen in terms of temperature

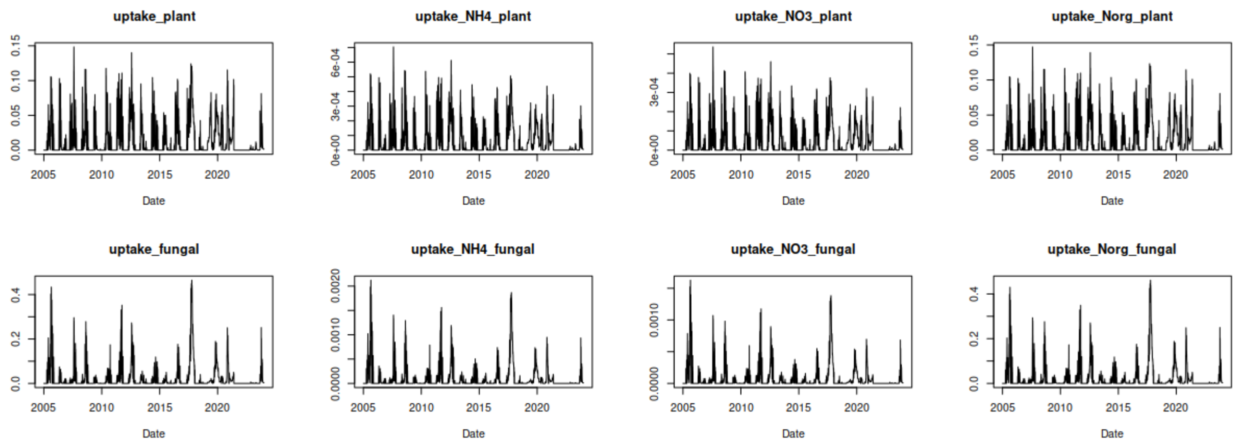

Figure 5: The uptake of nitrogen over the years 2005 to 2023 for the plant and mycorrhiza. Note the model is yet to be calibrated so the scales are not sensible.

Assumptions:

- Almost the same uptake priorities for all of the organisms (trees and mycorrhiza), similar to [Marschner et al., 1991]
- Mineral and organic uptake of N are in parallel due to the fact that when the N forms are found in a mixture the amino acid transfer doesn't decrease in proportion to the inorganic [Näsholm et al., 2009, Wallenda and Read, 1999] and as I could find relationships between NH_4^+ and NO_3^- uptake [Marschner et al., 1991].
- Currently ignoring mass flow: which is bad as Oyewole et al. [2017] notes that "the results suggest that mass flow, induced by transpiration, may be a strong driver for plant nitrogen acquisition in boreal forests by delivering higher amounts of amino acids and nitrate to plant roots and mycorrhizas." The water effect on growth will be added in the next iteration of the CASSIA model - so could be thought about at this stage. NOTE: Using the uptake as a reference from this paper anyway so the numbers are in the right range, but this could be a mistake if the processes are different to the ones in my model.

4.1.4 Mycorrhizal N Uptake

Like the plant uptake, this function uses the nitrogen uptake functions for each of the individual types of N compiled for the mycorrhiza. The demand is calculated by the decision function, although is currently 1 for all decision functions included [Meyer et al., 2010, Franklin et al., 2014]. Then the output is the N uptake of each of the types of nitrogen calculated in parallel [Wallenda and Read, 1999, Meyer et al., 2010] and then downscaled with the demand function.
Original formulation:

$$\begin{aligned}\text{N to mycorrhiza} = {} & \text{Mycorrhizal Biomass} \cdot \text{demand}\,(\text{mycorhiza C amount}) \cdot \\ & [u_{organic}(FOM, T, SWC) \\ & + u_{NH4}(NH4, T, SWC) + u_{NO3}(NO3, T, SWC)]\end{aligned} \tag{23}$$

New formulation: (to be added to code)

$$\begin{aligned}\text{Allocation factor for fungal} &= \text{demand}\,(\text{mycorhiza C amount}) &(24)\\ \text{N to root} &= \text{Mycorrhizal Biomass}\cdot[u_{organic}(FOM,T,SWC)\\ &\quad +u_{NH4}(NH4,T,SWC)+f(NH4)u_{NO3}(NO3,T,SWC)] &(25)\end{aligned}$$

Where u_{total} is the total mycorrhizal uptake. $u_{organic}$, u_{NO3} and u_{NH4}, are the mycorrhizal uptake of each of the forms of nitrogen. And demand is an input to the function calculated in the ectomycorrhiza decision function 4.2.2.

Assumption:

- There is no decomposition from ectomycorrhiza at the moment in the model!

4.1.5 Microbe Uptake

The microbe uptake holds half of the symphony model dynamics - the microbe side.
Original equations from Symphony paper

$$\begin{aligned}\text{Carbon Limitation} =& u_{\text{Norg}} C_{\text{Microbe}} &(26)\\ \text{Nitrogen Limitation} =& \frac{i(u_{\text{NH4}}+u_{\text{NO3}})+0.2\cdot(\text{N:C})_{\text{Microbes, opt}}C_{\text{Microbe}}}{(\text{N:C})_{\text{Litter}}-(\text{N:C})_{\text{Microbes, opt}}} &(27)\\ \text{Total N uptake} =& \max\{0,\min\{\text{Carbon Limitation},\text{Nitrogen Limitation}\}\} &(28)\\ \text{Total N uptaken} =& \text{Total N uptake}\cdot\Big(0.2\cdot(\text{N:C})_{\text{Microbes, opt}}C_{\text{Microbes}}+\\ & (\text{N:C})_{\text{Litter}}-(\text{N:C})_{\text{Microbes, opt}}\Big) &(29)\end{aligned}$$

Equations currently implemented

$$\begin{aligned}\text{Total C uptaken} &= C_{\text{Microbes}}\,[u_c(\text{Relevant C compartment})\\ &\quad +u_c(\text{Exudes})-(N:C)_{\text{opt}}+R(T_B)] &(30)\\ \text{Total } N_j \text{ Uptaken} &= C_{\text{microbe}}\left(u_{N_j}-(\text{N:C})_{\text{Microbes, opt}}\right)\left(\frac{N_j\text{ Pool}}{\text{Total Nitrogen}}\right) &(31)\\ & j\in[NH4,NO3,N_{\text{org}}]\end{aligned}$$

Where the uptake functions are the same as earlier, but calibrated for microbe uptake. i is immobilisation, 0.2 is a respiration parameter before the respiration is made dynamic, C, N are carbon and nitrogen respectively and $(N:C)$ are the nitrogen carbon ratios. j represents the NH4, NO3 and organic nitrogen pools. If the SOM decomposes don't get enough nitrogen from their own pools then they can uptake more from the FOM pool, as below.

$$\text{Extra FOM Uptake} = u_{\text{Organic}} \tag{32}$$

NOTE: the table of symbols will be added when the equations are finalised.

Assumptions:

- Carbon and nitrogen have the same units here - need to be careful that they are really made equivalent in the code.
- Exudates are uptaken by the microbes and not by the mycorrhiza. This allows for a limited priming effect.
- In terms of the carbon and nitrogen limitations missing here, they should be present in the soil model – namely immobilisation and growth.

4.2 Decisions: transfer between organisms of N and C

Model Lowdown: Optimisation and Game Theory - currently my own model.

Model type: Decision
Inputs: Max possible transfer of C and N
Scope: Just the transfer amounts of C and N between the organisms
Timestep: Daily
Reference: Meyer et al. [2010], Franklin et al. [2014]

There will be many different strategies here when the model is calibrated for the fixed ratios found in literature. Plans of these include, but are not limited to:

- Original MYCOFON dynamics [Meyer et al., 2010] *(Coded)*
- Näsholm et al. [2013] strategies *(Coded)*
- The trees / mycorrhiza want to optimise the system, not themselves [Baskaran et al., 2017]
- The trees / mycorrhiza want to optimise their growth (within this C, N and C:N)
- The trees / mycorrhiza want to optimise the a growth form (within this C, N and C:N) [Valverde-Barrantes et al., 2017, Bergmann et al., 2020]
- The trees / mycorrhiza want to optimise their limiting element uptake (within this C, N and C:N)
- The C surplus theory, that C is given proportionally to the overflow from the plant.
- Combinations of these strategies will make the system Game Theoretical

Some extra fun facts are:

- Mycorrhiza immobilise N during winter! [Heinonsalo et al., 2015] quoting [Kaiser et al., 2011] also miniralise N during winter in Kielland et al. [2006].

- If the plant is dying then the mycorrhiza will give resources to that plant because it will take less resources, not altruism [Sheldrake, 2020]

Reference values can come from Ingestad et al. [1986], Hobbie [2006], and behaviours from Johnson et al. [2006], Van't Padje et al. [2021], Högberg et al. [2010], Blaško et al. [2015].

4.2.1 Plant Decision

Currently two strategies are coded. These are derived from Näsholm et al. [2013] and the Mycofon model [Meyer et al., 2010]. The strategy of Mycofon gives a demand of 1 and and transfer amount stated in Equation 33.

$$\text{Transfer} = \max\{\text{allo}_{\text{max}} C_r, \text{allo}(C_r - (\text{root} : \text{mycorrhizal})_{\text{opt}}) - C_f\} \tag{33}$$

$$\text{allo}_{\text{max}} = \begin{cases} 1 - (1 - [\exp(-50 * N_r)]^3) & \text{for } N_r < 0.01 \\ 0.2 & \text{else} \end{cases} \tag{34}$$

$$\text{allo} = \begin{cases} \frac{N_{\text{allo}}}{N_r + N_{\text{allo}}} & \text{for } N_{\text{allo}} < 0.5 \\ 1 & \text{else} \end{cases} \tag{35}$$

Where C_r and C_f are the carbon in the roots and mycorrhiza respectively, $(\text{root} : \text{mycorrhizal})_{\text{opt}}$ is the optimal root mycorrhizal biomass ratio, N_r is the nitrogen in the roots and N_{allo} is the nitrogen allocated by the mycorrhiza.

The strategy of Näsholm gives a demand of 1 and and a transfer shown in Equation 36

$$\max\left[C^{\text{CASSIA}}_{\text{Allocated}}, 0.0\right] \tag{36}$$

where CASSIA is the maximum C allocation to the mycorrhiza calculated in CASSIA.

4.2.2 Mycorrhizal Decision

Currently two strategies are used. These are derived from Näsholm et al. [2013] and the Mycofon model [Meyer et al., 2010]. The strategy of Mycofon has a demand of 1 and a transfer function given as below 37.

$$\text{Transfer} = \max\left[N_f\left(1 - \frac{N_r}{C_r \cdot (N : C)_{\text{opt}}}\right), 0.0\right] \tag{37}$$

where N_f, N_r are the N in the mycorrhiza and root respectively, C_r is the C in the root and $(N : C)_{\text{opt}}$ is the optimal N:C ration in the root.

The strategy of Näsholm has a demand of 1 and a transfer of

$$\max\left[N_f - G_f, 0.0\right] \tag{38}$$

Where N and G are the nitrogen and growth of the mycorrhiza.
NOTE: add the table of symbols when the equations are finalised

4.3 Mycorrhizal Code

4.3.1 Mycorrhizal Growth

The growth of mycorrhiza is controlled currently by the same logic as CASSIA [Schiestl-Aalto et al., 2015], where the mycorrhizal growth is first calculated as possible growth based on temperature (Equation 42). Then the Non-Structural Carbon and Nitrogen form a limitation, as in Meyer et al. [2010] and Franklin et al. [2014]. NOTE: the timing of root growth is used for mycorrhiza temporarily for testing, parameterisation will soon follow.

$$g_F(t) = \begin{cases} 0 & T_a(t) < 0 \\ (1 - \exp(-\lambda M(t))(1 + \exp(-a(T_a(t) - b))^{-1} & T_a(t) \geq 0 \end{cases} \tag{39}$$

Where $g_R(t)$ is the first step in calculating the possible growth. λ is a parameter that decreases fine root growth during water deficiency, $M(t)$ is the soil moisture content, T_a is the temperature at soil depth a, finally a and b are fitted growth parameters.

$$f_F(t) = \begin{cases} 0 & s_i \leq 0 \\ \frac{1}{2}\left(\sin\left(\frac{2\pi}{s_i^c}\left(s_i(t) - \frac{s_i^c}{4}\right)\right) + 1\right) & 0 \leq s_i \leq s_i^c \\ 0 & s_i \geq s_i^c \end{cases} \tag{40}$$

$$G_F = \frac{L0}{\text{Mycelium Lifespan}} \cdot f_F(t) \cdot g_F(t) \tag{41}$$

$$\text{Potential Mycelium Growth} = \begin{cases} G_F & G_F > 0 \\ 0 & G_F \leq 0 \end{cases} \tag{42}$$

More information can be found in Schiestl-Aalto et al. [2015]! NOTE: the rest of the equations for the rest of the organs will be added to their respective sections at a later date. Now the rest of the equations not in CASSIA. The potential ectomycorrhizal growth is then limited by the stores of carbon and nitrogen.

$$f_C \approx \frac{C_{NS}^f}{C^f} \tag{43}$$

$$f_N \approx \frac{N_{NS}^f}{N^f} \tag{44}$$

$$\text{Mycelium Growth} = \text{Potential Mycelium Growth} \cdot f_C \cdot f_N \tag{45}$$

Assumptions:

- Need to assume a upper limit to the storage capacities and the effect that storage would have on growth.

4.3.2 Mycofon Balance

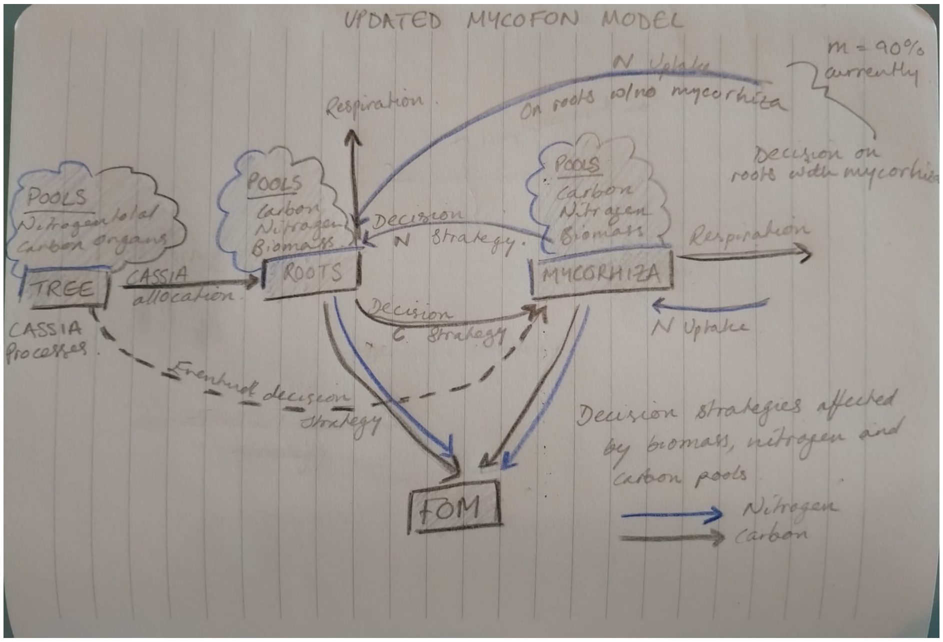

Figure 6: Flow chart for the updated MYOCFON model. Exact processes are represented by an arrow, more detailed processes are represented in the sections / flow diagrams referenced. The uptake rates etc. all have modifications by the environment, which are not written explicitly here.

Model Lowdown: MYCOFON Inspired.

Model type: Daily N and C cycling model, with a little bit of growth
Inputs: Temperature, N and C, biomass
Scope: Tree or stand level, depends on the inputs
Timestep: Daily
Reference: Version inspired by: Meyer et al. [2010]

The official MYCOFON model can be gotten by contacting Hongxing He (hongxing.he@gu.se). Due to the links with the Symphony and CASSIA models I have remade the MYCOFON model in C++ for this project.

The MYCOFON model (Meyer, 2010), with updates to include the uptake properties for three types of nitrogen as well as the decision functionality. This function brings together the C or N balance as in the original MYCOFON model, the decision functions for resource transfer, mycorrhizal growth and multiple N uptake functions. The equations in this function are below.

$$m = \frac{C_f}{B^{rf}_{opt} C^r} \tag{46}$$

$$\frac{dC^r}{dt} = \text{Growth from CASSIA} - (1-m)s^r C^r - m s^m C^r \tag{47}$$

$$\frac{dC^f}{dt} = g^f - s^{\text{mantle}} C^{\text{mantle}} - s^{\text{ERM}} C^{\text{ERM}} - R(T_{\text{B}}) C^f \tag{48}$$

$$\frac{dC^r_{\text{NonStruct}}}{dt} = C^{\text{CASSIA}}_{\text{Allocated}} - d^r(C^{\text{CASSIA}}) \tag{49}$$

$$\frac{dN^r_{\text{NonStruct}}}{dt} = d^f(C^f) + u^f C^f \tag{50}$$

$$\frac{dC^f_{\text{NonStruct}}}{dt} = d^r(C^{\text{CASSIA}}) - g^f \tag{51}$$

$$\frac{dN^f_{\text{NonStruct}}}{dt} = u^f C^f - g^f - d^f(C^f) \tag{52}$$

Table 4: Mycofon: table of symbols

Symbol	Function in the system	Units	Meaning
			Variable
t	Variable	Day	Time
N	Variable	kg N	Amount of nitrogen in specified organs
C	Variable	kg C	Amount of carbon in specified organs
B	Variable	kg C	Biomass
$C^{\text{CASSIA}}_{\text{Allocated}}$	Variable	kg C	The maximum amount of sugar that could be allocated from the CASSIA model
T	Variable / Input time-series	Degrees C	Temperature
m	Variable	0-1	Mycorrhized roots ratio. Although a formula is presented in the document, 0.9 is currently being used for the testing phase.
			Index
r, f	Index		Indexes for the roots and mycorrhiza respectively
opt	Index		Refers to the optimal value of the indicated variable
m, r	Index		Mycorrhized or non-mycorrhized roots
ERM	Index		Index referring to the extra-radical mycelium
Mantle	Index		Index referring to the mantle
B	Index		B soil horizon
			Parameter
s	Parameter	kg C day-1	Turnover
			Function
$d()$	Function	0-1	Decision function, gives the allocated amount of carbon or nitrogen depending on the direction of the function, see Section 4.2
R(Temperature)	Function	kg C	Respiration for indicated compartment, see Section 3
$g()$	Function	kg C	Growth function, for the mycorrhiza

Where N is nitrogen, C is carbon, r roots, f mycorrhiza, B biomass, opt is optimum. The uptake and decision functions are then calculated from the balance of the last iteration. Note that the plant decision requires the N allocated, so the mycorrhizal decision is calculated first in the code. Where, $C^{\text{CASSIA}}_{\text{Allocated}}$ is the carbon allocated from the CASSIA model, s is turnover, which is different for mycorrhized (m) and non-mycorrhized roots (r), T_B is temperature of the soil, $d()$ is decision (including exudes and transfer to mycorrhiza) and $R()$ is respiration, although for the roots this is calculated in CASSIA not here. Again, the growth process is currently handled in CASSIA so this is just the cumulative sum of the growth with the turnover negated. Growth for mycorrhiza is represented by $g()$.

Note: the m value is currently 0.9, although will be changed to this formulation when the model is fully tested.

Assumptions:

- Mycorrhiza is only taking organic and inorganic N, but not decomposing any itself - this is due to studies showing that although the decomposition is possible it is marginal [Meyer et al., 2010] - should I keep this assumption?
- As the root:mycorrhiza surface area ratio should control the mycorrhizal uptake of C from the tree, and in boreal systems there is a high colonisation rate [Smith and Read, 2010], therefore I assume that there is an optimal relationship one, this assumption could effect the underground dynamics, both in terms of the type of N as well as the colonisation dynamics

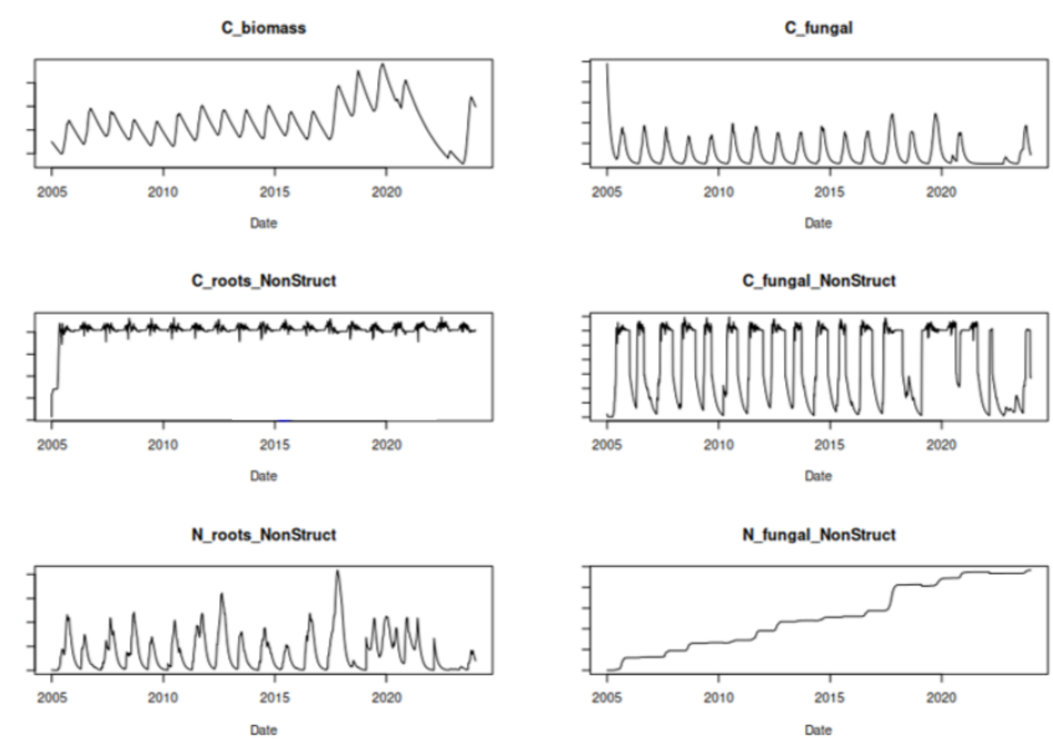

Figure 7: Figure to show the current growth in the model with the Näsholm et al. [2013] decision strategy.

4.4 Other Soil Processes: Symphony Model

Model Lowdown: SYMPHONY Inspired.

Model type: Soil C and N, Process-Organism Model [Perveen et al., 2014]
Inputs: Litter input, initial soil compartment amounts, temperature of air and soil
Scope: Microbial compartmentalisation of soil, with enzymatic N uptake
Timestep: Daily
Reference: Perveen et al. [2014]

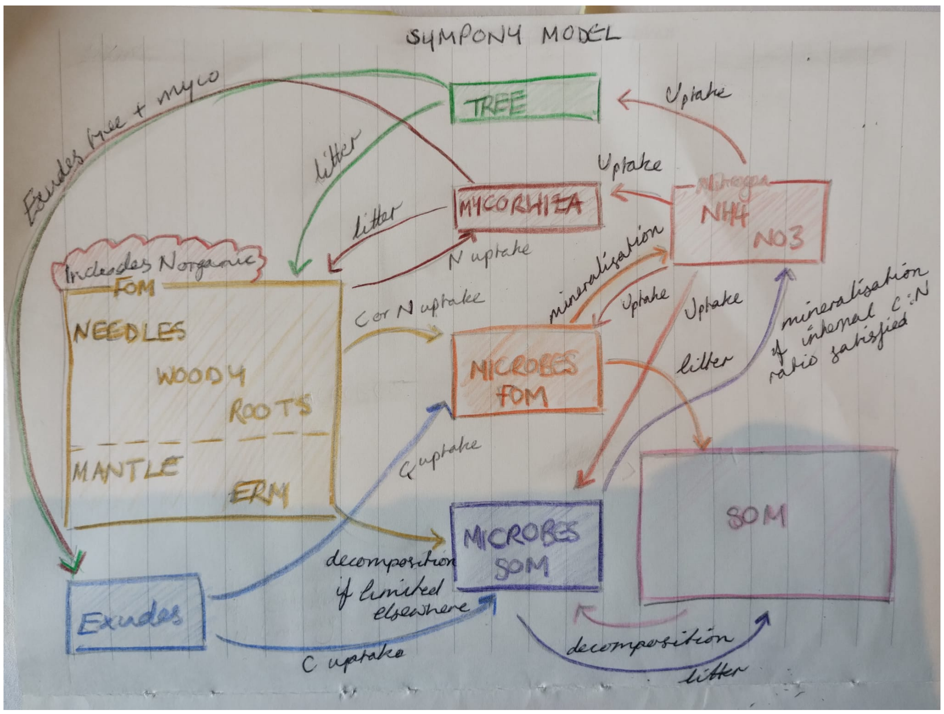

Figure 8: Temporary figure for the symphony model. Figure has all of the processes that are (hopefully) represented in the equations.

This model updates the soil states from CASSIA output (eventually).

$$
\begin{aligned}
\frac{dC_{\mathrm{SOM}}}{dt} =& - u_{\mathrm{C}}(C^{SOM})C^{\text{microbe, SOM}} + s\left(C^{\text{microbe, SOM}} + C^{\text{microbe, FOM}}\right) && (53)\\
C_{FOM} =& C^{needles}_{FOM} + C^{woody}_{FOM} + C^{roots}_{FOM} + C^{mantle}_{FOM} + C^{ERM}_{FOM} && (54)\\
N_{FOM} =& N^{needles}_{FOM}(N:C)^{needles} + N^{woody}_{FOM}(N:C)^{woody}\\
&+ N^{roots}_{FOM}(N:C)^{roots} + N^{mantle}_{FOM}(N:C)^{mantle} + N^{ERM}_{FOM}(N:C)^{ERM} && (55)\\
d_{total} =& u_C(C^{FOM})C^{microbes,SOM} + u_C(C^{FOM})C^{microbes,FOM} && (56)\\
\frac{dC^{needles}_{FOM}}{dt} =& L^{needles} - d_{total}\frac{C^{needles}_{FOM}}{C_{FOM}} && (57)\\
\frac{dC^{woody}_{FOM}}{dt} =& L^{woody} - d_{total}\frac{C^{woody}_{FOM}}{C_{FOM}} && (58)\\
\frac{dC^{roots}_{FOM}}{dt} =& L^{roots} - d_{total}\frac{C^{roots}_{FOM}}{C_{FOM}} && (59)\\
\frac{dC^{mantle}_{FOM}}{dt} =& L^{mantle} - d_{total}\frac{C^{mantle}_{FOM}}{C_{FOM}} && (60)\\
\frac{dC^{ERM}_{FOM}}{dt} =& L^{ERM} - d_{total}\frac{C^{ERM}_{FOM}}{C_{FOM}} && (61)
\end{aligned}
$$

Where C and N are carbon and nitrogen respectively, $(N : C)$ is the carbon nitrogen ratio of the indicated compartment, L is letter and the compartments are refereed to explicitly. FOM is fresh organic matter and SOM is soil organic matter. Where d is the decomposition, which is the uptake of both microbe pools, which is seen in more detail in Section 4.1.2. NOTE: the uptake is only from the aggregated FOM pool rather than each of the separate FOM pools and the decomposition from each pool is currently based on the size of the pool rather than the type of material. This will be changed to reflect the type of material.

$$
\begin{aligned}
\frac{dNH4}{dt} &= (\psi_{\mathrm{ims}} + \psi_{\mathrm{imf}})\frac{NH4}{NH4+NO3} - NH4^{p}_{used} - NH4^{f}_{used}\\
&- u_{NH4}C^{microbes,FOM} - u_{NH4}C^{microbes,SOM} && (62)\\
\frac{dNO3}{dt} &= (\psi_{\mathrm{ims}} + \psi_{\mathrm{imf}})\frac{NH4}{NH4+NO3} - NO3^{p}_{used} - NO3^{f}_{used}\\
&- u_{NO3}C^{microbes,FOM} - u_{NO3}C^{microbes,SOM} && (63)\\
\frac{dN^{FOM}}{dt} &= \text{Litter} - N^{FOM,p}_{used} - N^{FOM,f}_{used} - u_{Norg}C^{microbes,FOM} - u_{Norg}C^{microbes,SOM} && (64)\\
\frac{dN^{SOM}}{dt} &= \text{Microbe Litter} - u_{Norg}C^{microbes,SOM} && (65)
\end{aligned}
$$

NOTE: in the original symphony model there is leaching and fertilisation. These should be added, but currently not in the testing phase.

Where $NH4^{p}_{used}$ is the NH4 used for the plant, f represents the mycorrhizal uptake. This is an input to the function from the mycofon model. Next the microbe balance is considered.

$$\frac{dC^{\text{microbe, FOM}}}{dt} = u_{FOM} C^{\text{microbe, FOM}} - r(T_B) - s \tag{66}$$

$$\frac{dC^{\text{microbe, SOM}}}{dt} = u_{SOM} C^{\text{microbe, SOM}} - r(T_B) - s \tag{67}$$

Table 5: Symphony: table of symbols

Symbol	Function in the system	Units	Meaning
			Variable
t	Variable	Day	Time
N	Variable	kg N	Amount of nitrogen in specified organs
C	Variable	kg C	Amount of carbon in specified organs
T	Variable	Degrees C	Temperature
NH4	Variable	kg N	The amount of NH4 in the soil
NO3	Variable	kg N	The amount of NO3 in the soil
			Index
needles	Index		Subscript indicating the needles
woody	Index		Subscript indicating the woody biomass
roots	Index		Subscript indicating the roots
ERM	Index		Subscript indicating the extra-radical mycelium
mantle	Index		Subscript indicating the mantle
FOM	Index		Subscript indicating the fresh organic matter
SOM	Index		Subscript indicating the soil organic matter
p, f	Index		Subscripts indicating the plant and fungi respectively
B	Index		Soil B horison
NH4	Index		For processes related to NH4 pools
NO3	Index		For processes related to NO3 pools
Norg	Index		For processes related to Norg pools
microbe	Index		For processes related to microbes
			Parameter
s	Parameter	kg C day-1	Turnover
			Function
u	Function	kg N	Uptake for indicated compartment, see section 4.1.2

Assumptions and behaviours:

- Microbes assumed to be organisms that are not in symbiosis with the tree and that form competition for the nitrogen resources from the same pools as trees or ectomycorrhiza.
- Therefore the priming effect is still included as if there is more C in the soil then the decomposition will increase to a N storage bound value. The next day the N uptake can compensate for the N that was used the previous day with the C increase. This means that over time there would be a priming effect - but it is not instantaneous.
- Litter separated into sensible soil compartments
- Assumption that ammonium and nitrates are grouped - this could tell us if we have a mycorrhiza or bacteria dominated soil (TODO: reference)
- In the model there are no chemical processes - as the idea is to look at symbionts and microbes this make sense, but could be a bad assumption.
- Organic amount and C:N ratio dominate the decomposition rather than temperature, this is justified in literature [Kielland et al., 2006], but there is usually still some temperature effect.
- This model structure has (unintentionally) ended up quite similar to the CORPSE model [Sulman et al., 2014], although the N and two microbe dynamic is missing the CORPSE model has protected vs unprotected C dynamics which are similar to the SOM vs FOM formulation of the SYMOPHONY model. Could be a model to compare against if the parameters are not used.
- The respiration is not variable yet. Ryhti et al. [2022] data and models planning to be used for this.

Behaviours that should be eventually seen, added here as a reference!

Fig. 3 Net rates of (**a**) N mineralization, (**b**) nitrification, and (**c**) amino acid production over the growing season (June–October) across a primary successional sequence on the Tanana River floodplain, interior Alaska. Mean ± S.E., n = 3

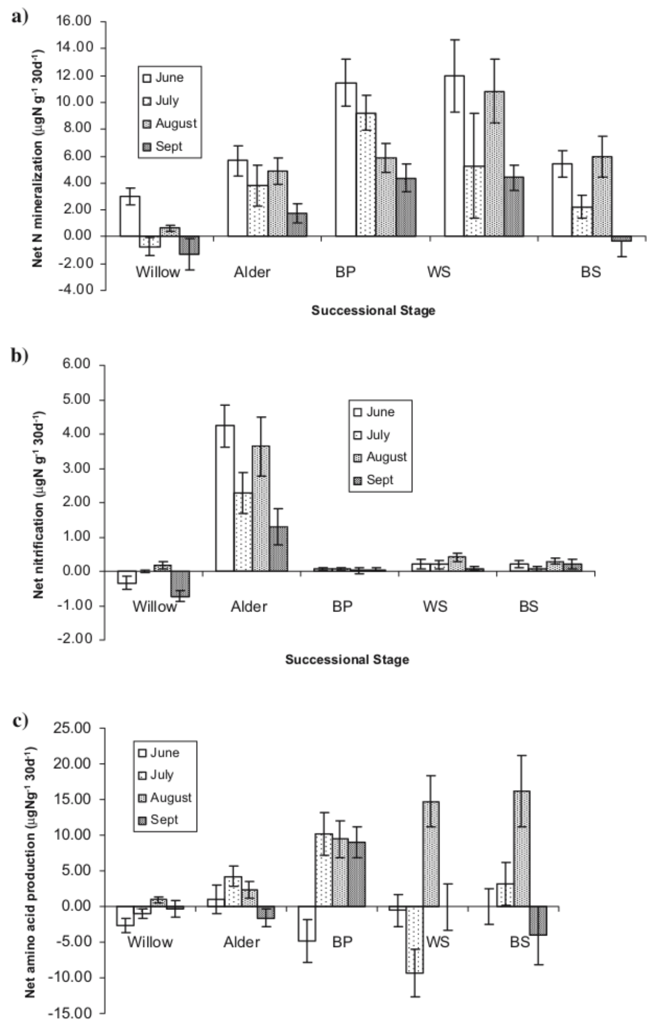

Figure 9: Kielland et al. [2006] Seasonal behaviours: flux

Fig. 6 Soil concentrations of (**a**) ammonium, (**b**) nitrate and (**c**) total free amino acids in over-winter incubations; initial concentrations in late autumn (October), mid-winter (January) and Spring (May). Mean ± S.E., n = 3

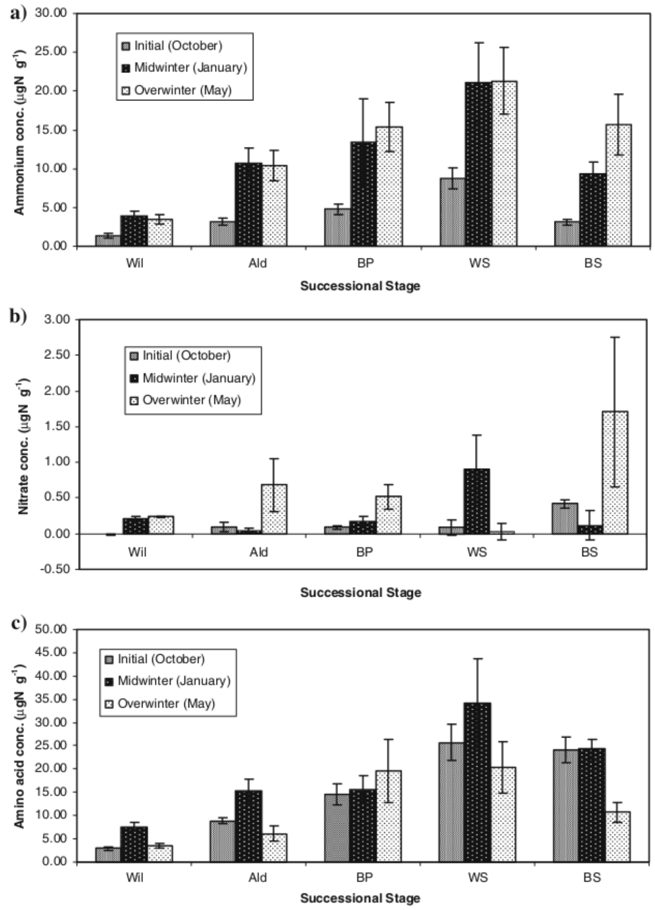

Figure 10: Kielland et al. [2006] Seasonal behaviours: winter production

5 Complete table of variables

TODO: update the following table with new equations.

Symbol	Function in the system	Units	Meaning
			Variable
W	Variable		Amount of of carbon in the organ indicated by the superscript
A	Variable		Amount of enzyme
T	Variable		Temperature, input to the model timeseries
t	Variable	Day	Time
N	Variable		Amount of nitrogen in specified organs
C	Variable		Amount of carbon in specified organs
B	Variable	kg C	Biomass

$C_{\text{Allocated}}^{\text{CASSIA}}$	Variable		The maximum amount of sugar that could be allocated from the CASSIA model
m	Variable	0-1	Mycorrhized roots ratio. Although a formula is presented in the document, 0.9 is currently being used for the testing phase.
NH4	Variable		The amount of NH4 in the soil
NO3	Variable		The amount of NO3 in the soil
			Index
r, f	Index		Indexes for the roots and mycorrhiza respectively
opt	Index		Refers to the optimal value of the indicated variable
m, r	Index		Mycorrhized or non-mycorrhized roots
ERM	Index		
Mantle	Index		
$needles$	Index		Subscript indicating the needles
$woody$	Index		Subscript indicating the woody biomass
$roots$	Index		Subscript indicating the roots
ERM	Index		Subscript indicating the extra-radical mycelium
$mantle$	Index		Subscript indicating the mantle
FOM	Index		Subscript indicating the fresh organic matter
SOM	Index		Subscript indicating the soil organic matter
p, f	Index		Subscripts indicating the plant and fungi respectively
B	Index		Soil B horison
NH4	Index		For processes related to NH4 pools
NO3	Index		For processes related to NO3 pools
Norg	Index		For processes related to Norg pools
microbe	Index		For processes related to microbes
			Parameter
λ	Parameter		Decay rate of enzymes
δ	Parameter		Emzymic parameter
A	Parameter		Rate of specified carbohydrate production
B	Parameter		$= log(Q10)/10$, $Q10$ for sugar synthesis and 1.8 for starch.
0.004211	Parameter		Scale factor from sugar concentration in mg g^{-1} to kg C to match the CASSIA units.
ρ	Parameter		density of organ
L	Parameter		Threshold for appropriate processes
W_{ala}	Parameter		lower bound for storage effects on growth
h	Parameter		Control of the sugar storage effects on growth
α	Parameter		Control of the sugar storage effects on growth
L_r^M	Parameter		Threshold for allocation to roots
W_b^{Ss}	Parameter		Threshold of sugar concentration for spring awaken / bud burst
s	Parameter	kg C day-1	Turnover
			Function
$d()$	Function	0-1	Decision function, gives the allocated amount of carbon or nitrogen depending on the direction of the function

u	Function		Uptake for indicated compartment, see section 4.1.2
R(Temperature)	Function		Respiration for indicated compartment, see section 3
$g()$	Function	kg C	Growth function, for the mycorrhiza
			Process
K	Process		Creation of sugar or starch
Q	Process		The Sperling model process amalgemated
$E(W^{Ss}, W^{St})$	Process		Emergency transfer when the sugar concentration is too low if there is enough starch to send an emergency transfer of starch.
$f(W_i^{all})$	Multiplier		Function between 0 and 1 which scales growth based on the carbohydrate reserves.
$B(W_r^{all})$	Process		Allocation to mycorrhiza
			Other
$P(t)$	Timeseries		Photosynthesis, timeseries input, calculated by the external model. Therefore, there is no dynamic effect on the daily photosynthesis input [Susiluoto et al., 2010].
$G(t)$	Input, state variable		Growth is worked out as in other CASSIA papers [Schiestl-Aalto et al., 2019]
$R(t)$	State variable		Respiration is worked out as in other CASSIA papers and includes growth and maintenance [Schiestl-Aalto et al., 2019]
D	Data		Data from observations at Hyytiälä
$CASSIA(\theta)$	Model		The CASSIA model with Hyytiälä inputs and certain parameters

6 Appexdix: Parameter Values in Code

6.1 repo_p Explanation

These parameters are from the paper Repola [2009] and is a multi-variable model fitted for Scots Pine and Norway Spruce in Finland.

Parameter Name	Parameter Value	Equations
b0.repo	-6.303	This model is from Repola [2009] and not explained further here. As the model is a mixed effect model, their parameters here do not have clear biological meanings, but are fixed effect parameters.
b1.repo	14.472	
b2.repo	-3.976	
uk.repo	0.109	
eki.repo	0.118	

Table 7: Explanation for the repo_p parameters built into the package.

6.2 common_p Explanation

Parameter Name (Name in Paper	Parameter value	Units	Comments and additional references
a (a)	0.185	Degree C^{-1}	Parameter of function g
b (b)	18.4	Degree C	Parameter of function g
TR0	0		Root temperature factor
abs_zero	273.15	K	Absolute zero temperature
b.s	4.14		Soil water potential and conductance
theetta.FC	0.62		Hölttä et al. 2009 Table 2
phi.e	-6.8×10^{-7}	MPa	Hölttä et al. 2009 Table 2, note psi.s should be psi.e
K.sat	24.5	mol m^{-1} s^{-1} MPa^{-1}	Hölttä et al 2009, Table 2
R.length	5300	m root m^{-2}	Index, Hölttä et al 2009
M.H2O	0.018	kg mol^{-1}	Hölttä et al 2009
r.cyl	4.25×10^{-3}	m	Hölttä et al 2009
r.root	3.0×10^{-3}	m	Hölttä et al 2009
ypsilon	1×10^{-14}		To prevent dividing by zero
Rg.N (r^g_R)	0.35	kg C(kg $C)^{-1}$	Growth respiration, share of growth (Needles)
Rg.S (r^g_{wood})	0.3	kg C(kg $C)^{-1}$	Growth respiration, share of growth (Wood)
Rg.R (r^g_N)	0.35	kg C(kg $C)^{-1}$	Growth respiration, share of growth (Fine roots)
gas.const (R)	8.314	J mol^{-1} K^{-1}	Gas constant
M.C (M_C)	12.01	g mol^{-1}	Molar mass of Carbon
M.H	1.008	g mol^{-1}	Molar mass of Hydrogen
M.O	16	g mol^{-1}	Molar mass of Oxygen
osmotic.sugar.conc	2000000	Pa	Osmotic sugar concentration 2 MPa Hölttä et al. 2000
m_n	0.02174605		
Uggla	1.95	–	Division to early/late wood

Table 8: Explanation for the common_p parameters built into the package

6.3 ratio_p Explanation

Parameter Name (Name in Paper)	Parameter value				Units	Comments and additional references
	Hyytiälä	Lettosuo	Väriö	Chinese Site		
form_factor (φ)	0.6	0.6	0.55		Ratio	Lettosuo: The multiplier between a cylinder (with diam=D0, height=h0) and the total biomass of stem, coarse roots and branches
needle_fineroot_ratio	NA	1/2.9	NA		Ratio	Depends on tree size, species and site and *
sapwood.share	0.8	0.8	0.8		Ratio	
height_growth_coefficient (α_S)	4.3	1	2.6		–	repeated value, Variö: leader shoot length / average measurement shoot length (average over years)
diameter_growth_coefficient (α_D)	1.6	1	0.8		–	repeated value
height_growth_coefficient_max	5.5	1.28	NA		–	repeated value, min if growth decreases
height_growth_coefficient_min	3.8	0.88	NA		–	repeated value, min if growth decreases
diameter_growth_coefficient_max	1.9	1.19	NA		–	repeated value, max if growth decreases
diameter_growth_coefficient_min	1.5	0.94	NA		–	repeated value, min if growth decreases

Table 9: Explanation for the ratios_p vector built into the package. Additional comment * "Lettosuo: Helmisaari et al. 2006 Tree physiology -¿ 2.0 for VT, 3.8 for MT, 5.7 for OMT. Very nice curve for needles / fine roots vs. fine root N % leads now to 100 gC m-2 (roots ¡ 2 mm) but result lower than in Leppälammi-Kujansuu et al. (2013, Plant Soil) where they found ca 225 gC m-2 (roots ¡ 2 mm) in control and 300-350 in fertilized ca 225 gC m-2 (roots ¡ 2 mm) in control and 300-350 in fertilized (Leppälammi-Kujansuu et al. 2013, Plant Soil)"

6.4 parameters_p Explanation

Table 10: Explanation for the parameters_p vector built into the package

Parameter Name (Name in Paper)	Parameter value				Units	Comments
	Hyde	Lettosuo	Väriö	HF China		
			Respiration			
Q10.N (q^{10}_{N})	1.898	1.898	1.898		–	Needles Q10
Rm.N (r^m_N)	0.00267	0.0020	0.004005		kg C(kg C)$^{-1}$	Needles R0
Q10.S (q^{10}_{Wood})	1.74788	1.74788	1.74788		–	Wood Q10
Rm.S (r^m_S)	5.5576e-5	5.5576e-5	8.3364e-5		kg C(kg C)$^{-1}$	Wood R0
Q10.R (q^{10}_{R})	2.5575	2.9662	2.0244		–	Fine roots Q10
Rm.R (r^m_R)	0.00958	0.0059	0.00945		kg C(kg C)$^{-1}$	Fine roots R0
			Growth			
sRc (S^c_R)	30	30	25		–	Root growth cessation
			Mycorrhiza			
growth.myco	0.1	0.1	0.1			Mycorrhiza growth
root.lifetime	1.7	2.01	2		years	Root lifetime
			Shoots			
HH0	10	10	10		mm	Initial shoot length
sH0	-1.359200388	-4.12008	-1.44		–	Shoot growth beginning
LH	8.226401284	8.226401284	9.0			Shoot growth rate
LH0	8.226401284	8.226401284	9.0			Initial shoot growth rate

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Table 10 continued from previous page

Parameter Name (Name in Paper)	Parameter value				Units	Comments
	Hyde	Lettosuo	Väriö	HF China		
sHc	14.59636279	12.8328	10.0		–	Shoot growth cessation
Needles						
sN0 (S_N^0)	-8.37584	-3.56589	-5.6		–	Needle growth beginning
TODO: the first LN parameter is a typo, it should be LN0, but will solve this issue later!						
LN	1.849493	1.849493	3.5		mm d^{-1}	Needle growth rate
LN0 (L_{N0})	1.849493	1.849493	3.5		mm d^{-1}	Initial needle growth rate
sNc (S_N^c)	5.263883	7.60671	4.327		–	Needle growth cessation
HN0	1	1	1		mm	Initial needle length
Diameter						
sD0.Trad	-3.724083738	-3.5	-2.434161213		–	Diameter growth beginning
TODO: the first LD parameter is a typo, it should be LD0, but will solve this issue later!						
LD	1.293443902	1.9	2.9		cells d^{-1}	Diameter growth rate
LD0 (L_{D0})	1.293443902	1.9	2.9		cells d^{-1}	Initial diameter growth rate
sDc (S_D^c)	5.077004992	5.2	4.093829285		–	Diameter growth cessation
sDc.T.count	NA	8.8	NA		–	Diameter growth cessation count
Duration parameters						

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Table 10 continued from previous page

Parameter Name (Name in Paper)	Parameter value				Units	Comments
	Hyde	Lettosuo	Väriö	HF China		
tau.Ee ($\tau_{\mathrm{e}}^{\mathrm{early}}$)	10.68685877	5.5	10.25174759		day	Early wood cell enlargement duration
tau.El ($\tau_{\mathrm{e}}^{\mathrm{late}}$)	8.789131263	4.8	4.510400352		day	Late wood cell enlargement duration
tau.We ($\tau_{\mathrm{wa}}^{\mathrm{early}}$)	25.29448857	17.8	51.60724145		day	Early wood cell wall formation duration
tau.Wl ($\tau_{\mathrm{wa}}^{\mathrm{late}}$)	35.12148687	19.2	17.76015932		day	Late wood cell wall formation duration
			GPP			
tau.GPP (τ_{GPP})	5	5	5		–	GPP effect on daily LD
Uggla	1.95	1.8	1.95		–	Division to early/late wood
			Buds			
sB0	171	171	181		day	Bud growth beginning
sBc	85	85	60		day	Bud growth cessation
LB	0.005	0.005	0.003			Bud growth rate
			Xylogenesis			
cell.d.ew ($d_{\mathrm{cell}}^{\mathrm{early}}$)	35.7e-6	32.1e-6	30e-6		m	Early wood cell diameter
cell.d.lw ($d_{\mathrm{cell}}^{\mathrm{late}}$)	24.2e-6	27.5e-6	20e-6		m	Late wood cell diameter
cell.l.ew ($l_{\mathrm{cell}}^{\mathrm{early}}$)	2.59e-3	2.89e-3	2.59e-3		m	Early wood cell length

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Table 10 continued from previous page

Parameter Name (Name in Paper)	Parameter value				Units	Comments
	Hyde	Lettosuo	Väriö	HF China		
cell.l.lw ($l_{\text{cell}}^{\text{late}}$)	2.73e-3	2.97e-3	2.73e-3		m	Late wood cell length
cell.wall.density.ew	57	570	557		kg C m^{-3}	Early wood cell wall density
cell.wall.density.lw	57	680	557		kg C m^{-3}	Late wood cell wall density
wall.thickness.ew	2.61e-6	3.1e-6	2.61e-6		m	Early wood wall thickness
wall.thickness.lw	5.23e-6	3.88e-6	5.23e-6		m	Late wood wall thickness
cell.volume.growth.per.day.ew	NA	5.49e-13	NA		m^3 day^{-1}	Early wood cell volume growth rate
cell.volume.growth.per.day.lw	NA	4.62e-13	NA		m^3 day^{-1}	Late wood cell volume growth rate
density_tree (ρ)	400	400	400		kg m^{-3}	Tree density
carbon_share	0.5	0.5	0.5		kg kg^{-1}	Carbon share
D0 (d_0)	0.175	0.175	0.154		m	Initial diameter
h0	17.9	17.9	9.5		m	Initial height
n_age	3	5	5		years	Needle lifespan
n_lenght	34.241	13	39.2		mm	Average needle length
h_increment	309.0938	309.0938	120.00		mm	Mean height increment
SLA	13	5.5	13		m^2 kg^{-1}	Specific leaf area
LR0 (L_R^0)	0.07446064	NA	0.02		kg C d^{-1}	LR0 parameter

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Table 10 continued from previous page

Parameter Name (Name in Paper)	Parameter value				Units	Comments
	Hyde	Lettosuo	Väriö	HF China		
Repola parameters						
b0_repo	-6.303	NA	NA		–	Repola [2009] Parameter
b1_repo	14.472	NA	NA		–	Repola [2009] Parameter
b2_repo	-3.976	NA	NA		–	Repola [2009] Parameter
Sperling parameters						
lower_bound_needles	0.02	NA	NA		kg C	Lower bound for needles
lower_bound_phloem	0.03	NA	NA		kg C	Lower bound for phloem
lower_bound_roots	0.05	NA	NA		kg C	Lower bound for roots
lower_bound_xylem_sh	0.03	NA	NA		kg C	Lower bound for shoot xylem
lower_bound_xylem_st	0.1	NA	NA		kg C	Lower bound for stem xylem
tau_emergancy_needles	3	NA	NA		–	Emergency time constant for needles
tau_emergancy_phloem	3	NA	NA		–	Emergency time constant for phloem
tau_emergancy_roots	3	NA	NA		–	Emergency time constant for roots

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Table 10 continued from previous page

Parameter Name (Name in Paper)	Parameter value				Units	Comments
	Hyde	Lettosuo	Väriö	HF China		
tau_emergancy_xylem_sh	3	NA	NA		–	Emergency time constant for shoot xylem
tau_emergancy_xylem_st	3	NA	NA		–	Emergency time constant for stem xylem
lower_bound_W	0.01	NA	NA		kg C	Lower bound for W
tau_emergancy	3	NA	NA		–	General emergency time constant
uk_repo	0.109	NA	0.109		–	Repola [2009] Parameter
eki_repo	0.118	NA	0.118		–	Repola [2009] Parameter
stem_no	3	NA	NA		–	Repola [2009] Parameter

6.5 sperling_p Explanation

Table 11: Explanation for the sperling_p vector built into the package

Parameter Name	Parameter value				Units	Comments
	Hyde	Lettosuo	Flakaliden	HF China		
starch0	0.3246781	0.40	0.40			Initial starch concentration
sugar0	0.4184208	0.35	0.35			Initial sugar concentration
starch.needles0	0.03	NA	NA			Initial needle starch concentration
starch.phloem0	0.037	NA	NA			Initial phloem starch concentration
starch.xylem.sh0	0.034	NA	NA			Initial shoot xylem starch concentration
starch.xylem.st0	0.166	NA	NA			Initial stem xylem starch concentration
starch.roots0	0.057	NA	NA			Initial root starch concentration
sugar.needles0	0.087	NA	NA			Initial needle sugar concentration
sugar.phloem0	0.27	NA	NA			Initial phloem sugar concentration
sugar.roots0	0.014	NA	NA			Initial root sugar concentration
sugar.xylem.sh0	0.0249	NA	NA			Initial shoot xylem sugar concentration
sugar.xylem.st0	0.021	NA	NA			Initial stem xylem sugar concentration
Wala	0.0	0.0	0.0			Wala parameter
carbon.sugar	0.4211	0.4211	NA			Carbon content in sugar
carbon.starch	0.4444	0.4444	NA			Carbon content in starch
alfa	3	3	3			Alfa parameter
tau.s	2	2	2			Tau s parameter
tau.t	2	2	2			Tau t parameter
starch00	0.3246781	0.40	0.40			Secondary initial starch concentration

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Table 11 continued from previous page

Parameter Name	Parameter value				Units	Comments
	Hyde	Lettosuo	Flakaliden_c	HF_China		
sugar00	0.4184208	0.35	0.35			Secondary initial sugar concentration
Q10s	3	NA	NA			Q10 for synthesis
Q10d	1.8	NA	NA			Q10 for decomposition
SCb	0.23	NA	NA		kg C	Storage carbon baseline
sugar.level	0.41	NA	0.35		kg C	Sugar level at senescence
Ad0.needles	0.017	NA	NA			Initial needle Ad0
Ad0.phloem	0.008	NA	NA			Initial phloem Ad0
Ad0.roots	2e-04	NA	NA			Initial root Ad0
Ad0.xylem.sh	2e-04	NA	NA			Initial shoot xylem Ad0
Ad0.xylem.st	0.047	NA	NA			Initial stem xylem Ad0
lamda.needles	0.197	NA	NA			Needle lamda parameter
lamda.phloem	0.05301	NA	NA			Phloem lamda parameter
lamda.roots	0.211	NA	NA			Root lamda parameter
lamda.xylem.sh	0.00401	NA	NA			Shoot xylem lamda parameter
lamda.xylem.st	0.00401	NA	NA			Stem xylem lamda parameter
delta.needles	0.729	NA	NA			Needle delta parameter
delta.phloem	0.832	NA	NA			Phloem delta parameter
delta.roots	0.853	NA	NA			Root delta parameter
delta.xylem.sh	0.762	NA	NA			Shoot xylem delta parameter
delta.xylem.st	0.294	NA	NA			Stem xylem delta parameter
k_np	0.3	NA	NA			k_np parameter
k_pr	0.072	NA	NA			k_pr parameter
k_pxsh	0.188	NA	NA			k_pxsh parameter
k_pxst	0.17	NA	NA			k_pxst parameter
myco.thresh	0.025	NA	NA			Mycorrhiza threshold

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