

# CASSIA Instruction Booklet

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## 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 [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 (April). 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 structure of the CASSIA model - equations will be added here when water dependencies are added (around April).

### 2.2 Sugar Model

CASSIA includes an organ level internal sugar model based of the logic from Sperling et al. [2019], which aims to predict the bloom dates of almond trees via the sugar level. When the sugar level drops below a threshold in spring the bloom is triggered. The sugar level is controlled by enzymes that convert sugar to starch. The enzyme activity is based on production and temperature. Plant production of enzymes is also generated by the difference between current sugar level and the "expected" sugar level (equilibrium point).

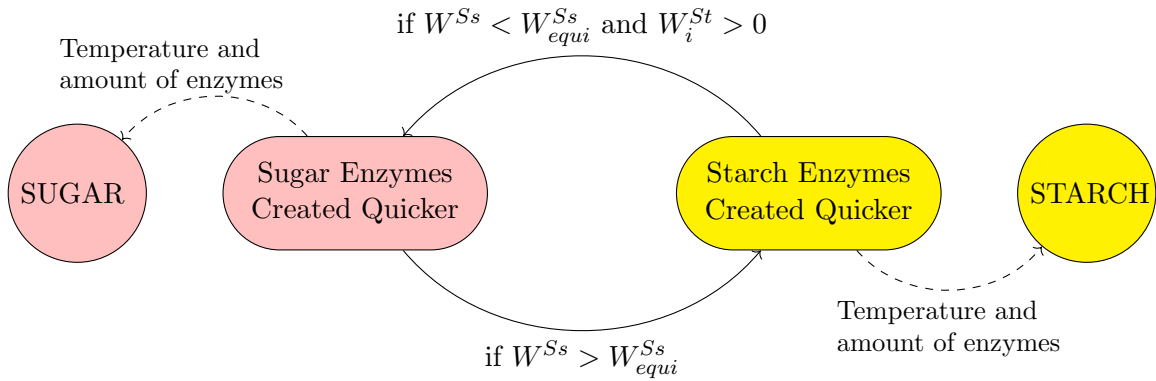


Figure 1: Figure to show the Sperling model process.

This is mathematically represented by;

$$W_i^{Ss} > W_{equi,i}^{Ss} : \quad (1)$$

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

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

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

$$K_i^{St}(T, A^{St}) = A^{St} e^{B^{St}T} \quad (2)$$

$$K_i^{Ss}(T, A^{Ss}) = A^{Ss} e^{B^{Ss}T} \quad (3)$$

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

Where  $W$  is the sugar concentration,  $Ss$  is sugar and  $St$  is starch,  $A$ ,  $\delta$ ,  $\lambda$ ,  $B$  are all parameters that control the enzymic behaviour and amount,  $T$  is temperature and  $\rho$  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).

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

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.

$$W^{\text{allocation}} = W_i^{\text{all}} - q_{i,j} W_j^{\text{all}} \quad (6)$$

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 carbon concentration.

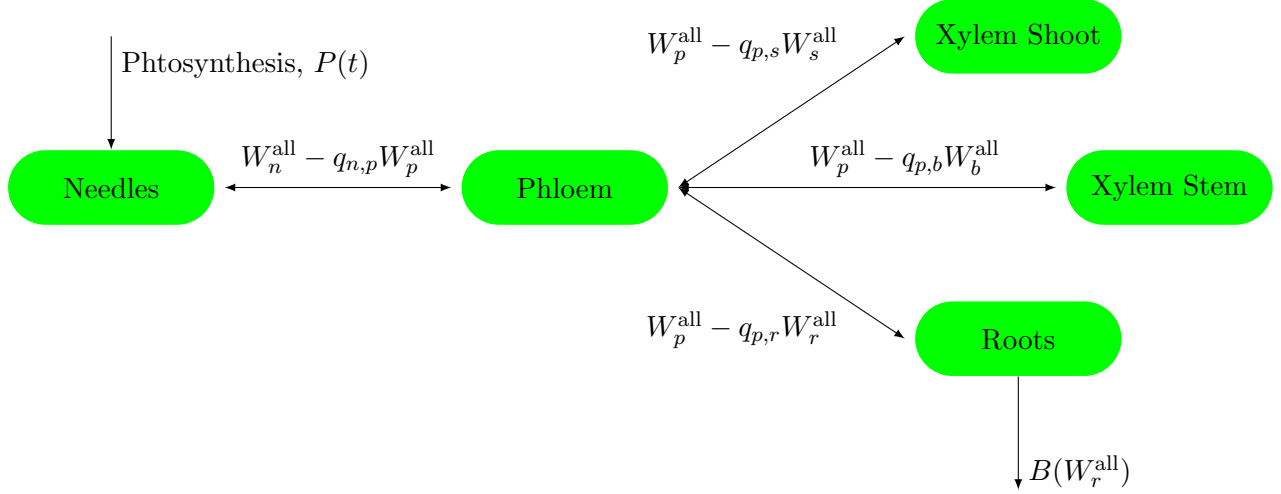


Figure 2: Figure to show the sugar transport of the model

$G(t)$  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 ( $f$ ).  $\alpha$ ,  $W_{ala}$  and  $h$  are fitted parameters.

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

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

$$B(W_r^{all}) = \min(\max(W_r^{all} - T_r^M, 0), W_r^{Ss}) \quad (8)$$

Therefore, sugar and starch transfer is calculated via:

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

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

The timing of bud burst is determined by a factor  $W_b^{Ss}$  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 1, with the new parameters with undetermined values again in Table parameters. As these are not found in the literature and have not been fitted before Bayesian calibration is applied. For the same reasons, the uniform distribution was chosen for the initial calibration.

Table 1: Table to define all of the symbols in the sugar model

Symbol	Function	Meaning
W	Variable	Concentration of carbon in the form of the superscript
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.
A	Variable	Amount of enzyme
$\lambda$	Parameter	Decay rate of enzymes
$\delta$	Parameter	Enzymic parameter
T	Variable	Temperature, input to the model timeseries
K	Process	Creation of sugar or starch
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 $\text{mg g}^{-1}$ to kg C to match the CASSIA units.
$\rho$	Parameter	density of organ
Q	Process	The Sperling model process amalgamated
$E(W^{Ss}, W^{St})$	Process	Emergency transfer when the sugar concentration is too low if there is enough starch to send an emergency transfer of starch.
L	Parameter	Threshold for appropriate processes
$G(t)$	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]
$f(W_i^{all})$	Multiplier	Function between 0 and 1 which scales growth based on the carbohydrate reserves.
$W_{ala}$	Parameter	lower bound for storage effects on growth
h	Parameter	Control of the sugar storage effects on growth
$\alpha$	Parameter	Control of the sugar storage effects on growth
$B(W_r^{all})$	Process	Allocation to mycorrhiza
$L_r^M$	Parameter	Threshold for allocation to roots
$P(t)$	Timeseries	Photosynthesis, timeseries input, calculated by the external model. Therefore, there is no dynamic effect on the daily photosynthesis input [Susiluoto et al., 2010].
$W_b^{Ss}$	Parameter	Threshold of sugar concentration for spring awaken / bud burst
D	Data	Data from observations at Hyytiälä
CASSIA( $\theta$ )	Model	The CASSIA model with Hyytiälä inputs and certain parameters

## 2.3 Photosynthesis

The original CASSIA model used SPP to calculate photosynthesis, this has changed to use PRELES as the photosynthesis model lately. Within this this model needs to consider the nitrogen effect on photosynthesis which is done by adding an extra function into the PRELES model.

### 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;

$$P = \beta \cdot \phi \cdot f_{\text{APAR}} \cdot f_L \cdot f_S \cdot \min(f_D, f_{W,P}) \cdot f_{\text{CO}_2,P} \quad (9)$$

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]:

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

Key factors:

- To get the function to be between 0 and 1 divide  $\epsilon$  with  $\epsilon_0$  (the point at the asymptote). Currently N limits at the average needle N concentration (9.1).
- 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.
- CASSIA used to generate the fAPAR as in Tian et al. [2021]

Calibration data:

- Peltoniemi
- Kainulainen and Holopainen [2002]



### 3 Soil Functions

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

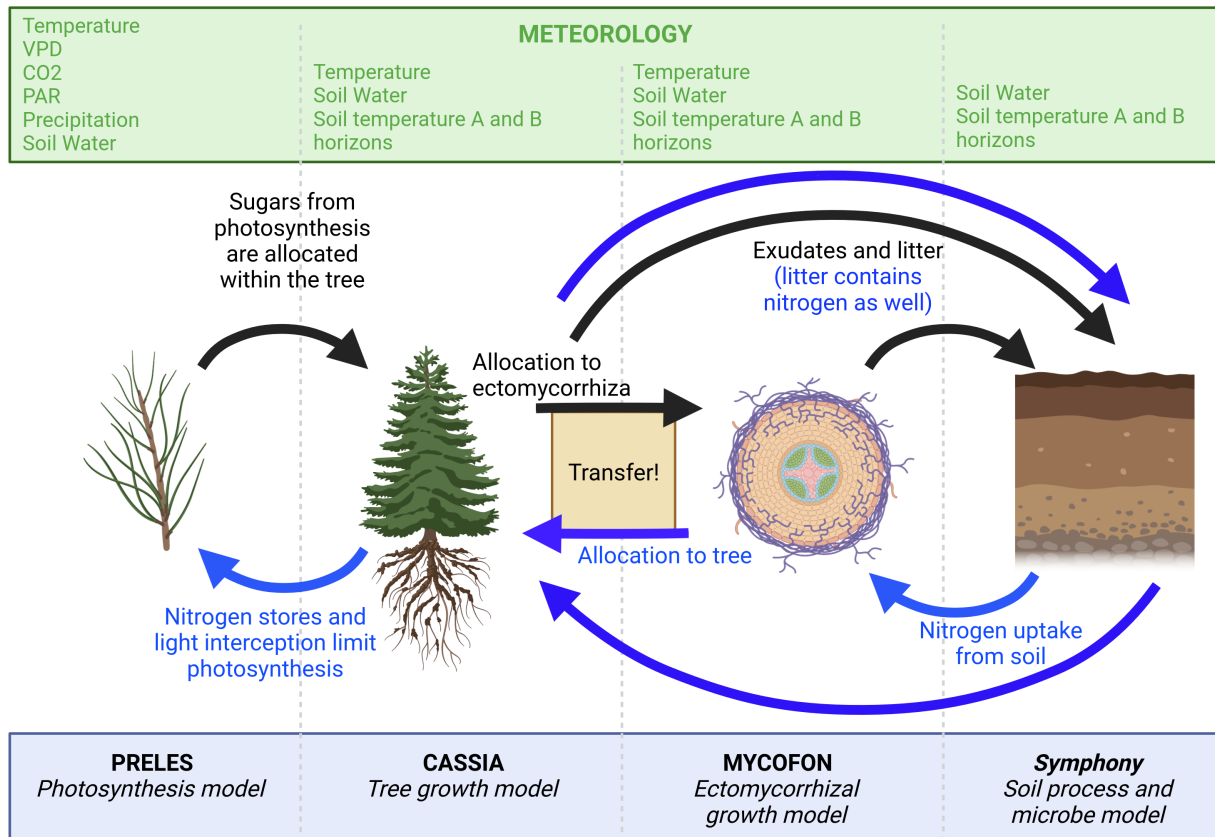


Figure 3: Figure to show the model process. Arrows show the most important inputs to the separate modules in terms of this question. Created with BioRender.com

#### 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 fungal species [Adamczyk et al., 2019]

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

### 3.1 Uptake Functions

#### 3.1.1 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.

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

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

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

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

Where  $f$ s are the environmental modification functions and  $f \in [0, 1]$ ,  $u()$  is the uptake. 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 and  $k$  are parameters. Equation 14 is the final nitrogen uptake effect. The parameters are dependant on the type of nitrogen.

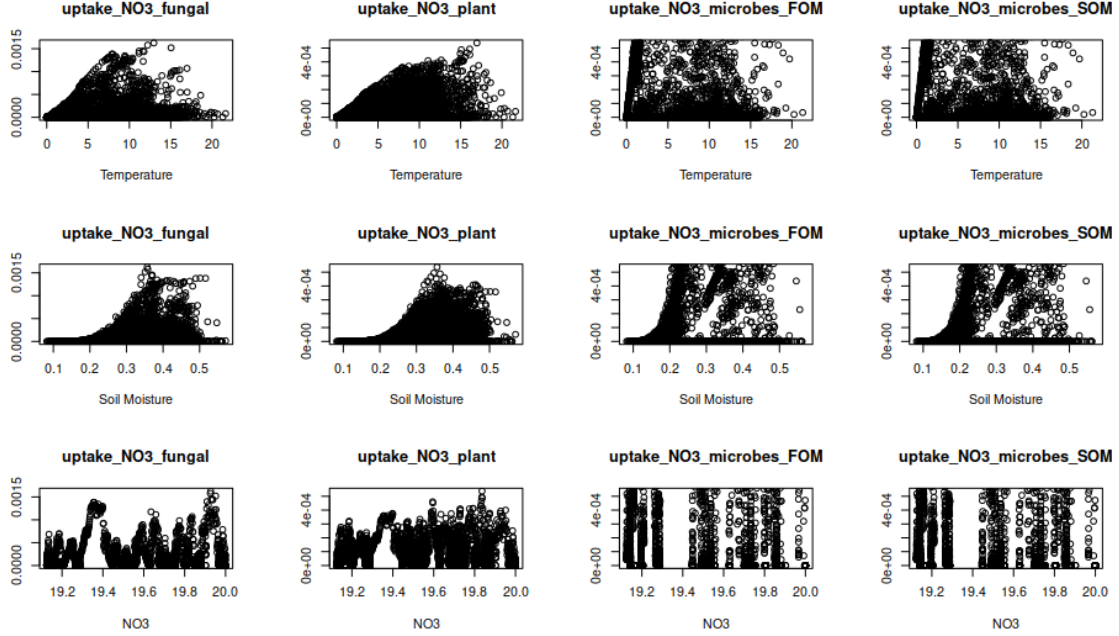


Figure 4: Figure to show the results of the uptake equation with respect to these environmental variables when the simulations are run for a few different years. Note the model is yet to be calibrated so the scales are not sensible.

### 3.1.2 Carbon uptake

This is formed using the same logic as the nitrogen uptake.

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

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

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

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

### 3.1.3 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 3.2.1. Although demand is currently 1 for all decision functions included until the code works better [Meyer et al., 2010, Franklin et al., 2014]. The nitrogen 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.

$$f(NH_4) = \frac{aNH_4^8}{NH_4^8 + b^8} \quad (19)$$

$$\begin{aligned} \text{N to root} = & \text{demand} \cdot [u_{\text{organic}}(FOM, T, SWC) \\ & + u_{NH_4}(NH_4, T, SWC) + f(NH_4)u_{NO_3}(NO_3, T, SWC)] \end{aligned} \quad (20)$$

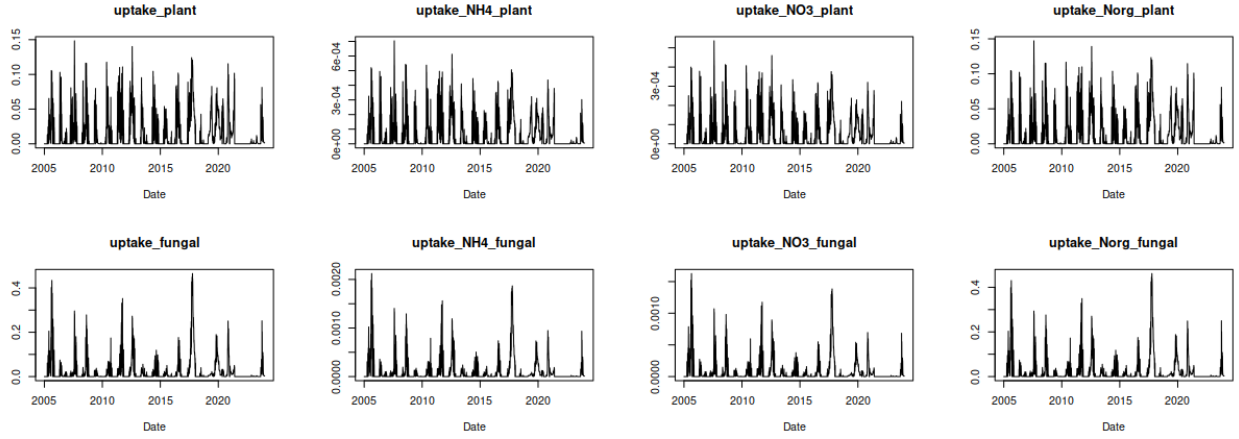


Figure 5: The uptake of nitrogen over the years 2005 to 2023 for the plant and mycorrhiza. Note the model is yet to be calibrated so the scales are not sensible.

### 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] and as I could find relationships between  $NH_4^+$  and  $NO_3^-$  uptake [Marschner et al., 1991].

#### 3.1.4 Fungal N Uptake

Like the plant uptake, this function uses the nitrogen uptake functions for each of the individual types of N compiled for the fungi. 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 [Meyer et al., 2010] and then downscaled with the demand function.

$$\begin{aligned} \text{N to fungi} = & \text{Fungal Biomass} \cdot \text{demand} \cdot [u_{\text{organic}}(FOM, T, SWC) \\ & + u_{NH_4}(NH_4, T, SWC) + u_{NO_3}(NO_3, T, SWC)] \end{aligned} \quad (21)$$

Where  $u_{total}$  is the total fungal uptake.  $u_{organic}$ ,  $u_{NO3}$  and  $u_{NH4}$ , are the fungal uptake of each of the forms of nitrogen. And demand is an input to the function calculated in the ectomycorrhiza decision function 3.2.2.

**Assumption:**

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

### 3.1.5 Microbe Uptake

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

$$\text{Carbon Limitation} = u_{Norg} C_{\text{Microbe}} \quad (22)$$

$$\text{Nitrogen Limitation} = \frac{i(u_{NH4} + u_{NO3}) + 0.2 \cdot (N:C)_{\text{Microbes, opt}} C_{\text{Microbe}}}{(N:C)_{\text{Litter}} - (N:C)_{\text{Microbes, opt}}} \quad (23)$$

$$\text{Total N uptake} = \max\{0, \min\{\text{Carbon Limitation}, \text{Nitrogen Limitation}\}\} \quad (24)$$

$$\text{Total N uptaken} = \text{Total N uptake} \cdot \left( 0.2 \cdot (N:C)_{\text{Microbes, opt}} C_{\text{Microbes}} + (N:C)_{\text{Litter}} - (N:C)_{\text{Microbes, opt}} \right) \quad (25)$$

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. If the SOM decomposes don't get enough nitrogen from their own pools then they can uptake more from the FOM pool, as below.

$$\text{Total N uptaken} = \text{Total N uptaken} + a C_{\text{Microbe}} \quad (26)$$

$$\text{Extra FOM Uptake} = u_{\text{Organic}} \quad (27)$$

Where  $a$  is assimilation of the microbes.

**Assumption:**

- Carbon and nitrogen have the same units here - need to be careful that they are really equivalent.
- Exudates are currently not considered in the carbon uptake in the model! Would like to add them to the first iteration of the model, but need to sort out the mechanics and priorities in the carbon limitation.

## 3.2 Decisions

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:

- Fungi immobilise N during winter! [Heinonsalo et al., 2015] quoting [Kaiser et al., 2011].
- 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 Padjé et al. [2021], Högberg et al. [2010], Blaško et al. [2015].

### 3.2.1 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 a transfer amount stated in Equation 28.

$$\text{Transfer} = \max\{\text{allo}_{\max}C_r, \text{allo}(C_r - (\text{root} : \text{fungal})_{\text{opt}}) - C_f\} \quad (28)$$

$$\text{allo}_{\max} = \begin{cases} 1 - (1 - [\exp(-50 * N_r)]^3) & \text{for } N_r < 0.01 \\ 0.2 & \text{else} \end{cases} \quad (29)$$

$$\text{allo} = \begin{cases} N_{\text{allo}}/(N_r + N_{\text{allo}}) & \text{for } N_{\text{allo}} < 0.5 \\ 1 & \text{else} \end{cases} \quad (30)$$

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

The strategy of Näsholm gives a demand of 1 and a transfer shown in Equation 31

$$\max [C_{\text{Allocated}}^{\text{CASSIA}}, 0.0] \quad (31)$$

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

### 3.2.2 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 32.

$$\text{Transfer} = \max \left[ N_f \left( 1 - \frac{\frac{N_r}{C_r}}{(N : C)_{\text{opt}}} \right), 0.0 \right] \quad (32)$$

where  $N_f$ ,  $N_r$  are the N in the fungi 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

$$\max [N_f - G_f, 0.0] \quad (33)$$

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

## 3.3 Mycorrhizal Code

### 3.3.1 Mycorrhizal Growth

The growth of mycorrhiza is controlled by the same logic as CASSIA [Schiestl-Aalto et al., 2015], where the fungal growth is first calculated as possible growth based on temperature (Equation 37). Then the Non-Structural Carbon and Nitrogen form a limitation, as in Meyer et al. [2010] and Franklin et al. [2014].

$$g_F(t) = \begin{cases} 0 & T_a(t) < 0 \\ (1 - \exp(-\lambda M(t)))(1 + \exp(-a(T_a(t) - b)))^{-1} & T_a(t) \geq 0 \end{cases} \quad (34)$$

Where  $g_R(t)$  is the first step in calculating the possible growth.  $\lambda$  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.

$$f_R(t) = \begin{cases} 0 & s_i \leq 0 \\ \frac{1}{2} \left( \sin \left( \frac{2\pi}{s_i^c} \left( s_i(t) - \frac{s_i^c}{4} \right) \right) + 1 \right) & 0 \leq s_i \leq s_i^c \\ 0 & s_i \geq s_i^c \end{cases} \quad (35)$$

$$G_R = \frac{L0}{\text{Root Life}} \cdot f_R(t) \cdot g_F(t) \quad (36)$$

$$\text{Potential Root Growth} = \begin{cases} G_R & G_R > 0 \\ 0 & G_R \leq 0 \end{cases} \quad (37)$$

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. The potential ectomycorrhizal growth is then limited by the stores of carbon and nitrogen.

$$f_C \approx \frac{C_{NS}^f}{C^f} \quad (38)$$

$$f_N \approx \frac{N_{NS}^f}{N^f} \quad (39)$$

$$\text{Root Growth} = \text{Potential Root Growth} \cdot f_C \cdot f_N \quad (40)$$

#### Assumptions:

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

### 3.3.2 Mycofon Balance

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, fungal growth and multiple N uptake functions. The equations in this function are below.

$$m = \frac{C_f}{B_{opt}^r C^r} \quad (41)$$

$$C^r = C^r - (1 - m)t^r C^r - mt^m C^r \quad (42)$$

$$C^f = C^f + g^f - t^{\text{mantle}} C^{\text{mantle}} - t^{\text{ERM}} C^{\text{ERM}} - r(T_{\text{mb}}) C^f \quad (43)$$

$$C_{\text{NonStruct}}^r = C_{\text{NonStruct}}^r + C_{\text{Allocated}}^{\text{CASSIA}} - d^r(C^{\text{CASSIA}}) \quad (44)$$

$$N_{\text{NonStruct}}^r = N_{\text{NonStruct}}^r + d^f(C^f) + u^f C^f \quad (45)$$

$$C_{\text{NonStruct}}^f = C_{\text{NonStruct}}^f + d^r(C^{\text{CASSIA}}) - g^f \quad (46)$$

$$N_{\text{NonStruct}}^f = N_{\text{NonStruct}}^f + u^f C^f - g^f - d^f(C^f) \quad (47)$$

Where N is nitrogen, C is carbon, r roots, f fungai, 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,  $t$  is turnover, which is different for mycorrhized ( $m$ ) and non-mycorrhized roots ( $r$ ),  $T_{\text{mb}}$  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 fungi is represented by  $g()$ .  $R_{C:N}^r$  fungal NC ratio.

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:fungi 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

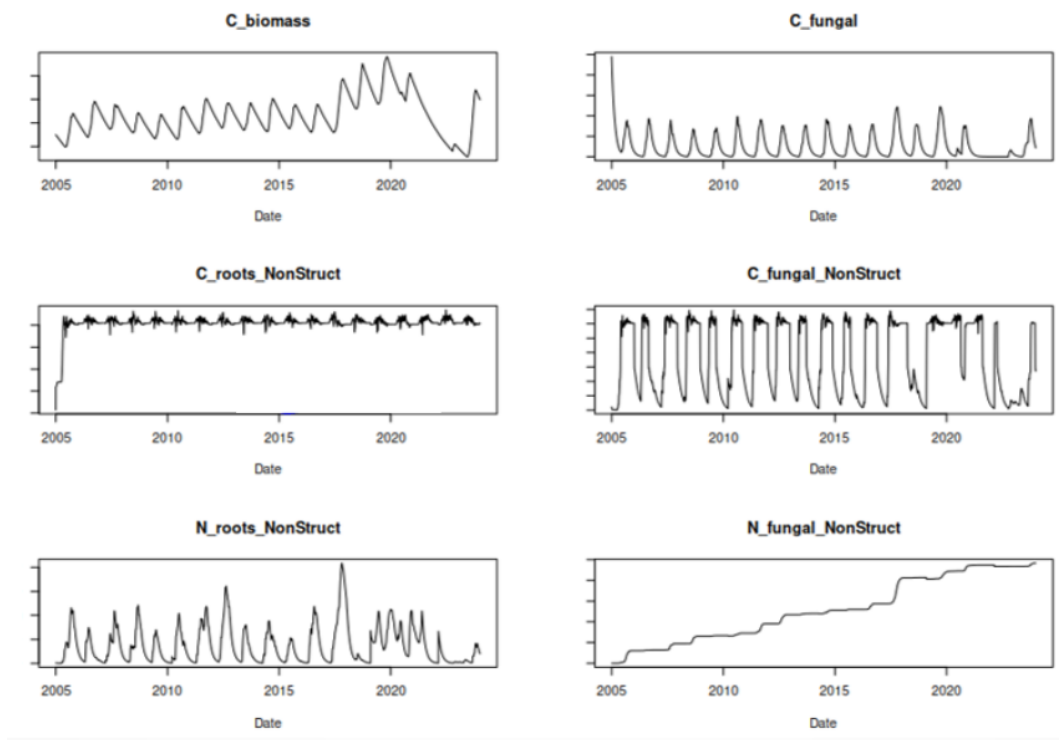


Figure 6: Figure to show the current growth in the model with the Näsholm et al. [2013] decision strategy.

### 3.4 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]

NOTE! The mathematical formatting is lacking here as this section is still under active development - so it is written more in a coding format.

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

$$C_{FOM}^{needles} = C_{FOM}^{needles} + L^{needles} \quad (48)$$

$$C_{FOM}^{woody} = C_{FOM}^{woody} + L^{woody} \quad (49)$$

$$C_{FOM}^{roots} = C_{FOM}^{roots} + L^{roots} \quad (50)$$

$$C_{FOM}^{mantle} = C_{FOM}^{mantle} + L^{mantle} \quad (51)$$

$$C_{FOM}^{ERM} = C_{FOM}^{ERM} + L^{ERM} \quad (52)$$

Where  $C$  and  $N$  are carbon and nitrogen respectively,  $L$  is letter and the compartments are referred to explicitly. FOM is fresh organic matter and SOM is soil organic matter. These values are then aggregated for the microbe model.

$$C_{FOM} = C_{FOM}^{needles} + C_{FOM}^{woody} + C_{FOM}^{roots} + C_{FOM}^{mantle} + C_{FOM}^{ERM} \quad (53)$$

$$N_{FOM} = N_{FOM}^{needles}(N : C)^{needles} + N_{FOM}^{woody}(N : C)^{woody} + N_{FOM}^{roots}(N : C)^{roots} + N_{FOM}^{mantle}(N : C)^{mantle} + N_{FOM}^{ERM}(N : C)^{ERM} \quad (54)$$

where  $C$  and  $N$  are carbon and nitrogen respectively, the compartment is indicated by the superscript and  $(N : C)$  is the carbon nitrogen ratio of the indicated compartment. Then the plant and microbe usages from the previous model / iteration are calculated.

$$NH4 = NH4 - NH4_{used}^p - NH4_{used}^f \quad (55)$$

$$NO3 = NO3 - NO3_{used}^p - NO3_{used}^f \quad (56)$$

$$N^{FOM} = N^{FOM} - N_{used}^{FOM,p} - N_{used}^{FOM,f} \quad (57)$$

$$N^{SOM} = N^{SOM} \quad (58)$$

Where  $NH4_{used}^p$  is the  $NH4$  used for the plant, f represents the fungal uptake. This is an input to the function from the mycofon model. Next the microbe uptake is considered, and this is taken away from the N type states and C. First nitrogen balance.

$$NH4 = NH4 - u_{NH4}C^{FOM} - u_{NH4}C^{SOM} \quad (59)$$

$$NO3 = NO3 - u_{NO3}C^{FOM} - u_{NO3}C^{SOM} \quad (60)$$

$$N^{FOM} = N^{FOM} - u_{Norg}C^{FOM} - u_{Norg}C^{SOM} \quad (61)$$

$$N^{SOM} = N^{SOM} - u_{Norg}C^{SOM} \quad (62)$$

Where u is the uptake. Next carbon balance.

$$d_{total} = u_C C^{SOM} + u_C C^{FOM} \quad (63)$$

Where d is decomposition. TODO: The distributed  $C_{FOM}$  decomposition is currently based on the size of the pool rather than the type of material. This should be changed!

$$C_{FOM}^{needles} = C_{FOM}^{needles} - d_{total} \frac{C_{FOM}^{needles}}{C_{FOM}} \quad (64)$$

$$C_{FOM}^{woody} = C_{FOM}^{woody} - d_{total} \frac{C_{FOM}^{woody}}{C_{FOM}} \quad (65)$$

$$C_{FOM}^{roots} = C_{FOM}^{roots} - d_{total} \frac{C_{FOM}^{roots}}{C_{FOM}} \quad (66)$$

$$C_{FOM}^{mantle} = C_{FOM}^{mantle} - d_{total} \frac{C_{FOM}^{mantle}}{C_{FOM}} \quad (67)$$

$$C_{FOM}^{ERM} = C_{FOM}^{ERM} - d_{total} \frac{C_{FOM}^{ERM}}{C_{FOM}} \quad (68)$$

$$C_{SOM} = C_{SOM} - u_C C^{microbe, SOM} + turnover * (C^{microbe, SOM} + C^{microbe, FOM}) \quad (69)$$

$$C^{microbe, FOM} = (1 + u_{SOM} C^{microbe, FOM} - r(Tmb) - turnover) C^{microbe, FOM} \quad (70)$$

$$C^{microbe, SOM} = (1 + u_{SOM} C^{microbe, SOM} - r(Tmb) - turnover) C^{microbe, SOM} \quad (71)$$

### 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 etcomycorrhiza.
- 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 fungi 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.

- 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.

## References

- Bartosz Adamczyk, Outi-Maaria Sietiö, Petra Straková, Judith Prommer, Birgit Wild, Marleena Hagner, Mari Pihlatie, Hannu Fritze, Andreas Richter, and Jussi Heinonsalo. Plant roots increase both decomposition and stable organic matter formation in boreal forest soil. *Nature Communications*, 10(1):1–9, 2019.
- Preetisri Baskaran, Riitta Hyvönen, S Linnea Berglund, Karina E Clemmensen, Göran I Ågren, Björn D Lindahl, and Stefano Manzoni. Modelling the influence of ectomycorrhizal decomposition on plant nutrition and soil carbon sequestration in boreal forest ecosystems. *New Phytologist*, 213(3):1452–1465, 2017.
- Joana Bergmann, Alexandra Weigelt, Fons van Der Plas, Daniel C Laughlin, Thom W Kuyper, Nathaly Guerrero-Ramirez, Oscar J Valverde-Barrantes, Helge Bruelheide, Grégoire T Freschet, Colleen M Iversen, et al. The fungal collaboration gradient dominates the root economics space in plants. *Science Advances*, 6(27):eaba3756, 2020.
- Róbert Blaško, Lisbet Holm Bach, Stephanie A Yarwood, Susan E Trumbore, Peter Högberg, and Mona N Högberg. Shifts in soil microbial community structure, nitrogen cycling and the concomitant declining n availability in ageing primary boreal forest ecosystems. *Soil Biology and Biochemistry*, 91:200–211, 2015.
- Michael C Dietze, Anna Sala, Mariah S Carbone, Claudia I Czimczik, Joshua A Mantooth, Andrew D Richardson, and Rodrigo Vargas. Nonstructural carbon in woody plants. *Annual review of plant biology*, 65(1):667–687, 2014.
- Alf Ekblad, Håkan Wallander, Douglas L Godbold, C Cruz, D Johnson, P Baldrian, RG Björk, Daniel Epron, B Kieliszewska-Rokicka, R Kjøller, et al. The production and turnover of extra-matrical mycelium of ectomycorrhizal fungi in forest soils: role in carbon cycling. *Plant and Soil*, 366(1):1–27, 2013.
- Oskar Franklin, Torgny Näsholm, Peter Högberg, and Mona N Högberg. Forests trapped in nitrogen limitation—an ecological market perspective on ectomycorrhizal symbiosis. *New Phytologist*, 203(2):657–666, 2014.
- Jussi Heinonsalo, Eija Juurola, Aki Linden, and Jukka Pumpanen. Ectomycorrhizal fungi affect scots pine photosynthesis through nitrogen and water economy, not only through increased carbon demand. *Environmental and Experimental Botany*, 109:103–112, 2015.

- Erik A Hobbie. Carbon allocation to ectomycorrhizal fungi correlates with belowground allocation in culture studies. *Ecology*, 87(3):563–569, 2006.
- Mona N Högberg, Maria JI Briones, Sonja G Keel, Daniel B Metcalfe, Catherine Campbell, Andrew J Midwood, Barry Thornton, Vaughan Hurry, Sune Linder, Torgny Näsholm, et al. Quantification of effects of season and nitrogen supply on tree below-ground carbon transfer to ectomycorrhizal fungi and other soil organisms in a boreal pine forest. *New Phytologist*, 187(2):485–493, 2010.
- Torsten Ingestad, Agneta S Arveby, and Monika Käfar. The influence of ectomycorrhiza on nitrogen nutrition and growth of pinus sylvestris seedlings. *Physiologia Plantarum*, 68(4):575–582, 1986.
- Nancy Collins Johnson, Jason D Hoeksema, James D Bever, V Bala Chaudhary, Catherine Gehring, John Klironomos, Roger Koide, R Michael Miller, John Moore, Peter Moutoglis, et al. From lilliput to brobdingnag: extending models of mycorrhizal function across scales. *Bioscience*, 56(11):889–900, 2006.
- Pirjo Kainulainen and JK Holopainen. Concentrations of secondary compounds in scots pine needles at different stages of decomposition. *Soil Biology and Biochemistry*, 34(1):37–42, 2002.
- Christina Kaiser, Lucia Fuchslueger, Marianne Koranda, Markus Gorfer, Claus F Stange, Barbara Kitzler, Frank Rasche, Joseph Strauss, Angela Sessitsch, Sophie Zechmeister-Boltenstern, et al. Plants control the seasonal dynamics of microbial n cycling in a beech forest soil by belowground c allocation. *Ecology*, 92(5):1036–1051, 2011.
- Annikki Mäkelä, Minna Pulkkinen, Pasi Kolari, Fredrik Lagergren, Paul Berbigier, Anders Lindroth, Denis Loustau, Eero Nikinmaa, Timo Vesala, and Pertti Hari. Developing an empirical model of stand gpp with the lue approach: analysis of eddy covariance data at five contrasting conifer sites in europe. *Global change biology*, 14(1):92–108, 2008.
- Horst Marschner, Max Häussling, and Eckhard George. Ammonium and nitrate uptake rates and rhizosphere ph in non-mycorrhizal roots of norway spruce [picea abies (l.) karst.]. *Trees*, 5:14–21, 1991.
- ROSS E McMURTRIE. Relationship of forest productivity to nutrient and carbon supply—a modeling analysis. *Tree Physiology*, 9(1-2):87–99, 1991.
- Astrid Meyer, Rüdiger Grote, Andrea Polle, and Klaus Butterbach-Bahl. Simulating mycorrhiza contribution to forest c-and n cycling-the mycofon model. *Plant and soil*, 327:493–517, 2010.
- F Minunno, Mikko Peltoniemi, Samuli Launiainen, M Aurela, A Lindroth, A Lohila, I Mammarella, K Minkinen, and A Mäkelä. Calibration and validation of a semi-empirical flux ecosystem model for coniferous forests in the boreal region. *Ecological Modelling*, 341:37–52, 2016.
- Torgny Näsholm, Knut Kielland, and Ulrika Ganeteg. Uptake of organic nitrogen by plants. *New phytologist*, 182(1):31–48, 2009.
- Torgny Näsholm, Peter Högberg, Oskar Franklin, Daniel Metcalfe, Sonja G Keel, Catherine Campbell, Vaughan Hurry, Sune Linder, and Mona N Högberg. Are ectomycorrhizal fungi alleviating or aggravating nitrogen limitation of tree growth in boreal forests? *New Phytologist*, 198(1):214–221, 2013.

- Mikko Peltoniemi, Minna Pulkkinen, Mika Aurela, Jukka Pumpanen, Pasi Kolari, and Annikki Mäkelä. A semi-empirical model of boreal-forest gross primary production, evapotranspiration, and soil water-calibration and sensitivity analysis. *Luke Open Documents*, 2015.
- Nazia Perveen, Sébastien Barot, Gaël Alvarez, Katja Klumpp, Raphael Martin, Alain Rapaport, Damien Herfurth, Frédérique Louault, and Sébastien Fontaine. Priming effect and microbial diversity in ecosystem functioning and response to global change: a modeling approach using the symphony model. *Global change biology*, 20(4):1174–1190, 2014.
- Kira Ryhti et al. Belowground carbon dynamics in scots pine stands. *Dissertationes Forestales*, 2022.
- Pauliina Schiestl-Aalto, Liisa Kulmala, Harri Mäkinen, Eero Nikinmaa, and Annikki Mäkelä. Cassia—a dynamic model for predicting intra-annual sink demand and interannual growth variation in scots pine. *New Phytologist*, 206(2):647–659, 2015.
- Pauliina Schiestl-Aalto, Kira Ryhti, Annikki Mäkelä, Mikko Peltoniemi, Jaana Bäck, and Liisa Kulmala. Analysis of the nsc storage dynamics in tree organs reveals the allocation to below-ground symbionts in the framework of whole tree carbon balance. *Frontiers in Forests and Global Change*, 2:17, 2019.
- Merlin Sheldrake. *Entangled life: how fungi make our worlds, change our minds & shape our futures*. Random House, 2020.
- Sally E Smith and David J Read. *Mycorrhizal symbiosis*. Academic press, 2010.
- Or Sperling, Tamir Kamai, Aude Tixier, Anna Davidson, Katherine Jarvis-Shean, Eran Raveh, Ted M DeJong, and Maciej A Zwieniecki. Predicting bloom dates by temperature mediated kinetics of carbohydrate metabolism in deciduous trees. *Agricultural and Forest Meteorology*, 276:107643, 2019.
- Benjamin N Sulman, Richard P Phillips, A Christopher Oishi, Elena Shevliakova, and Stephen W Pacala. Microbe-driven turnover offsets mineral-mediated storage of soil carbon under elevated co<sub>2</sub>. *Nature Climate Change*, 4(12):1099–1102, 2014.
- Sanna Susiluoto, Emmi Hilasvuori, and Frank Berninger. Testing the growth limitation hypothesis for subarctic scots pine. *Journal of Ecology*, 98(5):1186–1195, 2010.
- Xianglin Tian, Francesco Minunno, Pauliina Schiestl-Aalto, Jinshu Chi, Peng Zhao, Matthias Peichl, John Marshall, Torgny Näsholm, Hyungwoo Lim, Mikko Peltoniemi, et al. Disaggregating the effects of nitrogen addition on gross primary production in a boreal scots pine forest. *Agricultural and Forest Meteorology*, 301:108337, 2021.
- Oscar J Valverde-Barrantes, Grégoire T Freschet, Catherine Roumet, and Christopher B Blackwood. A worldview of root traits: the influence of ancestry, growth form, climate and mycorrhizal association on the functional trait variation of fine-root tissues in seed plants. *New Phytologist*, 215(4):1562–1573, 2017.
- Anouk Van’t Padje, Gijsbert DA Werner, and E Toby Kiers. Mycorrhizal fungi control phosphorus value in trade symbiosis with host roots when exposed to abrupt ‘crashes’ and ‘booms’ of resource availability. *New Phytologist*, 229(5):2933–2944, 2021.