

Forest growth and dynamics (theory)

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Outline

1. Simulation models and processes
2. Carbon pools and carbon balance
3. Growth and senescence
4. Mortality and recruitment
5. Biomass balance
6. Fire effects

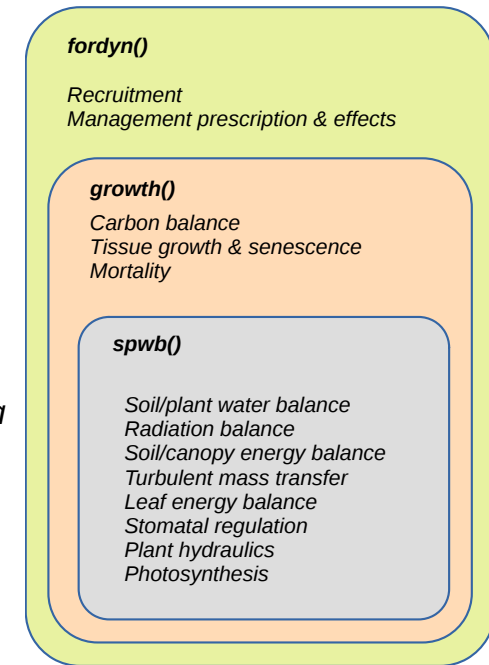
M.C. Escher - Three worlds, 1955



1. Simulation models and processes

About growth() and fordyn() models

1. Simulation functions in **medfate** have been designed and implemented in a **nested** manner.
2. The two water balance models (basic and advanced) are available for simulations with `growth()` and `fordyn()`.
3. The `growth()` model implements several **daily** processes:
 - i. Carbon balance processes resulting from the interplay of sources (photosynthesis) and sinks (maintenance respiration, growth respiration, root exudation, etc.).
 - ii. Growth and senescence processes that modulate changes in *leaf area*, *sapwood area* and *fine root area* of woody plant cohorts.
 - iii. Structural changes (diameter and height for trees; cover and height for shrubs) derived from growth and senescence processes.
 - iv. Tree mortality, which reduces cohort density.
4. For applications spanning more than a few years, users will use the `growth()` model indirectly, via calls to `fordyn()`, which includes other processes implemented at **annual** steps:
 - i. Natural regeneration (recruitment)
 - ii. The effect of disturbances (at present, only forest management and fire effects).



2. Carbon compartments, pools and carbon balance

Carbon compartments and pools

Carbon pool 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.

Pools

Compartment	Structural	Metabolic	Storage
<i>Leaves</i>	Leaf dry biomass B_{leaf}	Leaf sugar SS_{leaf}	Leaf starch ST_{leaf}
<i>Sapwood</i>	Sapwood dry biomass $B_{sapwood}$	Sapwood sugar $SS_{sapwood}$	Sapwood starch $ST_{sapwood}$
<i>Fine roots</i>	Fine root dry biomass $B_{fineroot}$		

Important

Sapwood carbon includes branches, stem and coarse roots

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}):

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

B. Changes in **leaf storage** carbon result from sugar-starch dynamics and translocation to sapwood storage (TT_{leaf}):

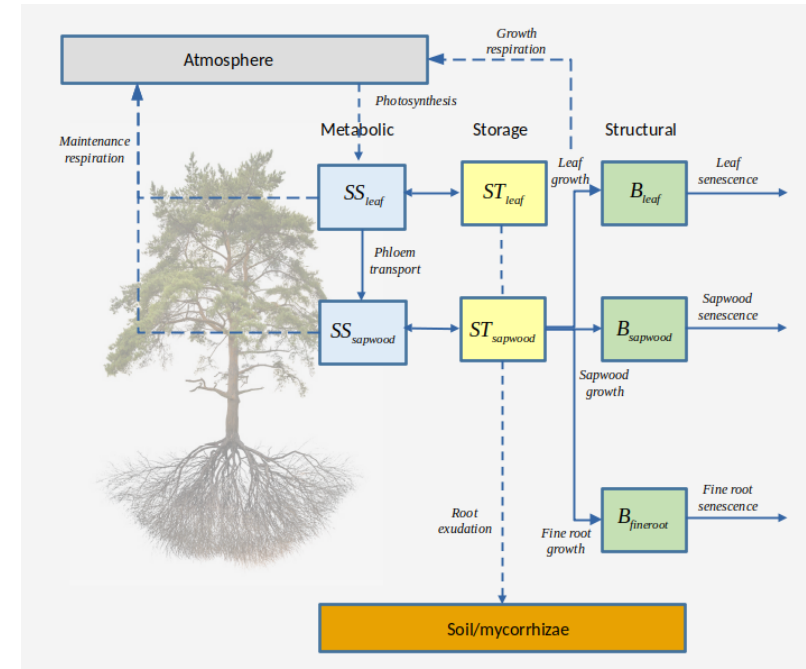
$$\Delta ST_{leaf} \cdot V_{storage,leaf} = SC_{leaf} - TT_{leaf}$$

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 ($TS_{sapwood}$):

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

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

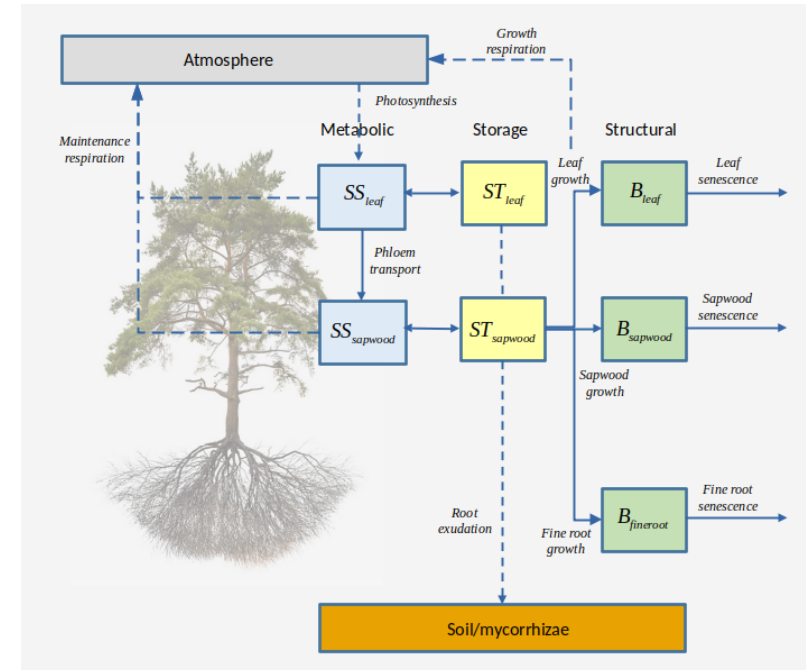
$$\Delta ST_{sapwood} \cdot V_{storage,sapwood} = SC_{sapwood} + TS_{leaf} + TT_{leaf} + TS_{sapwood} - G_{sapwood} - G_{leaf} - G_{fineroot} - RE_{sapwood}$$



Labile carbon balance equations

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

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



Design of labile carbon processes

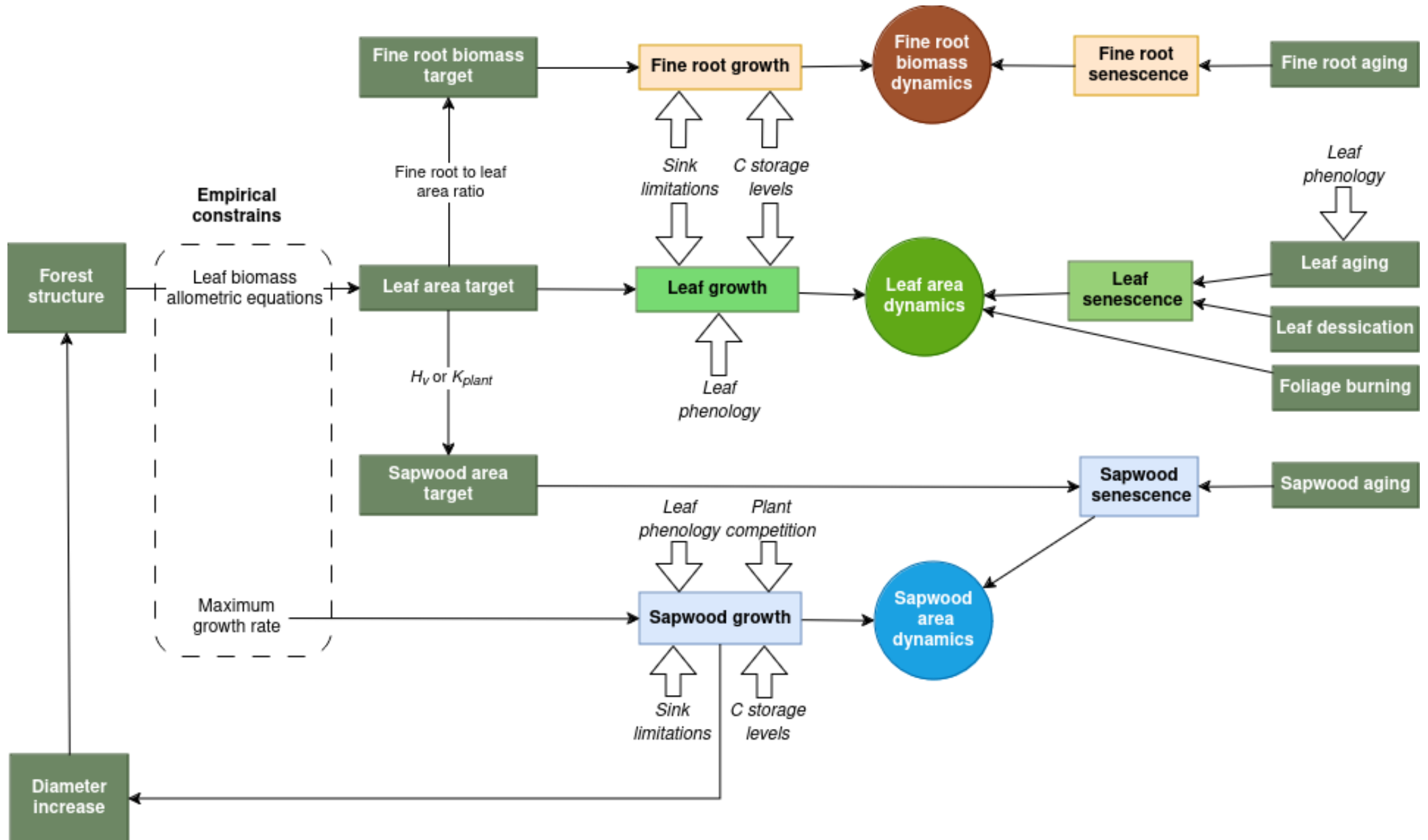
- **Phloem transport** is only explicitly modelled when using the **advanced water submodel**, following Hölttä et al. (2017)¹.
- **Sugar/starch dynamics** are meant to keep sugar levels at a prescribed equilibrium value.
- The usual separation between **maintenance** and **growth** respiration is followed, with maintenance costs depending on temperature and phenology.
- **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 surpassed².

1. Lindner et al (1997). Forest Ecology and Management, 95, 183–195.

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

3. Growth and senescence

Drivers of growth and senescence



Tissue growth

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

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

$$\Delta SA = \min(\Delta SA_{source}, \Delta SA_{sink})$$

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

- ΔLA_{alloc} and $\Delta B_{fineroot,alloc}$ are the increments allowed according to the targets set by **allocation rules**.
- ΔLA_{source} , ΔSA_{source} and $\Delta B_{fineroot,source}$ are the maximum increments allowed by current **starch availability**.
- ΔLA_{sink} , ΔSA_{sink} and $\Delta B_{fineroot,sink}$ are the increments expected due to **growth rates**, which are affected by temperature and turgor limitations ¹.

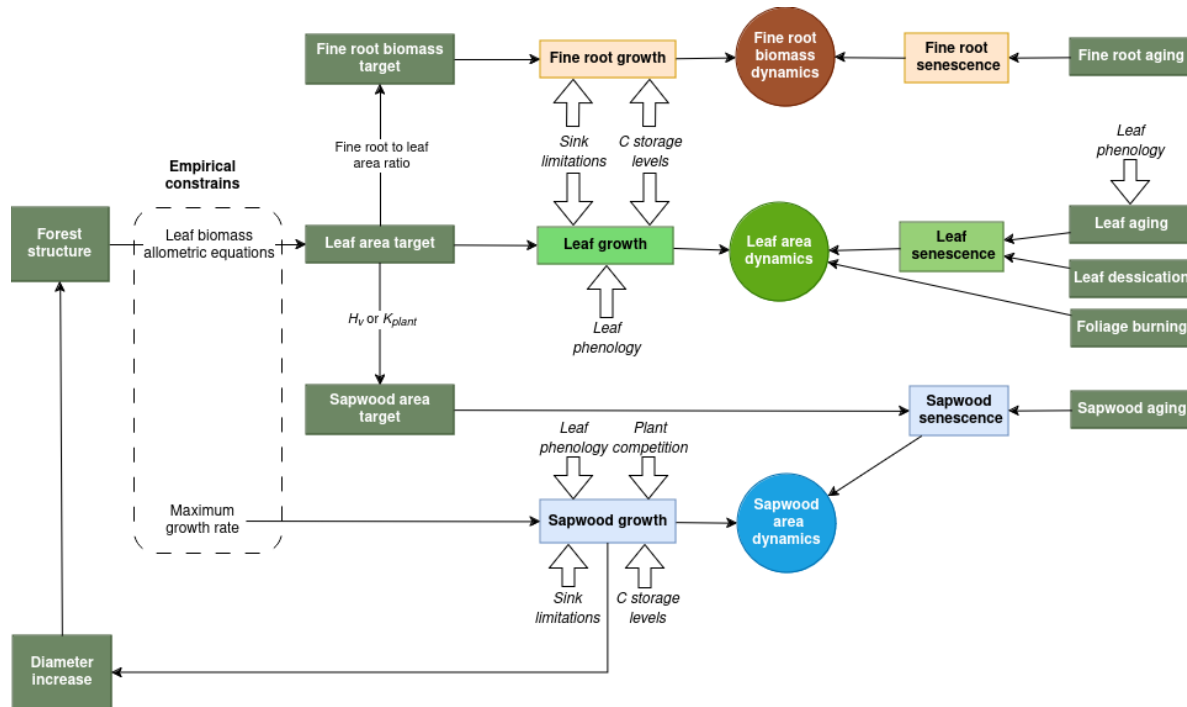
Important

- Sapwood area growth is **not limited** by allocation rules, effectively determining overall plant growth.
- Carbon is **preferentially** allocated to leaves and fine roots whenever storage levels are low because ΔSA_{source} is more restrictive than ΔLA_{source} or $\Delta B_{fineroot,source}$.

Tissue growth

Key growth parameters

Parameter	R	Definition	Explanation
$a_{fbt}, b_{fbt}, c_{fbt}$	$A_{fbt}, B_{fbt}, C_{fbt}$	Allometric coefficients for tree leaf biomass, including competition	Determine allocation target for tree leaf area and influence sapwood area growth rates
$RGR_{cambium,max}$	$RGR_{cambiummax}$	Maximum daily tree sapwood growth rate relative to cambium perimeter length	Determines overall maximum growth rates for tree species
$RGR_{sapwood,max}$	$RGR_{sapwoodmax}$	Maximum daily shrub sapwood growth rate relative to cambium perimeter length	Determines overall maximum growth rates for shrub species
$1/H_v$	A_{l2As}	Leaf area to sapwood area ratio	Determines allocation target for sapwood and, hence, sapwood senescence rates.
RGR	A_{r2Al}	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)



- **Leaf senescence rates** are determined by:
 - *Aging* (leaf lifespan)
 - *Phenology* (winter deciduous)
 - *Dessication* (via stem cavitation)
- **Sapwood senescence rates** are determined by:
 - *Aging* (depending on temperature)
 - *Sapwood area target* (only if $SA > SA_{target}$)
- **Fine root senescence rates** are determined by:
 - *Aging* (depending on temperature)

- Leaf and fine root senescence create a need to constantly replace tissues.
- Sapwood senescence aims to keep sapwood area close to its functional target (either constant leaf area to sapwood area ratio or a constant whole-plant conductance).

Updating structural variables

Trees

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

$$\Delta DBH = 2 \cdot \sqrt{(DBH/2)^2 + (\Delta SA/\pi)} - DBH$$

Increments in height are linearly related to increments in diameter through a coefficient depending on light conditions ¹, and are limited by a maximum height.

Crown ratios are updated following static allometric relationships.

Shrubs

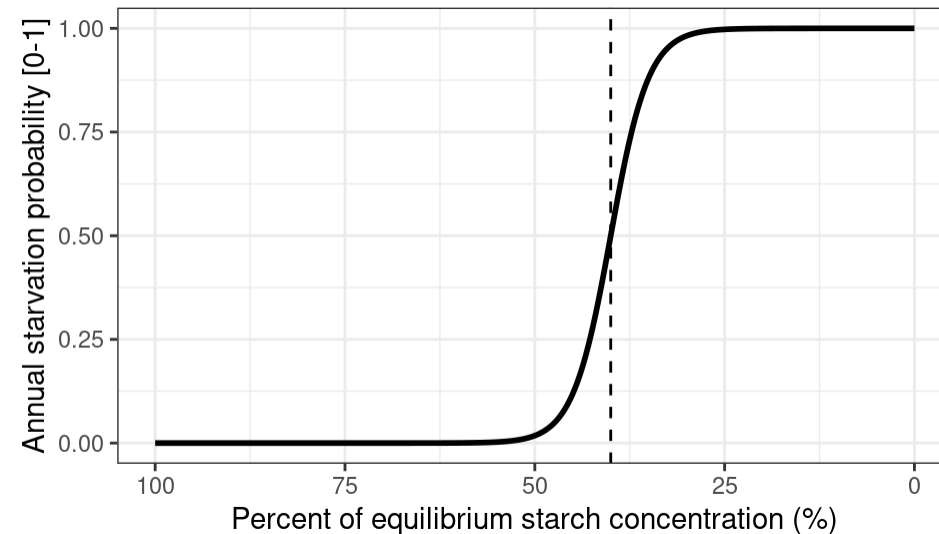
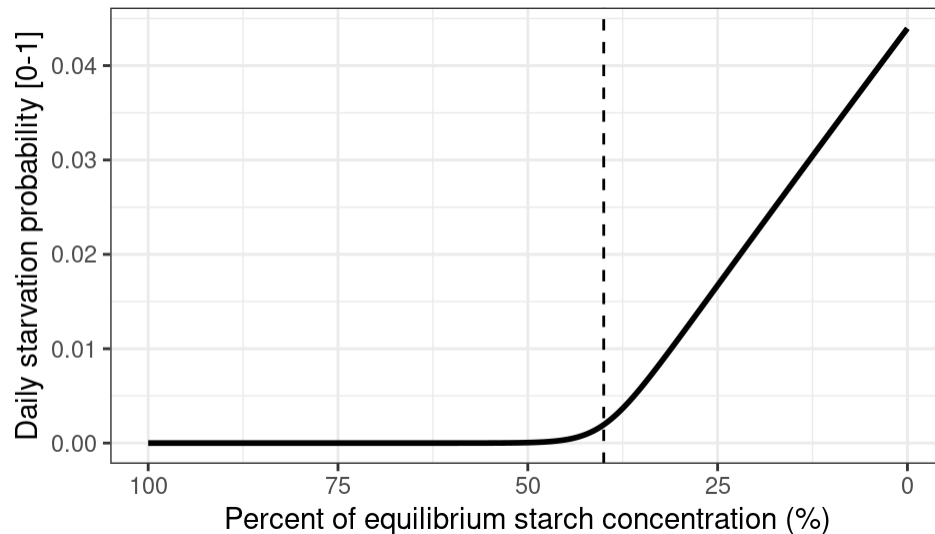
Leaf area changes are translated to changes in shrub volume, cover and shrub height via allometric equations.

As for trees, shrub height is limited to a maximum value.

4. Mortality and recruitment

Plant mortality

1. Small trees ($1 < DBH < 7.5$) die at a rate determined by a **self-thinning rule** depending on its size.
2. Species-specific parameters determine a daily constant **baseline mortality rate** for adults.
3. Daily mortality rates increase due to **carbon starvation** whenever sapwood metabolic carbon, $SS_{sapwood}$, becomes lower than a threshold, set by default to 40% of the homeostatic (equilibrium) concentrations. The daily starvation rate at the threshold corresponds to an annual mortality of 50%.



4. Daily mortality rates increase due to **dessication** whenever the average of *stem relative water content* and *stem relative hydraulic conductance* becomes lower than a pre-specified threshold, set to 40% by default.

Recruitment

Unlike mortality, recruitment is simulated *at the end of a simulated year* (only in `fordyn()`).

Recruitment from seed

- **Seed banks** are full whenever trees of the species are present with a **size above a maturity threshold** (or a seed rain is forced). Otherwise, they are reduced following an exponential decay function.
- The following conditions need to be met for a species to recruit:
 1. **Mean temperature of the coldest month** is above a bioclimatic threshold.
 2. The **fraction of light reaching the ground** is above a bioclimatic threshold.
 3. The **moisture index** (annual precipitation over annual evapotranspiration) is larger than a bioclimatic threshold.
- A **probability of recruitment** is used to stochastically determine whether recruitment actually occurs.

Resprouting

- Resprouting occurs if plants have been **cut, burned or dessicated**.
- Resprouting **survivorship** depends on the disturbance (different effects on buds).
- Resprouting **vigour** for trees depends on *DBH*.

5. Biomass balance

Biomass balance

Balance in structural carbon pools

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

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

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

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

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

$$\Delta B_{structure} = \Delta B_{leaves} + \Delta B_{sapwood} + \Delta B_{fineroot}$$

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:

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

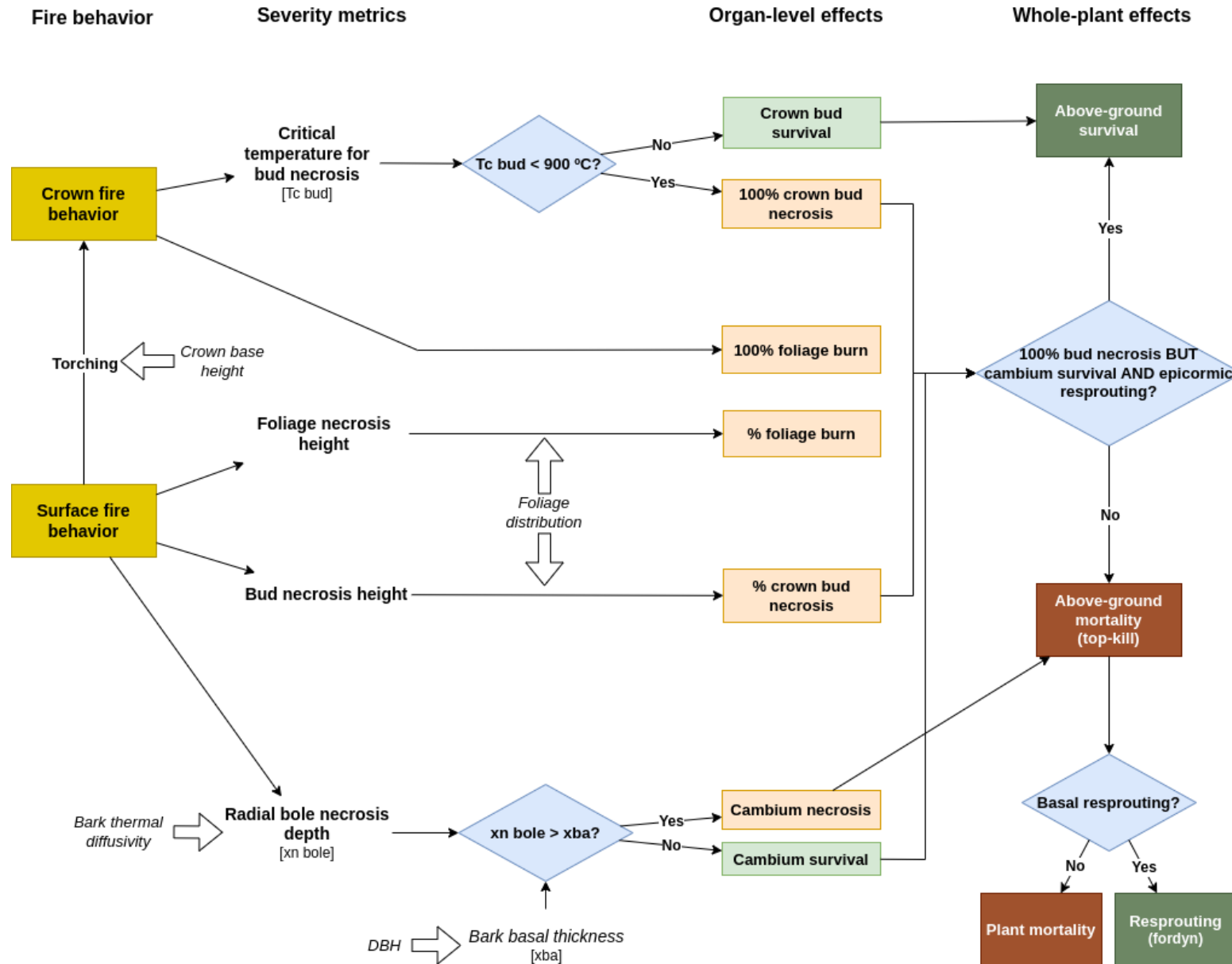
where N_{cohort} is the initial cohort density (before mortality occurred) and $B_{mortality}$ is the biomass loss due to mortality of individuals, which in order to close the balance has to be defined as:

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

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

6. Fire effects

Design of fire effects



M.C. Escher - Three worlds, 1955

