3.2 - Forest growth/dynamics (theory)

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2022-06-15

Outline

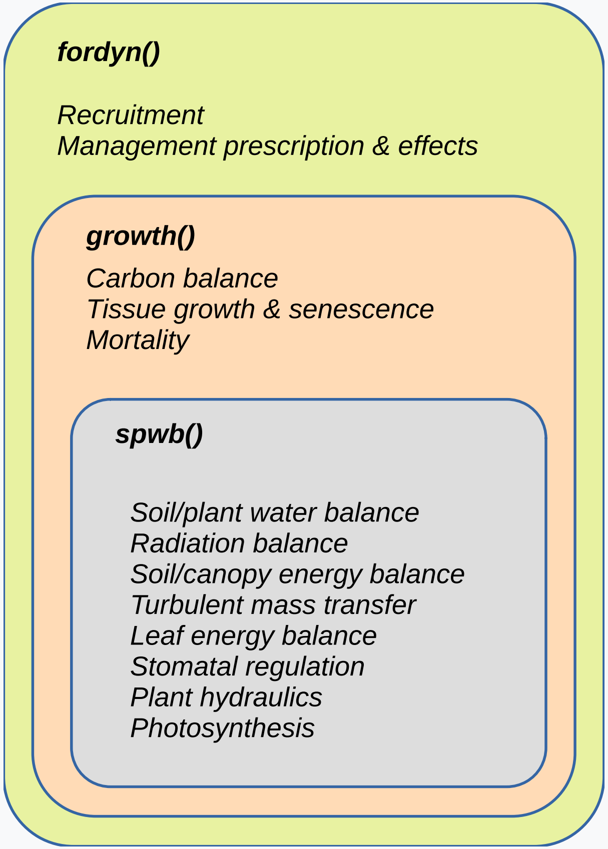
1. Simulation models and processes
2. Carbon pools and carbon balance
3. Growth and senescence
4. Mortality and recruitment

1. Simulation models and processes

Models in medfate and their processes

Simulation functions in **medfate** have been designed and implemented in a **nested** manner:

- Each upper-level function includes the processes of lower-level ones and adds new processes.
- Consequently, the two water balance models (basic and advanced) are available for simulations with `growth()` and `fordyn()`.
- In this presentation, we will focus on the state variables and processes that are added in simulations with `growth()` and `fordyn()`.



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The growth() and fordyn() models

The `growth()` model implements several **daily** processes:

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- Natural regeneration (recruitment)
- The effect of disturbances (at present, only forest management)

2. Carbon compartments, pools and carbon balance

Carbon compartments and pools

Types

Structural carbon - Cell membranes, cell walls & cytosolic machinery.

Metabolic carbon - Labile carbon (sugar) concentration used to sustain cell functioning.

Storage carbon - Labile carbon (starch) concentration used as long-term carbon source.

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Compartment	Structural	Metabolic	Storage
Leaves	Leaf dry biomass B_{leaf}	Leaf sugar SS_{leaf}	Leaf starch ST_{leaf}
Sapwood (branch/stem/coarse roots)	Sapwood dry biomass $B_{sapwood}$	Sapwood sugar $SS_{sapwood}$	Sapwood starch $ST_{sapwood}$
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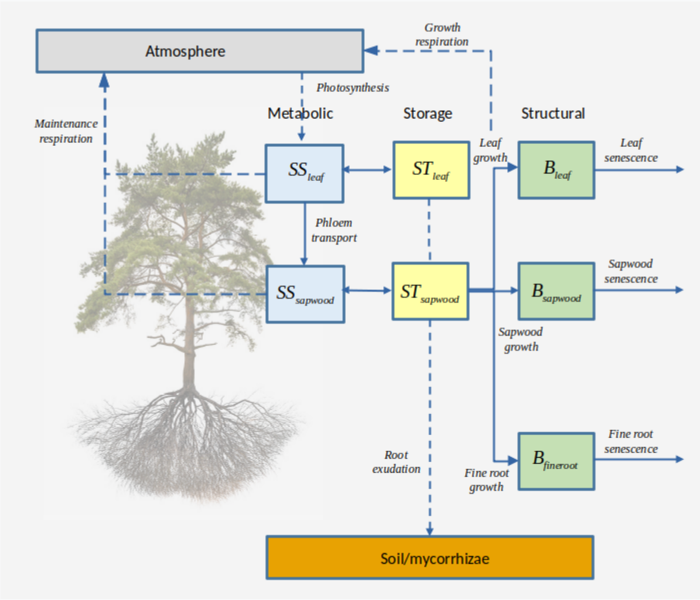
Fluxes



2. Carbon compartments, pools and carbon balance

Labile carbon balance equations

A. Changes in **leaf metabolic** carbon result from considering gross photosynthesis (A_g), leaf maintenance respiration (M_{leaf}), phloem transport (F_{phloem}) and sugar-starch dynamics (SC_{leaf}) and translocation to sapwood storage (TS_{leaf}):

$$\Delta SS_{leaf} \cdot V_{storage,leaf} = A_g - M_{leaf} - F_{phloem} - SC_{leaf} - TS_{leaf}$$

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C. Changes in **stem metabolic** carbon result from considering phloem transport, maintenance respiration of sapwood ($M_{sapwood}$) and fineroot ($M_{fineroot}$) tissues, sugar-starch dynamics and translocation to sapwood storage ($TS_{sapwood}$):

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C. Changes in **stem storage** carbon result from considering sugar-starch dynamics, translocation from other pools, growth respiration and root exudation:

$$\Delta ST_{sapwood} \cdot V_{storage,sapwood} = SC_{sapwood} + TS_{leaf} + TT_{leaf} + TS_{sapwood} - G_{sapwood} - G_{leaf} - G_{fineroot} - RE_{sapwood}$$

2. Carbon compartments, pools and carbon balance

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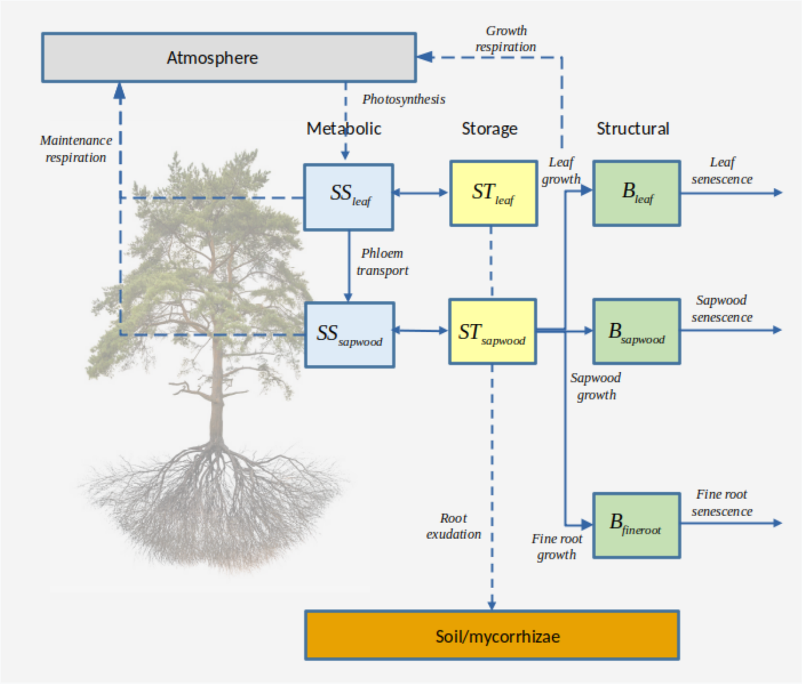
Changes in labile carbon pools can be reduced to the balance between gross photosynthesis (A_g), maintenance (M), growth (G) and root exudation (RE) components:

$$\Delta S_{labile} = A_g - M - G - RE$$



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Design of labile carbon processes

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- **Translocation** of labile carbon towards sapwood storage occurs whenever there is senescence in a given tissue (leaves, branches).
- **Root exudation** is not a process competing for metabolic carbon, but a consequence of plant storage capacity being surpassed (Prescott et al. 2020).

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Prescott et al (2020). Trends in Ecology & Evolution, 35, 1110–1118.

2. Carbon compartments, pools and carbon balance

Biomass balance

Balance in structural carbon pools

The change in structural biomass of each **compartment** results from the interplay between growth and senescence:

$$\Delta B_{leaves} = B_{leaves,growth} - B_{leaves,senescence}$$

$$\Delta B_{sapwood} = B_{sapwood,growth} - B_{sapwood,senescence}$$

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The following equation defines the structural biomass balance at the plant level:

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Balance at the individual level

The biomass balance at the **individual level** is completed if we add the labile biomass balance to the structural biomass balance:

$$\Delta B_{plant} = \Delta B_{structure} + \Delta S_{labile}$$

2. Carbon compartments, pools and carbon balance

Biomass balance

Balance at the cohort level

At the **cohort level** we need to take into account that some individuals will die, so that the biomass balance needs to incorporate mortality losses:

$$\Delta B_{cohort} = \Delta B_{plant} \cdot N_{cohort} - B_{mortality}$$

where N_{cohort} is the initial cohort density (before mortality occurred) and $B_{mortality}$ is the biomass loss due to mortality of individuals, which in order to close the balance has to be defined as:

$$B_{mortality} = (B_{plant} + \Delta B_{plant}) \cdot N_{dead}$$

where N_{dead} is the density of dead individuals and B_{plant} is the initial plant biomass.

3. Growth and senescence

Leaf area/fine root biomass growth

Daily leaf area increment ΔLA and fine root biomass increment $\Delta B_{fineroot}$ are defined as the minimum of three constraints:

$$\Delta LA = \min(\Delta LA_{alloc}, \Delta LA_{source}, \Delta LA_{sink})$$

$$\Delta B_{fineroot} = \min(\Delta B_{fineroot,alloc}, \Delta B_{fineroot,source}, \Delta B_{fineroot,sink})$$

1. ΔLA_{alloc} and $\Delta B_{fineroot,alloc}$ are the increments allowed according to the targets set by **allocation rules**.
2. ΔLA_{source} and $\Delta B_{fineroot,source}$ are the maximum increments allowed by current **carbon availability**.
3. ΔLA_{sink} and $\Delta B_{fineroot,sink}$ are the increments expected by taking into account maximum growth rates as well as **temperature and turgor limitations** (Cabon et al. 2020).

Cabon et al (2020). New Phytologist, 226, 1325–1340.

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Sapwood area growth

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Unlike leaf area or fine root biomass, sapwood formation is not explicitly constrained by any allocation rule.

However, newly assimilated carbon is preferentially allocated to leaves and fine roots whenever storage levels are low because ΔSA_{source} is more restrictive than ΔLA_{source} or $\Delta B_{fineroot,source}$.

3. Growth and senescence

Key growth parameters

Parameter	R	Definition	Explanation
$RGR_{cambium,max}$	`RGRcambiummax`	Maximum daily **tree** sapwood growth rate relative to cambium perimeter length	Determines overall maximum growth rates for tree species
$RGR_{sapwood,max}$	`RGRsapwoodmax`	Maximum daily **shrub** sapwood growth rate relative to cambium perimeter length	Determines overall maximum growth rates for shrub species
$1/H_v$	`Al2As`	Leaf area to sapwood area ratio	Determines allocation target for **leaves**
RGR	`Ar2Al`	Root area to leaf area ratio	Determines allocation target for **fine roots** and influences root maintenance costs
$RSSG$	`RSSG`	Minimum relative starch for sapwood growth to occur	Determines preference for maintenance over growth under low carbon availability (e.g. shade-tolerant species)

3. Growth and senescence

Drivers of tissue senescence

Compartment	Senescence cause	Description	Key parameter
Leaf	Aging	Defoliation in winter-deciduous. Evergreens lose leaves progressively or suddenly, but with an amount related to leaf lifespan	`LeafDuration`
	Cavitation	Increases in stem PLC are translated to proportional leaf area losses	
Sapwood	Aging	Daily rate of conversion from sapwood to heartwood, depending on temperature and plant height	`SRsapwood`
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Note: Stem cavitation reduces functional sapwood but does not lead to heartwood formation.

3. Growth and senescence

Updating structural variables

Trees

New sapwood area, ΔSA, is translated to an increment in DBH, ΔDBH, following:

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Plant mortality

Dynamic vegetation models implement mortality processes in very different ways, from purely-empirical to process-based (Hawkes 2000).

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3. Daily mortality rates increase due to **dessication** whenever stem relative water content becomes lower than a pre-specified threshold, set to 30% by default.

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Plants are recruited with specified structural characteristics (DBH and height) depending on species parameters.

M.C. Escher - Three worlds, 1955