

CASSIA+ Instruction and Plans Booklet

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1 What is the CASSIA model?

1.1 Introduction

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

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. 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. Further details for the individual functions can be found by writing `?function_name` in the terminal in R, although a list of functions included in this package can be found in Section 2.1. And tutorials are provided Section 2.

This document and package includes newer developments not yet published in papers such as a sugar internal allocation model and more detailed xylogenesis process. If there are questions about these sections, please get in contact with the people involved in making this package.

1.1.1 Coding plan

The model was originally written in R and then translated to C++. 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 2024-2025 a soil, mycorrhizal growth and photosynthesis model are being integrated.

All C++ functions should be accessible by an R interface.

1.1.2 Git and GitHub resources

If you are unfamiliar with GitHub then these are some helpful resources. If you would like to develop the model then using GitHub would be ideal, if you just want to use the model then you just need to know how to install the model from GitHub.

- **GitHub:** <https://docs.github.com/en>
- **GitHub:** <https://docs.github.com/en/get-started/quickstart/hello-world>
- **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 Tutorials

To be published: 09.05.2025 with documentation accessible from the code to also be updated around this time.

2.1 Function List

Table 1: Functions included in the CASSIA package grouped by function.

Function	Purpose	Documented
Tests		
all_tests	Tests the new CPP CASSIA function against the original CASSIA outputs (Pauliina's original R version).	
bound_checks	TODO	
preles_test_cpp		
repola_test_cpp		
respiration_test_cpp		
setup_export_data	Output dataset. Creates dataframes for the CASSIA model outputs, this isn't used yet.	N
tests		
update_model_settings	Input test. Check that the settings are defined in a way that makes sense for the model. As not all model settings work simultaneously.	N
validate_site	Input test. Function to check the parameters are from a site that is defined in the model. If a new site should be added contact Joanna.	N
validate_weather_data	Input test. The weather data should be within allowable bounds, these bounds are checked in this function	N
Plots		
plot_comparison		
plot_data		
plot_mycofon_data		
plot_nitrogen_uptake		
plot_respiration_data		
plot_soil_data		
plot_sugar_starch_comparison		
plot_total_ecosystem_respiration		
plot_weather_variables		

Continued on next page

Table 1 – continued from previous page

Function	Purpose	Documented
respiration_plot	Plot to test the cpp respiration formulation	N
xylem_plot	Plot to test the cpp xylogenesis_wrapper	N
C++ Model Functions		
CASSIA_cpp	The current CASSIA function using the cpp code and the sugar and soil options. TODO: check	Y
CASSIA_calibration	TODO?	
CASSIA_soil	TODO?	
CASSIA_yearly	TODO?	
Fungal_N_Uptake		
Microbe_Uptake		
myco_decision		
myco_growth		
mycofon_balance		
plant_decision		
Plant_N_Uptake		
uptake_C		
uptake_N		
symphony		
symphony_plus		
symphony_plus_daily		
xylogenesis_wrapper		
R Model Functions		
PRELES_GPP	R formulation of the PRELES function with the growth_photo_coef definition. Needs to be kept for the R version of the CASSIA model	Y
repola	R formulation of the repola function. Needs to be kept for the R version of the CASSIA model.	Y
Weather Processing		
calculate_VPD	This calculates the VPD from the temperature and the temperature at dew point. Needed for the ERA5 data.	Y
generating_max_values_monthly	Generates the monthly max values for the specific weather data	N
generating_mean_values_daily	Generates the daily mean values for the specific weather data	N
generating_mean_values_monthly	Generates the monthly mean values for the specific weather data	N
generating_sum_values_monthly	Generates the monthly sum values for the specific weather data	N

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Table 1 – continued from previous page

Function	Purpose	Documented
downloading_data	Downloading the SMEAR weather data for Hyytiälä [TODO: reference]	Y
Hyytiala_Data_Creation		
process_files		
process_files_co2		
process_weather_data		
importing_hyytiala_raw_data_into_list		
raw_to_daily_monthly_hyytiala		
rbinddatatable		
read_and_combine_weather_data		
reading_nc		
replace_value_DataFrame		
simplifying_names		
sort_CMIP	Sorts the pre-downloaded CMIP6 data for Hyytiälä.	
Data sets		
data_format	The best Hyytiälä formatting	
load_data	Function to load all of the Hyytiälä data gathered, mainly for calibrations and comparisons	
oyewole_2015_calibration_data		
weather_original		
Parameters		
common_p	The parameters needed for the common function are saved as a RData file so can be automatically accessed by the function	
parameters_p		
ratios_p		
repo_p		
sperling_p		
Calibration		
dhtn	An alternative to the normal distribution for the boreal calibration	N
nitrogen_uptake_calibration		
likelihood_nitrogen_uptake	Likelihood function for the nitrogen uptake function.	N
likelihood_soil_models	Likelihood function for the soil models.	N
likelihood_sugar_model	Likelihood function for the sugar model.	N
To be sorted TODO		

Continued on next page

Table 1 – continued from previous page

Function	Purpose	Documented
common		
daily_list		
daily_to_average		
envfac.data		
GPP_2009		
GPP_previous_sum		
GPP_ref		
growth_wrapper		
Hyde_daily_original		
Hyde_weather		
Hyde_yearly_original		
initialize_parameters		
karike_df_all		
leap_years		
nitrogen		
parameters.R		
printColumnNames		
ratios		
soil_model_calibration		
transform_variable		

3 CASSIA

3.1 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 [Schiestl-Aalto et al., 2015, 2019] 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). But the most important aspect is the carbon sink and source effect on seasonal growth:

$$\text{Actual Growth} = \text{Potential Growth Dependent on Environmental Conditions} \cdot \min[\text{Sugar limitation, Nitrogen Limitation}]$$

Note that the sugar limitation is the original formulation. The nitrogen limitation is currently being added to the system.

3.2 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).

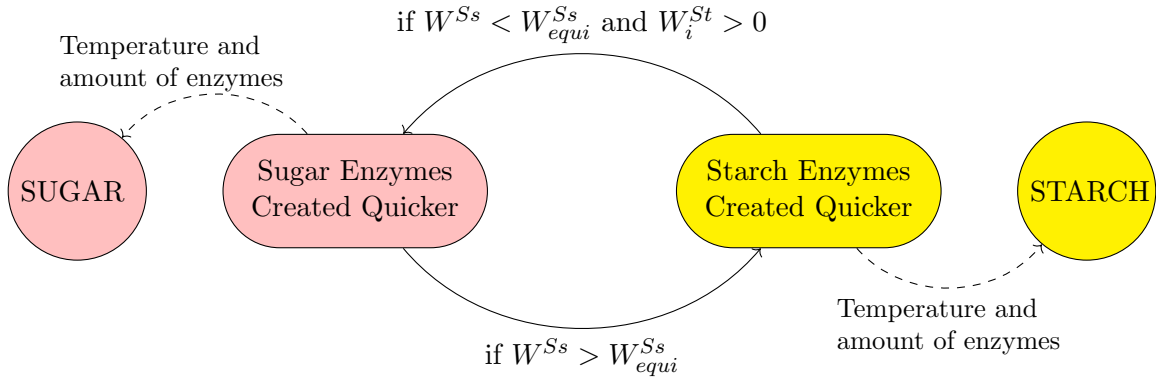


Figure 1: Figure to show the Sperling model process.

This is mathematically represented by;

$$W_i^{Ss} > W_{equi,i}^{Ss} : \tag{1}$$

$$\begin{cases} \frac{dD_i^{Ss}}{dt} = \lambda_i D_i^{Ss} + \delta_i \\ \frac{dD_i^{St}}{dt} = \lambda_i D_i^{St} \end{cases}$$

$$W_i^{Ss} < W_{equi,i}^{Ss} \text{ and } W_i^{St} > 0 :$$

$$\begin{cases} \frac{dD_i^{Ss}}{dt} = \lambda_i D_i^{Ss} \\ \frac{dD_i^{St}}{dt} = \lambda_i D_i^{St} + \delta_i \end{cases}$$

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

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

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

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).

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

3.2.1 Allocation of Sugar Within the Tree

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. The basic relationship is

$$W_{i,j}^{\text{allocation}} = \max \left[(W_i^{Ss} + W_i^{St}) \cdot (f(W_i^{Ss} + W_i^{St}) - f(W_j^{Ss} + W_j^{St})), (W_j^{Ss} + W_j^{St}) - cB_i \right] \quad (6)$$

Where f is a storage term between 0 and 1 which normalizes the concentration gradient. This means that the storage limitation is the driver in the system. This is updated for each iteration, where i is the sugar origin organ, and j , is the destination organ. This is then compared to the storage capacity of each organ cB , where c is the capacity – the percentage of biomass that can be used for storage. These values are fitted with sugar organ level data from Hyytiälä.

As a big debate in the field is the surplus C hypothesis of passive sugar movement compared to the active transfer, both should be considered in terms of their match for the data. Thus, when a carbohydrate conservative strategy is used we use the equation.

$$W_{i,j}^{\text{allocation}} = (W_j^{Ss} + W_j^{St}) - cB_i \quad (7)$$

More allocation strategies could be applied here, however the storage creating a gradient system is quite useful when different allocation strategies are considered in the system (3.2.2).

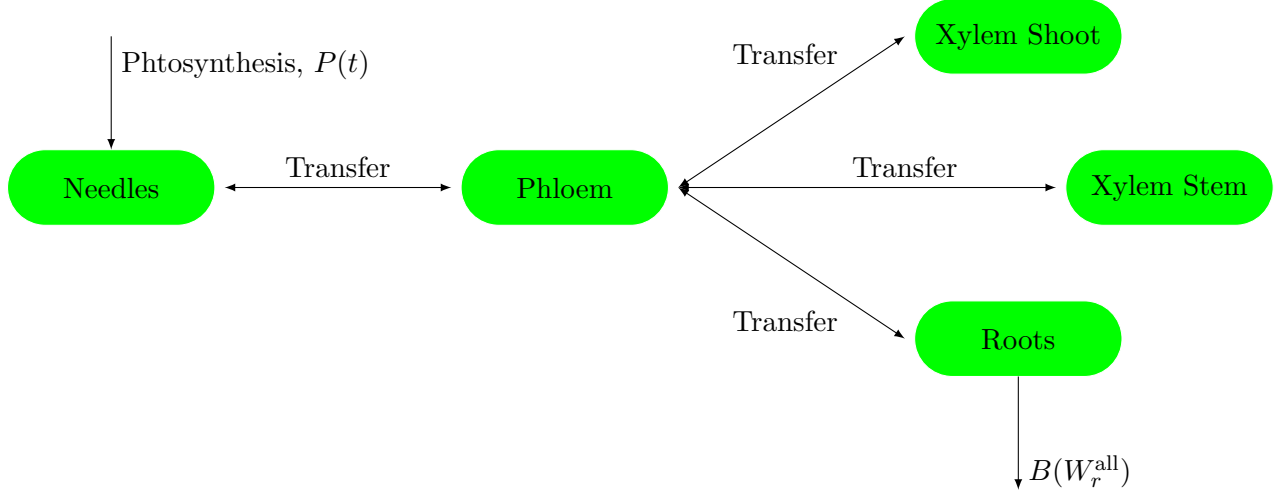


Figure 2: Figure to show the sugar transport of the model

Here $B(W_r^{all})$ is the allocation to fungal partners or the soil which is determined in the allocation alternatives section.

$G(t)$ 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.

Again this f function representing the storage has been formulated in different ways to test the model behaviour. The best ones are the moment are:

$$f(W_i^{all}) = \max \left[0, \min \left[1, h_i \left(1 - \frac{1}{e^{\alpha_i(W_i^{all} - W_i^{ala})}} \right) \right] \right] \quad (8)$$

$$f(W_i^{all}) = \max \left[0, \frac{1}{1 + \exp(-2(\text{Sugar} + \text{Starch} - \text{Storage Capacity}))} \right] \quad (9)$$

3.2.2 Allocation to Mycorrhiza / Soil

To understand the observed patterns we should consider a few different strategies. These strategies change the seasonality as well as the magnitude of allocation to the soil.

$$B(W_r^{all}) = \max(0.3 \cdot W_r^{all}, W_r^{all} - cB_r) \quad (10)$$

1. Observed: fitting the data with the sugar available considering a fixed percentage going to the mycorrhiza. This creates the desired effect in the starch. The value of this is approximately 30% of plant sugar being allocated to the soil. No nitrogen limitation.
2. Nitrogen feedback. However, rather than just considering the sugar leaving the system due to it fitting data could it be to harvest nitrogen? In this case consider the difference in growth, which thus effects the carbon fixed in growth and not available to be allocated below ground

3. Nitrogen investment. Again rather than considering this process to be passive, maybe it is active. In this case we consider the plant wanting to minimise the difference between the nitrogen and carbon limitation. Thus investing as much free carbon as it can to minimise this difference (ecoevolutionary inspired)
4. Strategies under development: nitrogen limitation within the model being driven by soil dynamics.

Note that the strategies above are considered due to the data available to us. Eventually the model should consider the ectomycorrhizal and plant decisions more explicitly as in 5.2.

3.2.3 Sugar and Starch complete process

Therefore, sugar and starch transfer is calculated via:

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

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

The timing of bud burst is determined by a factor W_{bud}^{Ss} 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 2. When the model is calibrated 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 2: Table to define all of the symbols in the sugar model. TODO: units and values

Symbol	Function	Units (day-1)	Meaning
<i>Variable</i>			
W	Variable	kg C	Amount of of carbon in the organ indicated by the super-script
D	Variable	mg g-1	Amount of enzyme
T	Variable	Degrees C	Temperature, input to the model timeseries
<i>Process in the model</i>			
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]
<i>Index</i>			
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.
<i>Parameter</i>			
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
c	Parameter	kg C	The threshold of sugar storage in each organ fitted for each organ with the sugar data collected from Hyyitälä.
<i>Other</i>			
$P(t)$	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].

3.3 Growth As Investment

Currently, we have considered fluxes and allocation as the key structure. Therefore, the plant investment is in sugars, however we do see a difference in the biomass allocated as well. Currently a framework is being thought of where the objective is to investigate how the cost of different root structures affects an optimisation problem where the cost of photosynthesis is dependent on nitrogen supply.

We seek to:

$$\max [\text{Photosynthesis dependent on nitrogen} - \text{Cost of root structures}] \quad (11)$$

Which is dependent on number of root tips, length of mycorrhized root tip and allocation of biomass to belowground infrastructure per leaf area. These traits are inspired by studies of the climate and soil fertility gradient in the hemiboreal to arctic soils [Ostonen et al., 2007], the root economic spectrum as explained by Kramer-Walter et al. [2016] and Kong et al. [2019] as well as conversations by boreal root experts.

This formulation has not been published so is not included in this documentation, but will be implemented in CASSIA when a calibration is completed. Expected Autumn 2025.

If interested ask send an email to Joanna for a preview.

3.4 Photosynthesis

In the original CASSIA model used SPP to calculate photosynthesis. The SPP model [TODO: reference] is first run and then the output is added into CASSIA as an input. In terms of integrated photosynthesis models PRELES [Mäkelä et al., 2008, Minunno et al., 2016] is now integrated and phydro [Joshi et al., 2022] with a nitrogen addition is being added.

Preles gives ecosystem level GPP considering environmental conditions and the nitrogen multiplier developed by Peltoniemi [TODO: reference] has been added to consider the entire nitrogen porcess in the model. This is explained further below. As PRELES is originally a canopy level model, the output of PRELES has been divided by the amount of trees in Hyytiälä (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.

phydro with a nitrogen factor is currently being added to CASSIA to give an eco-evolutionary approach alternative. The nitrogen limitation added will be published in the near future and then added here.

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;

$$P = \beta \cdot \phi \cdot f_{\text{APAR}} \cdot f_L \cdot f_S \cdot \min(f_D, f_{W,P}) \cdot f_{\text{CO}_2,P} \quad (12)$$

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]:

$$f_N(N) = \frac{\epsilon}{\epsilon_0} = \frac{\epsilon_0 \left(1 + \frac{N}{N_0}\right) - \sqrt{\left(\epsilon_0 \left(1 + \frac{N}{N_0}\right)\right)^2 - 4\theta\epsilon_0^2 \frac{N}{N_0}}}{2\theta\epsilon_0} \quad (13)$$

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 3: McMurtrie: table of symbols

Symbol	Function in the system	Units	Meaning
<i>Variable</i>			
N	Variable	Day	Nitrogen
<i>Parameter</i>			
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 $[N]$

4 Respiration

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

5 Soil Functions

The original extended model structure is shown in Figure 3. The equations are then stated afterwards according to the figure's sections. Note at the moment the Mycofon and symphony models are so altered that they don't necessarily reflect the original models.

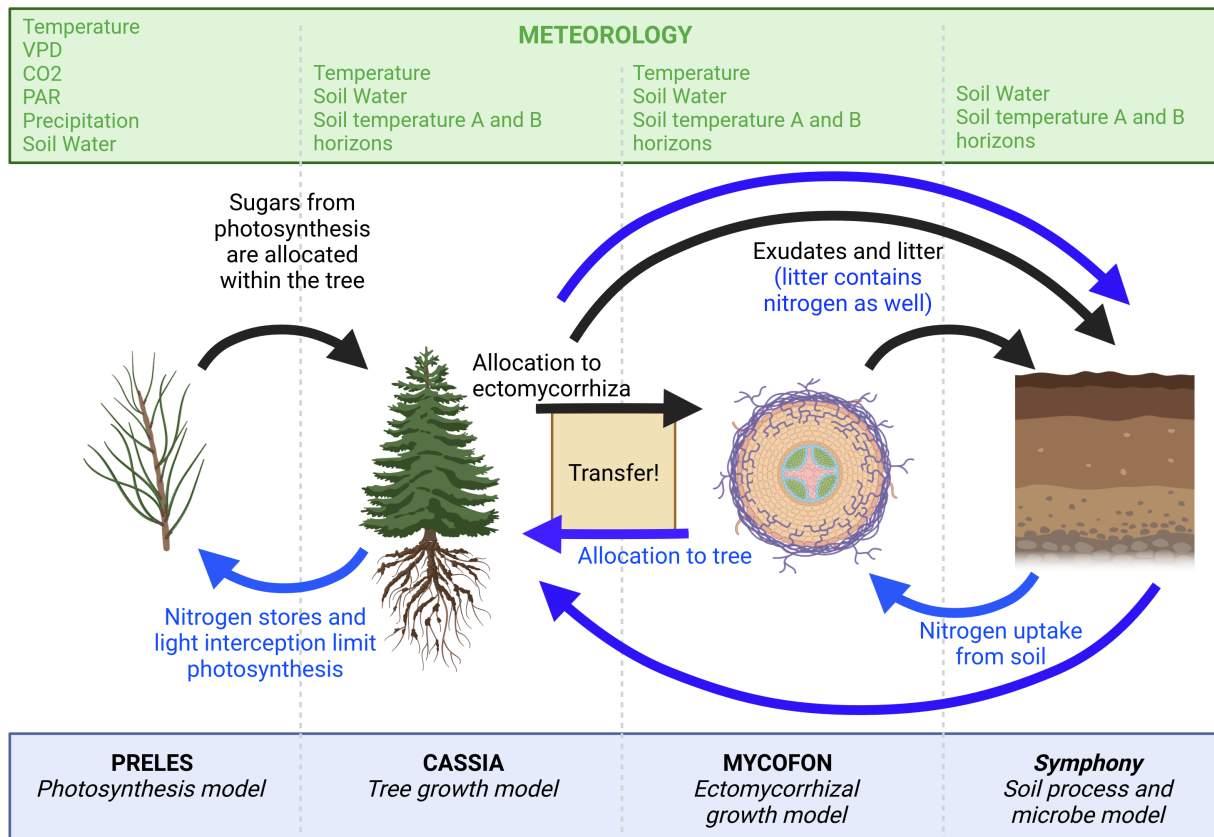


Figure 3: Figure to show the model process. Arrows show the most important inputs to the separate modules in terms of this question. Created with BioRender.com

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
- One nitrogen pool for the whole plant - this nitrogen affects the photosynthetic effect, but is not specifically leaf nitrogen nor organ nitrogen for the nitroge limitation on growth

- 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]

5.1 Uptake Functions

5.1.1 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.

$$u(N) = \frac{kN^8}{N_{limit}^8 + N^8} \quad (14)$$

$$f_T(T) = \begin{cases} \frac{T+20}{55} & T > 0 \\ 0 & T \leq 0 \end{cases} \quad (15)$$

$$f_{SWC}(SWC) = \frac{SWC^8}{0.3^8 + SWC^8} \quad (16)$$

$$u_{actual} = f_T(T)f_{SWC}(SWC)u(N) \quad (17)$$

Where f s are the environmental modification functions and $f \in [0, 1]$, $u()$ is the uptake. In equation 14, N is the concentration of a form of nitrogen, N_{limit} and k are parameters to control the uptake. Equation 15 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 16, where SWC is soil water content and 0.3 is a parameter (will change with calibration). Equation 17 is the final nitrogen uptake effect. The parameters are dependant on the type of nitrogen.

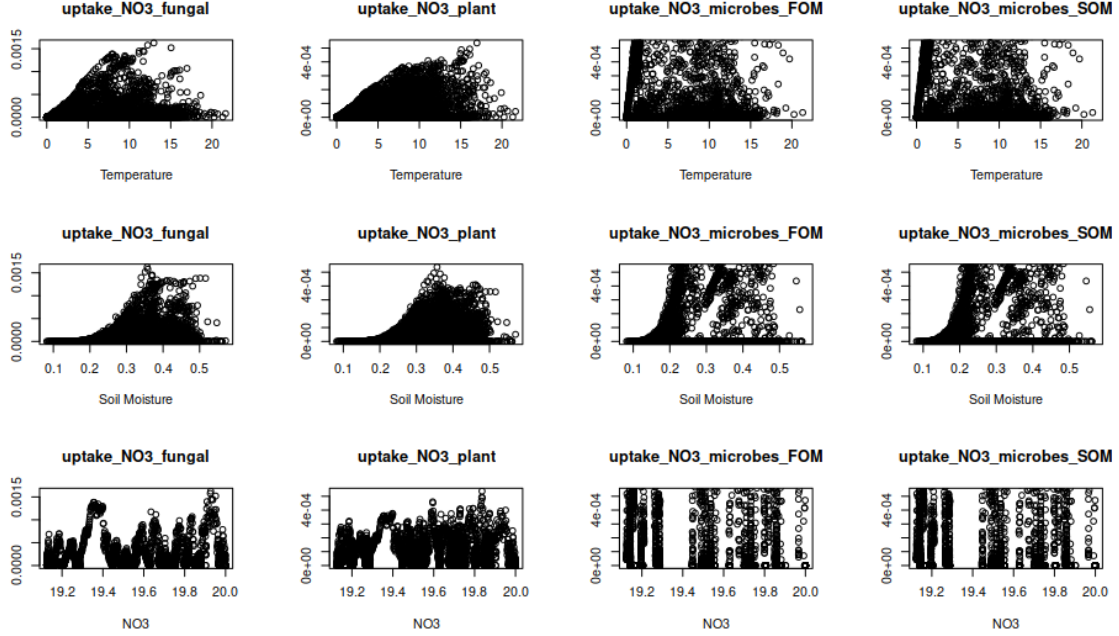


Figure 4: Figure to show the results of the uptake equation with respect to these environmental variables when the simulations are run for a few different years. Note the model is yet to be calibrated so the scales are not sensible.

5.1.2 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.

$$u(C) = \frac{kC^8}{C_{\text{limit}}^8 + C^8} \quad (18)$$

$$f_T(T) = \begin{cases} \frac{T+20}{55} & T > 0 \\ 0 & T \leq 0 \end{cases} \quad (19)$$

$$f_{SWC}(SWC) = \frac{SWC^8}{0.3^8 + SWC^8} \quad (20)$$

$$u_{\text{actual}} = f_T(T)f_{SWC}(SWC)u(C) \quad (21)$$

5.1.3 Plant N Uptake

NOTE: Uptake of nitrogen can also be considered as proportional to sugar exudated as well as a function of the nitrogen concentration in the soil. The following is considering a case when the soil model or at least nitrogen availability is an input.

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 5.2.1. 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:

$$f(NH4) = \frac{aNH4^8}{NH4^8 + b^8} \quad (22)$$

$$\begin{aligned} \text{N to root} = & (1 - m) \cdot \text{demand (plant N amount)} \cdot [u_{organic}(FOM, T, SWC) \\ & + u_{NH4}(NH4, T, SWC) + f(NH4)u_{NO3}(NO3, T, SWC)] \end{aligned} \quad (23)$$

New formulation: (to be added to code)

$$\text{Allocation factor for roots} = \text{demand (plant N amount)} \quad (24)$$

$$\begin{aligned} \text{N to root} = & (1 - m) \cdot [u_{organic}(FOM, T, SWC) \\ & + u_{NH4}(NH4, T, SWC) + f(NH4)u_{NO3}(NO3, T, SWC)] \end{aligned} \quad (25)$$

More formulations to be added!

Table 4: Uptake functions

Symbol	Function in the system	Units	Meaning
<i>Variable</i>			
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 49
<i>Parameter</i>			
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

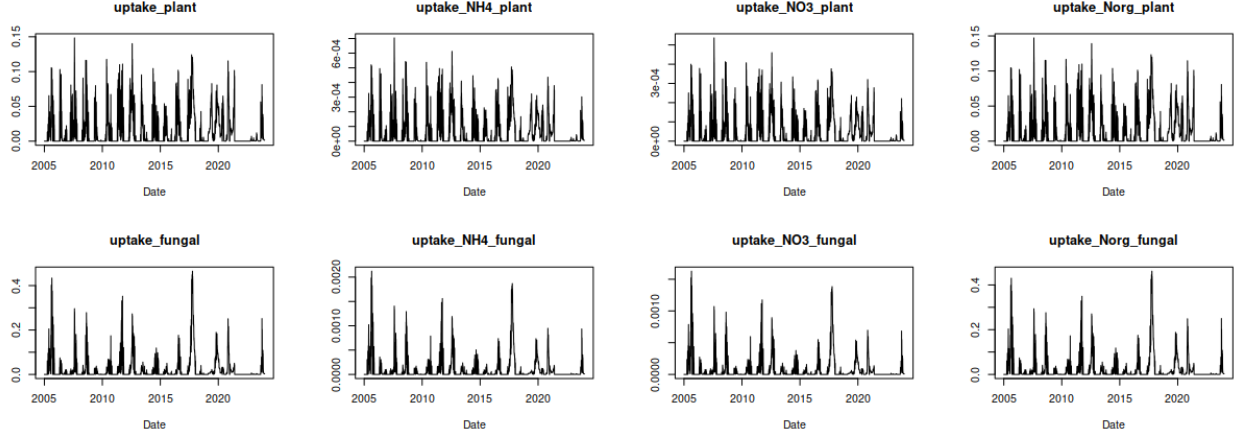


Figure 5: The uptake of nitrogen over the years 2005 to 2023 for the plant and mycorrhiza. Note the model is yet to be calibrated so the scales are not sensible. Behaviour is consistent with literature

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.

5.1.4 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:

$$\begin{aligned}
 \text{N to mycorrhiza} = & \text{Mycorrhizal Biomass} \cdot \text{demand}(\text{mycorrhiza C amount}) \cdot \\
 & [u_{\text{organic}}(FOM, T, SWC) \\
 & + u_{NH_4}(NH_4, T, SWC) + u_{NO_3}(NO_3, T, SWC)]
 \end{aligned} \tag{26}$$

New formulation: (to be added to code)

$$\text{Allocation factor for fungal} = \text{demand}(\text{mycorrhiza C amount}) \quad (27)$$

$$\begin{aligned} \text{N to root} = & \text{Mycorrhizal Biomass} \cdot [u_{\text{organic}}(FOM, T, SWC) \\ & + u_{NH4}(NH4, T, SWC) + f(NH4)u_{NO3}(NO3, T, SWC)] \end{aligned} \quad (28)$$

More formulations to be added!

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 5.2.2.

Assumption:

- Although in the original model there was no mycorrhizal decomposition. Decomposition is currently under development as inspired by [Lindahl et al., 2007, Baskaran et al., 2017]

5.1.5 Microbe Uptake

The microbe uptake holds half of the symphony model dynamics - the microbe side.

Original equations from Symphony paper

$$\text{Carbon Limitation} = u_{\text{Norg}} C_{\text{Microbe}} \quad (29)$$

$$\text{Nitrogen Limitation} = \frac{i(u_{NH4} + u_{NO3}) + 0.2 \cdot (N:C)_{\text{Microbes, opt}} C_{\text{Microbe}}}{(N:C)_{\text{Litter}} - (N:C)_{\text{Microbes, opt}}} \quad (30)$$

$$\text{Total N uptake} = \max\{0, \min\{\text{Carbon Limitation}, \text{Nitrogen Limitation}\}\} \quad (31)$$

$$\begin{aligned} \text{Total N uptaken} = & \text{Total N uptake} \cdot \left(0.2 \cdot (N:C)_{\text{Microbes, opt}} C_{\text{Microbes}} + \right. \\ & \left. (N:C)_{\text{Litter}} - (N:C)_{\text{Microbes, opt}} \right) \end{aligned} \quad (32)$$

Equations currently implemented

$$\begin{aligned} \text{Total C uptaken} = & C_{\text{Microbes}} [u_c(\text{Relevant C compartment}) \\ & + u_c(\text{Exudes}) - (N : C)_{\text{opt}} + R(T_B)] \end{aligned} \quad (33)$$

$$\begin{aligned} \text{Total } N_j \text{ Uptaken} = & C_{\text{microbe}} \left(u_{N_j} - (N:C)_{\text{Microbes, opt}} \right) \left(\frac{N_j \text{ Pool}}{\text{Total Nitrogen}} \right) \\ & j \in [NH4, NO3, N_{\text{org}}] \end{aligned} \quad (34)$$

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.

$$\text{Extra FOM Uptake} = u_{\text{Organic}} \quad (35)$$

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.

5.2 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 and tested as is currently happening in 3.2.2. 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

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

5.2.1 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 36.

$$\text{Transfer} = \max\{\text{allo}_{\max}C_r, \text{allo}(C_r - (\text{root} : \text{mycorrhizal})_{\text{opt}}) - C_f\} \quad (36)$$

$$\text{allo}_{\max} = \begin{cases} 1 - (1 - [\exp(-50 * N_r)]^3) & \text{for } N_r < 0.01 \\ 0.2 & \text{else} \end{cases} \quad (37)$$

$$\text{allo} = \begin{cases} \frac{N_{\text{allo}}}{N_r + N_{\text{allo}}} & \text{for } N_{\text{allo}} < 0.5 \\ 1 & \text{else} \end{cases} \quad (38)$$

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 39

$$\max [C_{\text{Allocated}}^{\text{CASSIA}}, 0.0] \quad (39)$$

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

5.2.2 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 40.

$$\text{Transfer} = \max \left[N_f \left(1 - \frac{N_r}{C_r \cdot (N : C)_{\text{opt}}} \right), 0.0 \right] \quad (40)$$

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

$$\max [N_f - G_f, 0.0] \quad (41)$$

Where N and G are the nitrogen and growth of the mycorrhiza.

NOTE: add the table of symbols when the equations are finalised

5.3 Mycorrhizal Code

5.3.1 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 45). 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.

$$g_F(t) = \begin{cases} 0 & T_a(t) < 0 \\ (1 - \exp(-\lambda M(t))(1 + \exp(-a(T_a(t) - b)))^{-1} & T_a(t) \geq 0 \end{cases} \quad (42)$$

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.

$$f_F(t) = \begin{cases} 0 & s_i \leq 0 \\ \frac{1}{2} \left(\sin \left(\frac{2\pi}{s_i^c} \left(s_i(t) - \frac{s_i^c}{4} \right) \right) + 1 \right) & 0 \leq s_i \leq s_i^c \\ 0 & s_i \geq s_i^c \end{cases} \quad (43)$$

$$G_F = \frac{L0}{\text{Mycelium Lifespan}} \cdot f_F(t) \cdot g_F(t) \quad (44)$$

$$\text{Potential Mycelium Growth} = \begin{cases} G_F & G_F > 0 \\ 0 & G_F \leq 0 \end{cases} \quad (45)$$

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.

$$f_C \approx \frac{C_{NS}^f}{C^f} \quad (46)$$

$$f_N \approx \frac{N_{NS}^f}{N^f} \quad (47)$$

$$\text{Mycelium Growth} = \text{Potential Mycelium Growth} \cdot f_C \cdot f_N \quad (48)$$

Assumptions:

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

5.3.2 Mycofon Balance

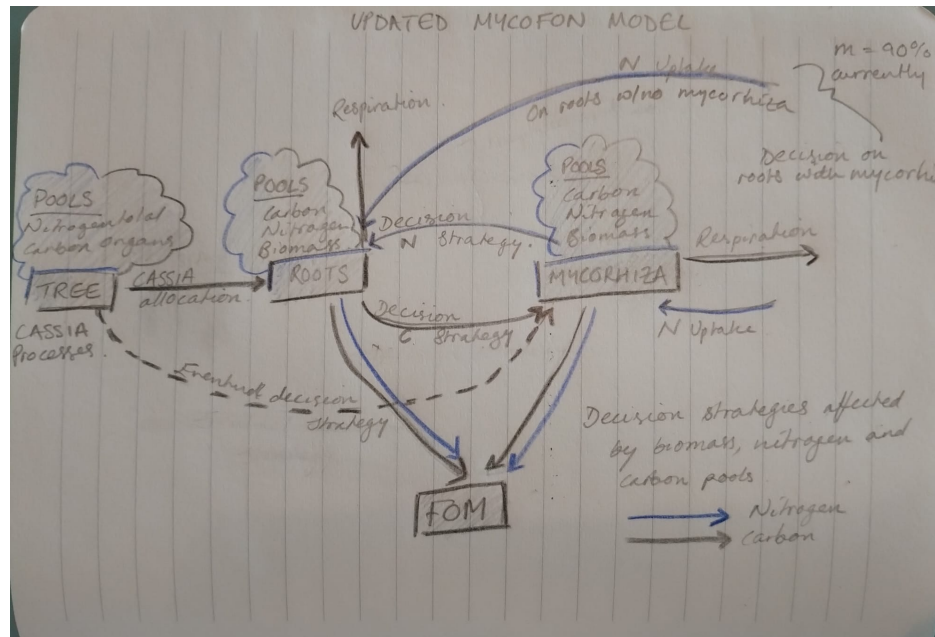


Figure 6: Flow chart for the updated MYOCFON model. Exact processes are represented by an arrow, more detailed processes are represented in the sections / flow diagrams referenced. The uptake rates etc. all have modifications by the environment, which are not written explicitly here.

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.

$$m = \frac{C_f}{B_{opt}^{rf} C^r} \quad (49)$$

$$\frac{dC^r}{dt} = \text{Growth from CASSIA} - (1 - m)s^r C^r - ms^m C^r \quad (50)$$

$$\frac{dC^f}{dt} = g^f - s^{\text{mantle}} C^{\text{mantle}} - s^{\text{ERM}} C^{\text{ERM}} - R(T_B) C^f \quad (51)$$

$$\frac{dC_{\text{NonStruct}}^r}{dt} = C_{\text{Allocated}}^{\text{CASSIA}} - d^r(C^{\text{CASSIA}}) \quad (52)$$

$$\frac{dN_{\text{NonStruct}}^r}{dt} = d^f(C^f) + u^f C^f \quad (53)$$

$$\frac{dC_{\text{NonStruct}}^f}{dt} = d^r(C^{\text{CASSIA}}) - g^f \quad (54)$$

$$\frac{dN_{\text{NonStruct}}^f}{dt} = u^f C^f - g^f - d^f(C^f) \quad (55)$$

Table 5: Mycofon: table of symbols

Symbol	Function in the system	Units	Meaning
<i>Variable</i>			
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
$C_{\text{Allocated}}^{\text{CASSIA}}$	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.
<i>Index</i>			
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
<i>Parameter</i>			
s	Parameter	kg C day-1	Turnover
<i>Function</i>			
$d()$	Function	0-1	Decision function, gives the allocated amount of carbon or nitrogen depending on the direction of the function, see Section 5.2
$R(\text{Temperature})$	Function	kg C	Respiration for indicated compartment, see Section 4
$g()$	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, $C_{\text{Allocated}}^{\text{CASSIA}}$ 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:

- 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

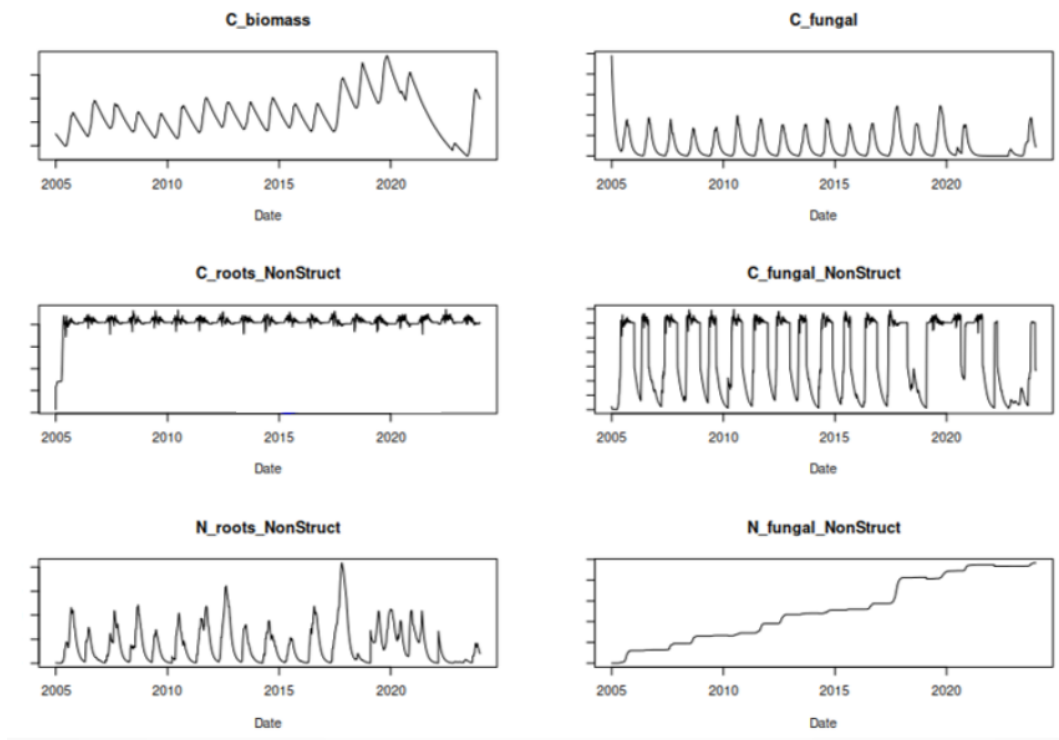


Figure 7: Figure to show the current growth in the model with the Näsholm et al. [2013] decision strategy.

5.4 Soil Processes: Soil Model

Whilst the aim of the project is **to account for nitrogen and carbon transfer between trees and ectomycorrhiza in a boreal ecosystem**, to do this a soil model is needed. As the amount of nitrogen in the soil depends on the fungal competition, it doesn't make sense to study the strategic transfer between the tree and their symbionts without the other functional group competition between microbes in the soils. And also the feedback of the competitive advantage this symbiosis gives to the ectomycorrhiza in the soil.

Model Lowdown: Soil Model.

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] Baskaran et al. [2017]

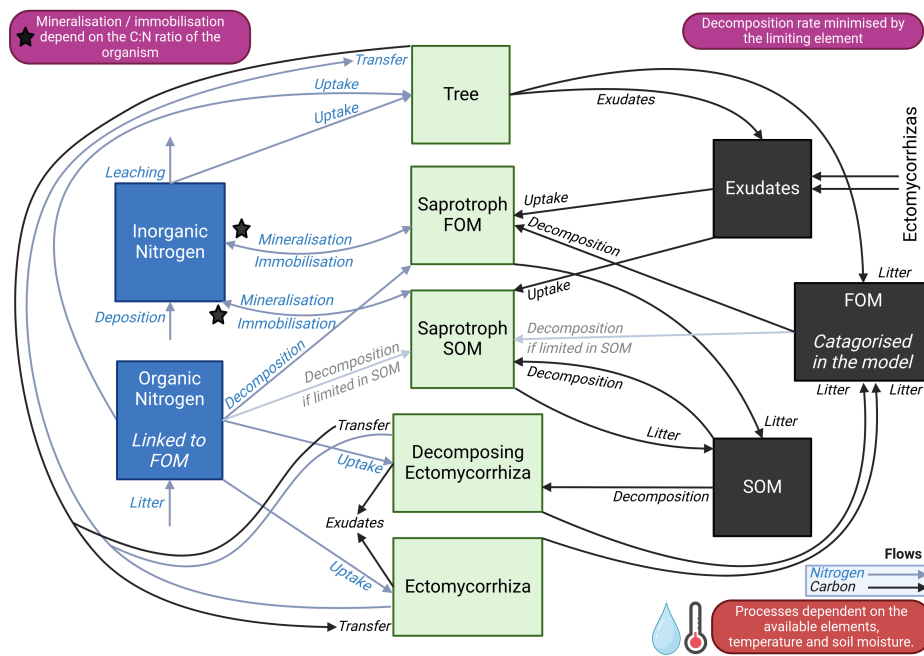


Figure 8: Temporary figure for the soil model. Figure has all of the processes that we want to be represented in the equations.

As the model is seasonal and conceptual so the model should be looked at at two levels: Short term results:

- Priming effect from trenching experiments (*priming effect can be seen*) [Ryhti et al., 2021, 2022]

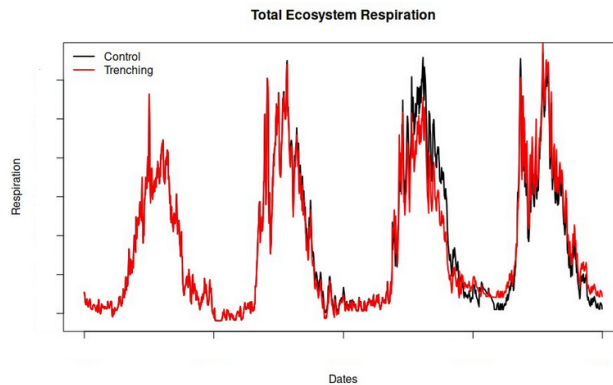
- Nitrogen and Carbon transfer tracked at Hyyitälä (data being gathered)
- Growth patterns within the seasonal pattern [Ekblad et al., 2013] (roots come from the tree model [Ding et al., 2020] and nitrogen availability based root strategy being added)

The long term results should respond to disturbance:

- Change in fungal composition / dominance of fungal strategy Lindahl et al. [2021]
- Changes in carbon stock after disturbances reflecting the different recycling strategies of the different microbes Clemmensen et al. [2015], Sterkenburg et al. [2015]
- Nitrogen immobilisation in old growth forests Sterkenburg et al. [2015]
- Inorganic vs organic nitrogen stock changes after disturbances Lindahl et al. [2010]

This soil model was originally inspired by Perveen et al. [2014], but in order to make the model fit for boreal forests the model has ended up looking a lot like Baskaran et al. [2017] and to a lesser extent [Sulman et al., 2014]. Only with a seasonal timestep and some small differences in the equations. This is encouraging in terms of the understanding of the system, however should be carefully considered in terms of the model use. Exploring using another soil model is also in progress.

The behaviour so far:



NOTE: Equations are from an old iteration of the model so exudation and decomposing ectomycorrhiza are missing.

$$\frac{dC_{SOM}}{dt} = -u_C(C^{SOM})C^{microbe, SOM} + s \left(C^{microbe, SOM} + C^{microbe, FOM} \right) \quad (56)$$

$$C_{FOM} = C_{FOM}^{needles} + C_{FOM}^{woody} + C_{FOM}^{roots} + C_{FOM}^{mantle} + C_{FOM}^{ERM} \quad (57)$$

$$N_{FOM} = N_{FOM}^{needles} (N : C)^{needles} + N_{FOM}^{woody} (N : C)^{woody} + N_{FOM}^{roots} (N : C)^{roots} + N_{FOM}^{mantle} (N : C)^{mantle} + N_{FOM}^{ERM} (N : C)^{ERM} \quad (58)$$

$$d_{total} = u_C(C^{FOM})C^{microbes, SOM} + u_C(C^{FOM})C^{microbes, FOM} \quad (59)$$

$$\frac{dC_{FOM}^{needles}}{dt} = L^{needles} - d_{total} \frac{C_{FOM}^{needles}}{C_{FOM}} \quad (60)$$

$$\frac{dC_{FOM}^{woody}}{dt} = L^{woody} - d_{total} \frac{C_{FOM}^{woody}}{C_{FOM}} \quad (61)$$

$$\frac{dC_{FOM}^{roots}}{dt} = L^{roots} - d_{total} \frac{C_{FOM}^{roots}}{C_{FOM}} \quad (62)$$

$$\frac{dC_{FOM}^{mantle}}{dt} = L^{mantle} - d_{total} \frac{C_{FOM}^{mantle}}{C_{FOM}} \quad (63)$$

$$\frac{dC_{FOM}^{ERM}}{dt} = L^{ERM} - d_{total} \frac{C_{FOM}^{ERM}}{C_{FOM}} \quad (64)$$

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 5.1.2. 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.

$$\begin{aligned} \frac{dNH4}{dt} &= (\psi_{ims} + \psi_{imf}) \frac{NH4}{NH4 + NO3} - NH4_{used}^p - NH4_{used}^f \\ &\quad - u_{NH4}C^{microbes, FOM} - u_{NH4}C^{microbes, SOM} \end{aligned} \quad (65)$$

$$\begin{aligned} \frac{dNO3}{dt} &= (\psi_{ims} + \psi_{imf}) \frac{NH4}{NH4 + NO3} - NO3_{used}^p - NO3_{used}^f \\ &\quad - u_{NO3}C^{microbes, FOM} - u_{NO3}C^{microbes, SOM} \end{aligned} \quad (66)$$

$$\frac{dN^{FOM}}{dt} = Litter - N_{used}^{FOM, p} - N_{used}^{FOM, f} - u_{Norg}C^{microbes, FOM} - u_{Norg}C^{microbes, SOM} \quad (67)$$

$$\frac{dN^{SOM}}{dt} = Microbe Litter - u_{Norg}C^{microbes, SOM} \quad (68)$$

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

Where $NH4_{used}^p$ 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.

$$\frac{dC^{\text{microbe, FOM}}}{dt} = u_{FOM} C^{\text{microbe, FOM}} - r(T_B) - s \quad (69)$$

$$\frac{dC^{\text{microbe, SOM}}}{dt} = u_{SOM} C^{\text{microbe, SOM}} - r(T_B) - s \quad (70)$$

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.
- 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.
- The respiration is not variable yet. Ryhti et al. [2022] data and models planning to be used for this.

Table 6: Soil Model: table of symbols

Symbol	Function in the system	Units	Meaning
<i>Variable</i>			
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
<i>Index</i>			
<i>needles</i>	Index		Subscript indicating the needles
<i>woody</i>	Index		Subscript indicating the woody biomass
<i>roots</i>	Index		Subscript indicating the roots
<i>ERM</i>	Index		Subscript indicating the extra-radical mycelium
<i>mantle</i>	Index		Subscript indicating the mantle
FOM	Index		Subscript indicating the fresh organic matter
SOM	Index		Subscript indicating the soil organic matter
<i>p, f</i>	Index		Subscripts indicating the plant and fungi respectively
<i>B</i>	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
<i>Parameter</i>			
<i>s</i>	Parameter	kg C day-1	Turnover
<i>Function</i>			
<i>u</i>	Function	kg N	Uptake for indicated compartment, see section 5.1.2

6 Complete table of variables

TODO: update the following table with new equations.

Table 7: All Sections: Table of Symbols

Symbol	Function in the System	Units	Meaning
<i>Variable</i>			
W	Variable		Amount of carbon in the indicated organ
A	Variable		Amount of enzyme
T	Variable	°C	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		Maximum sugar allocatable from the CASSIA model
m	Variable	0–1	Mycorrhized roots ratio (0.9 used in testing phase)
NH_4	Variable		Amount of NH_4 in soil
NO_3	Variable		Amount of NO_3 in soil
<i>Index</i>			
r, f	Index		Roots and mycorrhiza indices
opt	Index		Refers to the optimal value of the variable
m, r	Index		Mycorrhized or non-mycorrhized roots
ERM	Index		Extra-radical mycelium
Mantle	Index		Mantle tissue
<i>needles</i>	Index		Needles
<i>woody</i>	Index		Woody biomass
<i>roots</i>	Index		Roots
<i>ERM</i>	Index		Extra-radical mycelium
<i>mantle</i>	Index		Mantle
FOM	Index		Fresh organic matter
SOM	Index		Soil organic matter
p, f	Index		Plant and fungi
B	Index		Soil B horizon
NH_4	Index		Related to NH_4 pools
NO_3	Index		Related to NO_3 pools
Norg	Index		Related to organic nitrogen pools
Microbe	Index		Related to microbial processes
<i>Parameter</i>			
λ	Parameter		Decay rate of enzymes
δ	Parameter		Enzymatic parameter
A	Parameter		Rate of carbohydrate production

B	Parameter		$= \log(Q_{10})/10$, with Q_{10} for sugar synthesis and 1.8 for starch
0.004211	Parameter		Scale factor from mg g^{-1} sugar concentration to kg C
ρ	Parameter		Density of organ tissue
L	Parameter		Threshold for certain processes
W_{ala}	Parameter		Lower bound for storage effects on growth
h	Parameter		Control parameter for storage effects on growth
α	Parameter		Another control parameter for storage effects on growth
L_r^M	Parameter		Threshold for allocation to roots
W_b^{Ss}	Parameter		Threshold of sugar concentration for spring awakening / bud burst
s	Parameter	kg C day^{-1}	Turnover rate
<i>Function</i>			
$d()$	Function	0–1	Decision function allocating C or N depending on context
$u()$	Function		Uptake for specified compartment (see Section 5.1.2)
$R(\text{Temperature})$	Function		Respiration function (see Section 4)
$g()$	Function	kg C	Growth function for mycorrhiza
<i>Process</i>			
K	Process		Creation of sugar or starch
Q	Process		Sperling model amalgamated process
$E(W^{Ss}, W^{St})$	Process		Emergency transfer of starch to sugar under low sugar conditions
$f(W_i^{all})$	Multiplier		Scaling function (0–1) for growth based on carbohydrate reserves
$B(W_r^{all})$	Process		Allocation to mycorrhiza
<i>Other</i>			
$P(t)$	Timeseries		Photosynthesis (input timeseries; no feedback)
$G(t)$	Input, state variable		Growth based on CASSIA model [Schiestl-Aalto et al., 2019]
$R(t)$	State variable		Respiration including growth and maintenance [Schiestl-Aalto et al., 2019]
D	Data		Observational data from Hyytiälä
CASSIA(θ)	Model		CASSIA model with Hyytiälä-specific inputs and parameters

7 Appendix: Parameter Values in Code

7.1 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 8: Explanation for the repo_p parameters built into the package.

7.2 common_p Explanation

Parameter Name (Name in Paper)	Parameter value	Units	Comments and additional references
a (<i>a</i>)	0.185	Degree C ⁻¹	Parameter of function g
b (<i>b</i>)	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_R^g)	0.35	kg C(kg C) ⁻¹	Growth respiration, share of growth (Needles)
Rg.S (r_{wood}^g)	0.3	kg C(kg C) ⁻¹	Growth respiration, share of growth (Wood)
Rg.R (r_N^g)	0.35	kg C(kg C) ⁻¹	Growth respiration, share of growth (Fine roots)
gas.const (<i>R</i>)	8.314	J mol ⁻¹ K ⁻¹	Gas constant
M.C (<i>M_C</i>)	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		
Ugglä	1.95	–	Division to early/late wood

Table 9: Explanation for the common_p parameters built into the package

7.3 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, Väriö: 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 10: Explanation for the ratios_p vector built into the package. Additional comment * "Lettosuo: Helmisaari et al. 2006 Tree physiology -i, 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)"

7.4 parameters_p Explanation

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

Parameter Name (Name in Paper)	Parameter value				Units	Comments
	Hyde	Lettosuo	Väriö	HF China		
<i>Respiration</i>						
Q10.N (q_N^{10})	1.898	1.898	1.898		–	Needles Q10
Rm.N (r_N^m)	0.00267	0.0020	0.004005		kg C(kg C) ⁻¹	Needles R0
Q10.S (q_{Wood}^{10})	1.74788	1.74788	1.74788		–	Wood Q10
Rm.S (r_S^m)	5.5576e-5	5.5576e-5	8.3364e-5		kg C(kg C) ⁻¹	Wood R0
Q10.R (q_R^{10})	2.5575	2.9662	2.0244		–	Fine roots Q10
Rm.R (r_R^m)	0.00958	0.0059	0.00945		kg C(kg C) ⁻¹	Fine roots R0
<i>Growth</i>						
sRc (S_R^c)	30	30	25		–	Root growth cessation
<i>Mycorrhiza</i>						
growth.myco	0.1	0.1	0.1			Mycorrhiza growth
root.lifetime	1.7	2.01	2		years	Root lifetime
<i>Shoots</i>						
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 11 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
<i>Needles</i>						
sN0 (S_N^0)	-8.37584	-3.56589	-5.6		–	Needle growth beginning
<i>TODO: the first LN parameter is a typo, it should be LN0, but will solve this issue later!</i>						
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
<i>Diameter</i>						
sD0.Trad	-	-3.5	-		–	Diameter growth beginning
	3.724083738		2.434161213			
<i>TODO: the first LD parameter is a typo, it should be LD0, but will solve this issue later!</i>						
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
<i>Duration parameters</i>						

Continued on next page

Table 11 continued from previous page

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

Continued on next page

Table 11 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 11 continued from previous page

Parameter Name (Name in Paper)	Parameter value				Units	Comments
	Hyde	Lettosuo	Väriö	HF China		
<i>Repola parameters</i>						
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
<i>Sperling parameters</i>						
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

Continued on next page

Table 11 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 emergancy 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

7.5 sperling_p Explanation

Table 12: 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 12 continued from previous page

Parameter Name	Parameter value			Units	Comments
	Hyde	Lettosuo	Flakaliden_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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