

# MAECS

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# Symbols

**Symbols used in formulas, respective model parameters, and their descriptions**

---

$P_{max}$     P\_max : phyto max. growth rate

# Chapter 1

## MAECS: Model for Adaptive Ecosystems in Coastal Seas

### 1.1 General Overview

With regard to the conceptualization of trophic interactions, MAECS resembles the classical N-P-Z-D models (1). The emphasis is on the regulation of a number of physiological processes in the phytoplankton unit, which are resolved following a sophisticated optimization scheme. Energy & nutrient allocation scheme of the phytoplankton, as well as the optimization concept used in MAECS is hinted by the model described by [Wirtz and Pahlow \(2010\)](#). See the last section (2) (available only in the pdf form of the documentation) for a detailed description and model equations with some narration.

**Todo** (1) include a diagram here

**Todo** (2) find out how to refer to latex-only sections from the mainpage

In order to re-generate this documentation, make sure the prerequisites (doxygen, latex, bibtex) installed in your system, then type:

```
make
```

inside:

```
$FABMDIR/src/models/hzg/maecs/doc/
```

## Chapter 2

## Todo List

page [MAECS: Model for Adaptive Ecosystems in Coastal Seas](#)

(1) include a diagram here<p>(2) find out how to refer to latex-only sections from the mainpage

Subprogram [maecs\\_functions::calc\\_internal\\_states](#) (maecs, phy, det, dom, zoo)

: add equations

Subprogram [maecs\\_functions::calc\\_sensitivities](#) (maecs, sens, phy, env, nut)

: add a better description and equations

Subprogram [maecs\\_functions::foptupt](#) (Aff0, Vmax0, Nut)

: add equations

Subprogram [maecs\\_functions::min\\_mass](#) (maecs, phy, method)

: add equations

Subprogram [maecs\\_functions::queuederiv](#) (n, x)

: add equations

Subprogram [maecs\\_functions::queuefunc](#) (n, x, qfunc, qderiv)

: add equations

Subprogram [maecs\\_functions::queuefunc1](#) (n, x, qfunc, qderiv)

: add equations

Subprogram [maecs\\_functions::sinking](#) (vS, phys\_status, sinkvel)

: add equations

Subprogram [maecs\\_functions::smooth\\_small](#) (x, eps)

: add a description and details

Subprogram [maecs\\_functions::uptflex](#) (Aff0, Vmax0, Nut, fAv)

: add equations

Type [maecs\\_types](#)

: !!! documentation is interfering with the parser !!!

Type [maecs\\_types::type\\_maecs\\_base\\_model](#)

: complete the parameter list

Type [maecs\\_types::type\\_maecs\\_rhs](#)

: need for a parameter list?

## Chapter 3

# Data Type Index

### 3.1 Class Hierarchy

This inheritance list is sorted roughly, but not completely, alphabetically:

|  |    |
|--|----|
| fabm_hzg_maecs . . . . .                               | 8  |
| maecs_functions . . . . .                              | 8  |
| fabm_hzg_maecs::maecs_get_vertical_movement . . . . .  | 11 |
| maecs_grazing . . . . .                                | 12 |
| maecs_primprod . . . . .                               | 12 |
| maecs_types . . . . .                                  | 12 |
| maecs_types::stoichiometry_pointer . . . . .           | 13 |
| type_base_model  |    |
| maecs_types::type_maecs_base_model . . . . .           | 14 |
| maecs_types::type_maecs_allocation_fractions . . . . . | 13 |
| type_maecs_base_model                                  |    |
| fabm_hzg_maecs::type_hzg_maecs . . . . .               | 13 |
| maecs_types::type_maecs_basic_traits . . . . .         | 14 |
| maecs_types::type_maecs_env . . . . .                  | 14 |
| maecs_types::type_maecs_om . . . . .                   | 15 |
| maecs_types::type_maecs_life . . . . .                 | 15 |
| maecs_types::type_maecs_phy . . . . .                  | 15 |
| maecs_types::type_maecs_zoo . . . . .                  | 17 |
| maecs_types::type_maecs_rhs . . . . .                  | 16 |
| maecs_types::type_maecs_sensitivities . . . . .        | 16 |
| maecs_types::type_maecs_switch . . . . .               | 16 |
| maecs_types::type_maecs_traitdyn . . . . .             | 16 |

## Chapter 4

# Data Type Index

### 4.1 Data Types List

Here are the data types with brief descriptions:

|  |    |
|--|----|
| <a href="#">fabm_hzg_maecs</a>   |    |
| This is the module registered in FABM . . . . .                              | 8  |
| <a href="#">maecs_functions</a>  |    |
| All functions called by maecs_do are defined here . . . . .                  | 8  |
| <a href="#">fabm_hzg_maecs::maecs_get_vertical_movement</a>                  |    |
| Handles vertical movement for depth-varying movement rates . . . . .         | 11 |
| <a href="#">maecs_grazing</a> . . . . .                                      | 12 |
| <a href="#">maecs_primprod</a> . . . . .                                     | 12 |
| <a href="#">maecs_types</a>  |    |
| Data types used in <a href="#">fabm_hzg_maecs</a> are defined here . . . . . | 12 |
| <a href="#">maecs_types::stoichiometry_pointer</a> . . . . .                 | 13 |
| <a href="#">fabm_hzg_maecs::type_hzg_maecs</a>                               |    |
| This is the model type FABM uses to create the mode . . . . .                | 13 |
| <a href="#">maecs_types::type_maecs_allocation_fractions</a> . . . . .       | 13 |
| <a href="#">maecs_types::type_maecs_base_model</a>                           |    |
| Stores standard fabm model types and self-parameters . . . . .               | 14 |
| <a href="#">maecs_types::type_maecs_basic_traits</a> . . . . .               | 14 |
| <a href="#">maecs_types::type_maecs_env</a>                                  |    |
| Stores environmental dependencies . . . . .                                  | 14 |
| <a href="#">maecs_types::type_maecs_life</a> . . . . .                       | 15 |
| <a href="#">maecs_types::type_maecs_om</a> . . . . .                         | 15 |
| <a href="#">maecs_types::type_maecs_phy</a> . . . . .                        | 15 |
| <a href="#">maecs_types::type_maecs_rhs</a>                                  |    |
| Stores right hand sides . . . . .  | 16 |
| <a href="#">maecs_types::type_maecs_sensitivities</a> . . . . .              | 16 |
| <a href="#">maecs_types::type_maecs_switch</a> . . . . .                     | 16 |
| <a href="#">maecs_types::type_maecs_traitdyn</a> . . . . .                   | 16 |
| <a href="#">maecs_types::type_maecs_zoo</a> . . . . .                        | 17 |



## Chapter 5

# File Index

### 5.1 File List

Here is a list of all documented files with brief descriptions:

|                                     |    |  |
|-------------------------------------|----|--|
| <a href="#">maecs.F90</a>           |    |  |
| Main MAECS module                   | 18 |  |
| <b>maecs_do.F90</b>                 | ?? |  |
| <a href="#">maecs_functions.F90</a> |    |  |
| Various maecs functions             | 18 |  |
| <b>maecs_grazing.F90</b>            | ?? |  |
| <b>maecs_primprod.F90</b>           | ?? |  |
| <a href="#">maecs_types.F90</a>     |    |  |
| Maecs_types module                  | 19 |  |
| <b>mainpage.doxygen</b>             | ?? |  |

## Chapter 6

# Data Type Documentation

### 6.1 fabm\_hzg\_maecs Module Reference

This is the module registered in FABM.

#### Data Types

- interface [maecs\\_get\\_vertical\\_movement](#)  
*handles vertical movement for depth-varying movement rates*
- type [type\\_hzg\\_maecs](#)  
*this is the model type FABM uses to create the mode*

#### 6.1.1 Detailed Description

This is the module registered in FABM.

all the [maecs\\_types](#) are made available to this module

Definition at line 10 of file maecs.F90.

The documentation for this module was generated from the following file:

- [maecs.F90](#)

### 6.2 maecs\_functions Module Reference

all functions called by maecs\_do are defined here

#### Public Member Functions

- pure real(rk) function, public [smooth\\_small](#) (x, eps)  
*smoothly ..?*
- pure real(rk) function, public [uptflex](#) (Aff0, Vmax0, Nut, fAv)  
*calc's pot nut upt as f(external conc, allocations)*
- pure real(rk) function [foptupt](#) (Aff0, Vmax0, Nut)  
*opt. partitioning between surf upt sites and intern. enzymes for nut assim.*

- subroutine, public [queuefunc](#) (n, x, qfunc, qderiv)  
*the queue function*
- subroutine [queuefunc1](#) (n, x, qfunc, qderiv)  
*approximation of the queue function*
- real(rk) function, public [queuederiv](#) (n, x)  
*derivative of the queue function ??*
- subroutine, public [sinking](#) (vS, phys\_status, sinkvel)  
*calculation of the sinking rate*
- subroutine, public [min\\_mass](#) (maecs, phy, method)  
*minimum mass*
- subroutine, public [calc\\_sensitivities](#) (maecs, sens, phy, env, nut)  
*calculate sensitivities*
- subroutine, public [calc\\_internal\\_states](#) (maecs, phy, det, dom, zoo)  
*calculate the internal states*

### 6.2.1 Detailed Description

all functions called by maecs\_do are defined here

Definition at line 10 of file maecs\_functions.F90.

### 6.2.2 Member Function/Subroutine Documentation

6.2.2.1 pure real(rk) function, public maecs\_functions::smooth\_small ( real(rk), intent(in) x, real(rk), intent(in) eps )

smoothly ..?

Returns

smooth\_small

**Todo** : add a description and details

Definition at line 30 of file maecs\_functions.F90.

Referenced by [calc\\_internal\\_states\(\)](#), [calc\\_sensitivities\(\)](#), and [min\\_mass\(\)](#).

6.2.2.2 pure real(rk) function, public maecs\_functions::uptflex ( real(rk), intent(in) Aff0, real(rk), intent(in) Vmax0, real(rk), intent(in) Nut, real(rk), intent(in) fAv )

calc's pot nut upt as f(external conc, allocations)

Returns

uptflex

**Todo** : add equations

Definition at line 53 of file maecs\_functions.F90.

Referenced by [calc\\_sensitivities\(\)](#).

6.2.2.3 pure real(rk) function maecs\_functions::foptupt ( real(rk), intent(in) *Aff0*, real(rk), intent(in) *Vmax0*, real(rk), intent(in) *Nut* )

opt. partitioning between surf upt sites and intern. enzymes for nut assim.

Returns

fOptUpt

**Todo** : add equations

Definition at line 71 of file maecs\_functions.F90.

Referenced by calc\_sensitivities().

6.2.2.4 subroutine, public maecs\_functions::queuefunc ( real(rk), intent(in) *n*, real(rk), intent(in) *x*, real(rk), intent(out) *qfunc*, real(rk), intent(out) *qderiv* )

the queue function

n->inf :liebig n~1:product

**Todo** : add equations

Definition at line 84 of file maecs\_functions.F90.

6.2.2.5 subroutine maecs\_functions::queuefunc1 ( real(rk), intent(in) *n*, real(rk), intent(in) *x*, real(rk), intent(out) *qfunc*, real(rk), intent(out) *qderiv* )

approximation of the queue function

n->inf :liebig n~1:product

**Todo** : add equations

Definition at line 106 of file maecs\_functions.F90.

6.2.2.6 real(rk) function, public maecs\_functions::queuederiv ( real(rk), intent(in) *n*, real(rk), intent(in) *x* )

derivative of the queue function ??

Returns

queuederiv

**Todo** : add equations

Definition at line 129 of file maecs\_functions.F90.

6.2.2.7 subroutine, public maecs\_functions::sinking ( real(rk), intent(in) *vS*, real(rk), intent(in) *phys\_status*, real(rk), intent(out) *sinkvel* )

calculation of the sinking rate

**Todo** : add equations

Definition at line 144 of file maecs\_functions.F90.

6.2.2.8 subroutine, public maecs\_functions::min\_mass ( type (type\_maecs\_base\_model), intent(in) *maecs*, type (type\_maecs\_phy), intent(inout) *phy*, integer, intent(in), optional *method* )

minimum mass

**Todo** : add equations

Definition at line 206 of file maecs\_functions.F90.

References smooth\_small().

6.2.2.9 subroutine, public maecs\_functions::calc\_sensitivities ( type (type\_maecs\_base\_model), intent(in) *maecs*, type (type\_maecs\_sensitivities), intent(out) *sens*, type (type\_maecs\_phy), intent(in) *phy*, type (type\_maecs\_env), intent(in) *env*, type (type\_maecs\_om), intent(in) *nut* )

calculate sensitivities

**Todo** : add a better description and equations

Definition at line 311 of file maecs\_functions.F90.

References foxtupt(), smooth\_small(), and uptflex().

6.2.2.10 subroutine, public maecs\_functions::calc\_internal\_states ( type (type\_maecs\_base\_model), intent(in) *maecs*, type (type\_maecs\_phy), intent(inout) *phy*, type (type\_maecs\_om), intent(inout) *det*, type (type\_maecs\_om), intent(inout) *dom*, type (type\_maecs\_zoo), intent(inout) *zoo* )

calculate the internal states

**Todo** : add equations

Definition at line 372 of file maecs\_functions.F90.

References smooth\_small().

The documentation for this module was generated from the following file:

- [maecs\\_functions.F90](#)

## 6.3 fabm\_hzg\_maecs::maecs\_get\_vertical\_movement Interface Reference

handles vertical movement for depth-varying movement rates

### 6.3.1 Detailed Description

handles vertical movement for depth-varying movement rates

phyto sinking rate depends on the nutritional state, so for each node:

$phy\%relQ$  obtained by calling calc\_internal\_states(self,phy,det,dom,zoo)

then  $phyQstat = phy\%relQ\%N * phy\%relQ\%P$

finally, vsink = sinking(self%vS\_phy, phyQstat, vsink)

Definition at line 41 of file maecs.F90.

The documentation for this interface was generated from the following file:

- [maecs.F90](#)

## 6.4 maecs\_grazing Module Reference

### 6.4.1 Detailed Description

Definition at line 9 of file `maecs_grazing.F90`.

The documentation for this module was generated from the following file:

- `maecs_grazing.F90`

## 6.5 maecs\_primprod Module Reference

### 6.5.1 Detailed Description

Definition at line 7 of file `maecs_primprod.F90`.

The documentation for this module was generated from the following file:

- `maecs_primprod.F90`

## 6.6 maecs\_types Module Reference

Data types used in `fabm_hzg_maecs` are defined here.

### Data Types

- type `stoichiometry_pointer`
- type `type_maecs_allocation_fractions`
- type `type_maecs_base_model`  
*stores standard fabm model types and self-parameters*
- type `type_maecs_basic_traits`
- type `type_maecs_env`  
*stores environmental dependencies*
- type `type_maecs_life`
- type `type_maecs_om`
- type `type_maecs_phy`
- type `type_maecs_rhs`  
*stores right hand sides*
- type `type_maecs_sensitivities`
- type `type_maecs_switch`
- type `type_maecs_traitdyn`
- type `type_maecs_zoo`

### 6.6.1 Detailed Description

Data types used in `fabm_hzg_maecs` are defined here.

**Todo** : !!! documentation is interfering with the parser !!!

Definition at line 12 of file `maecs_types.F90`.

The documentation for this module was generated from the following file:

- [maecs\\_types.F90](#)

## 6.7 `maecs_types::stoichiometry_pointer` Type Reference

### 6.7.1 Detailed Description

Definition at line 124 of file `maecs_types.F90`.

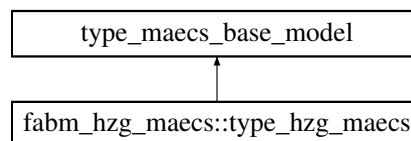
The documentation for this type was generated from the following file:

- [maecs\\_types.F90](#)

## 6.8 `fabm_hzg_maecs::type_hzg_maecs` Type Reference

this is the model type FABM uses to create the mode

Inheritance diagram for `fabm_hzg_maecs::type_hzg_maecs`:



### 6.8.1 Detailed Description

this is the model type FABM uses to create the mode

the parent type (`type_maecs_base_model`) was defined in [maecs\\_types](#) module

Definition at line 26 of file `maecs.F90`.

The documentation for this type was generated from the following file:

- [maecs.F90](#)

## 6.9 `maecs_types::type_maecs_allocation_fractions` Type Reference

### 6.9.1 Detailed Description

Definition at line 74 of file `maecs_types.F90`.

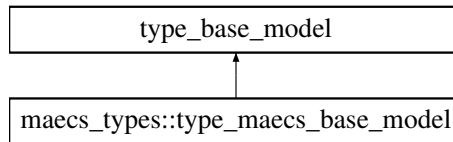
The documentation for this type was generated from the following file:

- [maecs\\_types.F90](#)

## 6.10 `maecs_types::type_maecs_base_model` Type Reference

stores standard fabm model types and self-parameters

Inheritance diagram for `maecs_types::type_maecs_base_model`:



### 6.10.1 Detailed Description

stores standard fabm model types and self-parameters

this model type parents the FABM-recognized [type\\_maecs\\_base\\_model](#)

Model parameters, descriptions and corresponding symbols used in formulas:

Parameters

|           |                                    |
|-----------|------------------------------------|
| $P_{max}$ | $P_{max}$ : phyto max. growth rate |
|-----------|------------------------------------|

**Todo** : complete the parameter list

Definition at line 43 of file `maecs_types.F90`.

The documentation for this type was generated from the following file:

- [maecs\\_types.F90](#)

## 6.11 `maecs_types::type_maecs_basic_traits` Type Reference

### 6.11.1 Detailed Description

Definition at line 69 of file `maecs_types.F90`.

The documentation for this type was generated from the following file:

- [maecs\\_types.F90](#)

## 6.12 `maecs_types::type_maecs_env` Type Reference

stores environmental dependencies

### 6.12.1 Detailed Description

stores environmental dependencies

Definition at line 28 of file `maecs_types.F90`.

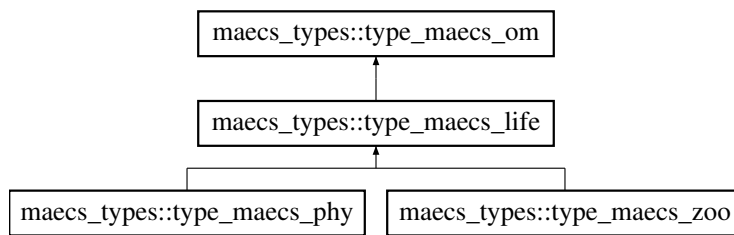
The documentation for this type was generated from the following file:

- [maecs\\_types.F90](#)



## 6.13 maecs\_types::type\_maecs\_life Type Reference

Inheritance diagram for maecs\_types::type\_maecs\_life:



### 6.13.1 Detailed Description

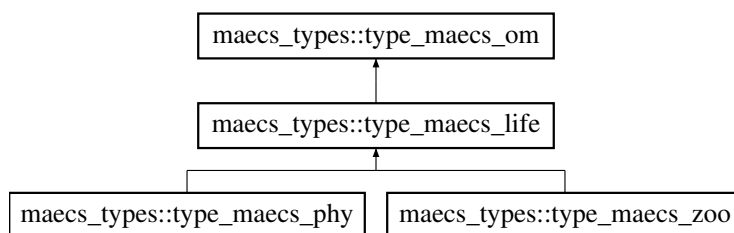
Definition at line 81 of file `maecs_types.F90`.

The documentation for this type was generated from the following file:

- [maecs\\_types.F90](#)

## 6.14 maecs\_types::type\_maecs\_om Type Reference

Inheritance diagram for maecs\_types::type\_maecs\_om:



### 6.14.1 Detailed Description

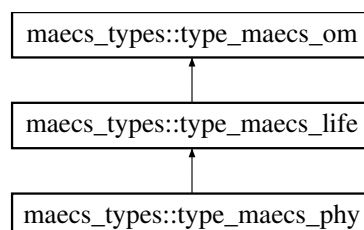
Definition at line 65 of file `maecs_types.F90`.

The documentation for this type was generated from the following file:

- [maecs\\_types.F90](#)

## 6.15 maecs\_types::type\_maecs\_phy Type Reference

Inheritance diagram for maecs\_types::type\_maecs\_phy:



### 6.15.1 Detailed Description

Definition at line 86 of file maecs\_types.F90.

The documentation for this type was generated from the following file:

- [maecs\\_types.F90](#)

## 6.16 maecs\_types::type\_maecs\_rhs Type Reference

stores right hand sides

### 6.16.1 Detailed Description

stores right hand sides

**Todo** : need for a parameter list?

Definition at line 34 of file maecs\_types.F90.

The documentation for this type was generated from the following file:

- [maecs\\_types.F90](#)

## 6.17 maecs\_types::type\_maecs\_sensitivities Type Reference

### 6.17.1 Detailed Description

Definition at line 115 of file maecs\_types.F90.

The documentation for this type was generated from the following file:

- [maecs\\_types.F90](#)

## 6.18 maecs\_types::type\_maecs\_switch Type Reference

### 6.18.1 Detailed Description

Definition at line 61 of file maecs\_types.F90.

The documentation for this type was generated from the following file:

- [maecs\\_types.F90](#)

## 6.19 maecs\_types::type\_maecs\_traitdyn Type Reference

### 6.19.1 Detailed Description

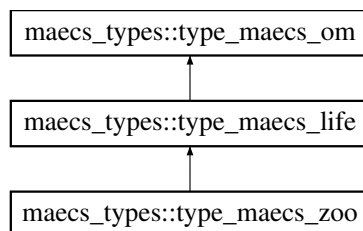
Definition at line 103 of file maecs\_types.F90.

The documentation for this type was generated from the following file:

- [maecs\\_types.F90](#)

## 6.20 maecs\_types::type\_maecs\_zoo Type Reference

Inheritance diagram for maecs\_types::type\_maecs\_zoo:



### 6.20.1 Detailed Description

Definition at line 97 of file `maecs_types.F90`.

The documentation for this type was generated from the following file:

- [maecs\\_types.F90](#)

# Chapter 7

## File Documentation

### 7.1 `maecs.F90` File Reference

main MAECS module

```
#include "fabm_driver.h"
```

#### Data Types

- module [fabm\\_hzg\\_maecs](#)  
*This is the module registered in FABM.*
- type [fabm\\_hzg\\_maecs::type\\_hzg\\_maecs](#)  
*this is the model type FABM uses to create the mode*
- interface [fabm\\_hzg\\_maecs::maecs\\_get\\_vertical\\_movement](#)  
*handles vertical movement for depth-varying movement rates*

#### 7.1.1 Detailed Description

main MAECS module

Author

Richard Hofmeister, Markus Schartau, Kai Wirtz, Onur Kerimoglu

Copyright

HZG [dates?]

Author

Richard Hofmeister, Markus Schartau, Kai Wirtz, Onur Kerimoglu

Copyright

HZG

Definition in file [maecs.F90](#).

### 7.2 `maecs_functions.F90` File Reference

various maecs functions

```
#include "fabm_driver.h"
```

## Data Types

- module [maecs\\_functions](#)

*all functions called by maecs\_do are defined here*

### 7.2.1 Detailed Description

various maecs functions

Author

Richard Hofmeister, Markus Schartau, Kai Wirtz, Onur Kerimoglu

Copyright

HZG

Definition in file [maecs\\_functions.F90](#).

## 7.3 maecs\_types.F90 File Reference

[maecs\\_types](#) module

```
#include "fabm_driver.h"
```

## Data Types

- module [maecs\\_types](#)

*Data types used in [fabm\\_hzg\\_maecs](#) are defined here.*

- type [maecs\\_types::type\\_maecs\\_env](#)

*stores environmental dependencies*

- type [maecs\\_types::type\\_maecs\\_rhs](#)

*stores right hand sides*

- type [maecs\\_types::type\\_maecs\\_base\\_model](#)

*stores standard fabm model types and self-parameters*

- type [maecs\\_types::type\\_maecs\\_switch](#)

- type [maecs\\_types::type\\_maecs\\_om](#)

- type [maecs\\_types::type\\_maecs\\_basic\\_traits](#)

- type [maecs\\_types::type\\_maecs\\_allocation\\_fractions](#)

- type [maecs\\_types::type\\_maecs\\_life](#)

- type [maecs\\_types::type\\_maecs\\_phy](#)

- type [maecs\\_types::type\\_maecs\\_zoo](#)

- type [maecs\\_types::type\\_maecs\\_traitdyn](#)

- type [maecs\\_types::type\\_maecs\\_sensitivities](#)

- type [maecs\\_types::stoichiometry\\_pointer](#)

### 7.3.1 Detailed Description

[maecs\\_types](#) module

Author

Richard Hofmeister, Kai Wirtz, Onur Kerimoglu

Copyright

HZG

Definition in file [maecs\\_types.F90](#).

## Chapter 8

# Textual Model Description

### 8.1 Model structure

MAECS resolves major functional groups and their dynamics not unlike simple state-of-the-art ecosystem models. All energy and material fluxes in the ecosystem derive from primary production of phytoplankton, here expressed in terms of biomass carbon (C) concentration. Phytoplankton experiences various local and trait dependent loss rates, from sinking, respiration, exudation, to grazing. MAECS versions differ in the degree of resolution in ecological processes; a full account of grazing interactions in the plankton is only addressed by versions that includes size as a major trait. Grazers convert only a fraction of captured phytoplankton to their own biomass; in size-based variants of MAECS we have implemented different formulations for whether this fraction immediately contributes to the biomass of adult grazers or their egg stage, or how many grazer groups are simulated (see below).

Physiological regulation in unicellular autotrophs makes the very kernel of the MAECS version documented here. The intracellular nutrient quotas, in this model version resolved for nitrogen (N), phosphorus (P), and silicon (Si), change over time when uptake does not match demand due to biomass build-up. Differential uptake regulation then leads to highly variable stoichiometries, that not only reflect ambient nutrient and light concentration, but also generalized optimality criteria.

For describing the living compartment of plankton ecosystems MAECS employs much more trait variables (e.g., allocation coefficients) compared to bulk variables (e.g., phytoplankton or zooplankton biomass). The adaptive trait dynamics infers the need of calculating (sometimes long) derivative terms, which also challenges this documentation; however, the gradient-derived terms include very few additional process parameters, so that the number of tunable parameters in relation to simulated and testable dynamics is significantly reduced compared to models that share a similar resolution in plankton physiology or ecology. Most importantly, MAECS seeks to account for biophysical and evolutionary principles as much as possible; resulting in expressions replacing heuristic functions such as Michaelis-Menten approximations of nutrient uptake, Droop representation of cell growth, or Liebig's rule of minimum. Biophysical origins of model formulations further reduces the number of tunable parameters, in particular in the ecological part. Prominent counter-examples, i.e. yet uncertain model formulations or parameters, comprise aggregation dynamics or variations in metabolic interdependency.

#### 8.1.1 Mass equations

Basic mass equations common to the two MAECS variants (size and physiology). All coefficients and their meanings are listed in Table ??.

Net change in autotroph C, N, P, Si (cf. Eq.(8.8) and Eq.(8.29)) ...

$$\frac{d}{dt}\text{Phy}_C = \mu_{\text{tot}} \cdot \text{Phy}_C \quad (8.1)$$

$$\frac{d}{dt}\text{Phy}_X = V_X \cdot \text{Phy}_C - M \cdot \text{Phy}_X \quad \text{with } X = \text{N, P, Si} \quad (8.2)$$

... in dissolved inorganic nutrients ( $X=N, P$ ), optionally including silicate

$$\frac{d}{dt}DIX = -V_X \text{Phy}_C + \omega_{\text{DOM}}^{(8.7)} DOX \quad (8.3)$$

$$\frac{d}{dt}DSi = -V_{Si} \text{Phy}_C + \omega_{\text{Det}}^{(8.7)} \text{Det}_{Si} \quad (8.4)$$

[TODO: include DIC into code]

... in dissolved organic nutrients ( $X=C, N, P$ ),

$$\frac{d}{dt}DOX = E \text{Phy}_X + \omega_{\text{Det}} \text{Det}_X - \omega_{\text{DOM}} DOX \quad (8.5)$$

... and in the detrital pool ( $X=C, N, P, Si$ ).

$$\frac{d}{dt}\text{Det}_X = M' \text{Phy}_X + M_Z \text{Zoo}_X - \omega_{\text{Det}} \text{Det}_X \quad (8.6)$$

where the phytoplankton mortality  $M'$  collects contributions from sloppy grazing  $((1-y)G)$  and, in 0D setups, and from sinking ( $S$  in Eq.(8.33)). Remineralization of DOM  $\omega_{\text{DOM}}$  and hydrolysis of detritus  $\omega_{\text{Det}}$  both change with ambient temperature and substrate quality

$$\omega_{\text{DOM}} = f_T \frac{\text{DON}}{\text{DOC}} \omega_{\text{DOM}}^* \quad \omega_{\text{Det}} = f_T \frac{\text{Det}_N}{\text{Det}_C} \omega_{\text{Det}}^* \quad (8.7)$$

Because of the quality dependency in degradation rates [TODO: justify], element cycles in the water column are easily decoupled within MAECS.

Note that in a chemostat mode, to the dynamics of *all* concentration variables a dilution ( $D$ ) loss is added, which only for dissolved nutrients also contains reservoir inflow  $(-D \cdot (DIX - DIX^0))$ .

[TODO: Parameter table]

## 8.2 Process Descriptions

### 8.2.1 Growth rate components and primary production

Temporal changes of the bulk phytoplankton concentration  $\text{Phy}_C$  are per construction given in terms of the over all relative growth rate  $\mu_{\text{tot}}$ :

$$\frac{d}{dt}\text{Phy}_C = \mu_{\text{tot}} \cdot \text{Phy}_C \quad (8.8)$$

The relative growth rate of autotrophic unicells (phytoplankton) collects primary production and a number of loss terms

$$\mu_{\text{tot}} = \underbrace{P - \underbrace{R}_{(8.12)}}_{\mu} - \underbrace{\left( \underbrace{E}_{(8.43)} + \underbrace{\frac{G \text{Zoo}_C}{\text{Phy}_C}}_{(8.32)} + \underbrace{S}_{(8.33)} + \underbrace{AF}_{(8.38)} + D \right)}_M = \mu - M \quad (8.9)$$

with sinking loss given in Eq.(8.33) (relevant only in 0D), aggregate formation in Eq.(8.38) [TODO: living cells in aggregates], grazing  $G$  explained in Sec. 8.2.6, exudation rate  $E$  formulated in Eq.(8.43), dilution rate  $D$  (for running the model in a chemostat mode), and respiration  $R$  in Eq.(8.12).

Gross C assimilation  $P$  changes with stoichiometric balance as expressed by the multi-nutrient co-limitation factor  $LF$ (Eq.(8.14)), maximal photosynthetic capacity  $P_{\text{max}}$  (further depending on, e.g. partitioning, Eq.(8.20), or size in the ecological version, Wirtz (2011, 2013)) and light harvesting success  $LH$

$$P = \underbrace{P_{\text{max}}}_{(8.20)} \cdot \underbrace{LF}_{(8.14)} \cdot LH \quad (8.10)$$



Light harvesting LH is primarily controlled by ambient light intensity PAR and light adsorption by chloroplasts  $\alpha \cdot \theta$  proportional to the chlorophyll concentration  $\theta$  (cf. Eq.(8.21)). Its functional form derives from Poisson arrival statistics of photons

$$LH = 1 - e^{-\alpha \theta PAR / P_{\max}} \quad (8.11)$$

### 8.2.2 Respiration and temperature

Respiratory losses reflect costs of N uptake (Raven, 1984; Pahlow, 2005), while neglecting energetic costs of P- and Si-assimilation

$$R = \zeta V_N \quad (8.12)$$

Temperature dependency of respiration thus follows from the factor  $f_T$  in the uptake coefficients in Eq.(8.24). In the current MAECS version, all metabolic rates equally increase with rising temperature following the Arrhenius equation,

$$f_T = e^{-E_a(T^{-1} - T_0^{-1})} \quad \text{with} \quad E_a = \frac{T_0^2}{10} \cdot \log(Q_{10}) \quad (8.13)$$

with a reference temperature  $T_0$  (here 18°C) where  $f_T$  equals one.

### 8.2.3 Multi-nutrient co-limitation

The co-limitation factor LF is constructed within a metabolic network view of cellular physiology. There, LF reflects not only the availability of singular resources (nutrients) but also how dependent the sub-networks (protein turnover) associated to those nutrients can evolve. In this view, LF quantifies the turnover of the first sub-process (here intracellular nitrogen turnover) times the queuing function that gives the intermittency between the first and the other sub-processes (associated to elements X):

$$LF = q_N \cdot \underset{(8.16)}{g_h} (q'_X / q_N) \cdot c_{hq} \quad \text{with} \quad c_{hq} = 1 + \underset{(8.17)}{c_h} + h \cdot q_N \underset{(8.18)}{q'_X} \quad (8.14)$$

The relative quota  $q_X$  expresses the availability of nutrient X above a subsistence threshold  $Q_X^0$  normalized by a reference pool size  $Q_X^* - Q_X^0$ . In contrast to most other models resolving variable internal stores (e.g. Morel, 1987),  $Q_X^*$  does not impose [TODO: 'does not impose'=? is it rather 'is not a prescribed'? but what is it then?] an upper boundary of the cell quota  $Q_X$ .

$$q_X = \frac{Q_X - Q_X^0}{\Delta Q_X} \quad \text{with} \quad \Delta Q_X = Q_X^* - Q_X^0 \quad \text{and} \quad X = N, P, Si, \dots \quad (8.15)$$

In Eq.(8.14), the product  $h q_N q'_X$  describes the non-linear metabolic interdependency between intracellular turnover of element N and X that is not covered by the simple queuing function.  $g_h$  expresses a "stop and go" dependency while neglecting possible amplification and inhibition effects as explained by Wirtz&Kerimoglu (in prep.). The product term leads to a quadratic influence of the first element ( $q_N$ ) and can be considered as most simple account of non-linear metabolic interdependency. It also ensures symmetry of LF with respect to exchanging the order of nutrients as  $q_1 g_h(q'_2 / q_1) c_{hq12} \approx q_2 g_h(q'_1 / q_2) c_{hq21}$ .

The queuing function  $g_h$  can be derived from assuming Poisson statistics in phase-locking of sub-networks [TODO: 'Poisson statistics in phase-locking of sub-networks' sounds scary, please expand!]:

$$g_h(x) = \frac{x - x_h}{1 - x_h} \quad \text{with} \quad x_h = x^{1+h^{-1}} \quad (8.16)$$

The function  $g_h$  introduces as new control parameter the metabolic interdependency  $h$ .  $h$  resembles the processing intermittency introduced by Wirtz (2012), which describes the probability of phase-locking [TODO: 'phase-locking' is again an unusual term: expand with a sentence?] in independent sub-steps in a process chain.

The correction coefficient  $c_h$  in Eq.(8.14) follows from imposing convergence of LF to the product and Liebig rules. Compliance to the Liebig rule leads to  $c_0 = 0$  since  $g_0$  describes a stepwise linear function [TODO: it's not clear: when  $h=0$ , Eq.(8.14) reduces to  $q_N g_0(q'_X/q_N)$ , with  $g_0 = -\inf / -\inf$ ]. For the product rule, we use the identity  $g_h(1) = 1/(1+h)$  and assume that  $q_X = q_Y = 1/2$ , to obtain  $1/4 = 1/2 \cdot (1 + h/4 + c_h)/(1+h)$  [TODO: it's very unclear where this equation came from], or  $c_h = -1/2 + h/4$ . However, the offset in this linear relation conflicts with the condition  $c_0 = 0$ . Both conditions can be approximately reconciled by a logarithmic function [TODO: does Eq.(8.17) have something to do with all the other equations in this paragraph? if so, how? if not, why not directly listing those 'conditions', providing Eq.(8.17) saying that it is one of the potentially many pragmatic solutions?]

$$c_h = \log(1/4^h + h/2) \quad (8.17)$$

It is mandatory in MAECS to resolve nitrogen. If optionally one, two, or more further nutrients are considered (e.g., P or Si, P and Si, or a micro-nutrient), a recursive scheme is applied. The limiting effect of element  $X+1$  on the processing of element  $X$  ( $q'_X$ ) is then formally equivalent to the LF of the first element (N) limited by the remainder metabolism (LF =  $q'_N$ ) as given in Eq.(8.14):

$$q'_X = q_X \cdot g_h(q'_{X+1}/q_X) \cdot c_{hq} \quad X = \text{P, Si, } \dots \quad (8.18)$$

For the final element we have  $q'_X = q_X$ . From the (subjective) ordering of elements in the recursive scheme only a small asymmetry arises. [TODO: no matter how small it is, the asymmetry probably requires us to document (and maybe also provide justification, if any) the order we chose]

## 8.2.4 Uptake system allocation and PI-coefficients

It is assumed that the fraction of free proteins or allocatable resources does not change. [TODO: it is not clear what this means: maybe a diagram helps?] Structural compounds such as cell wall, nucleus, or other non directly functional components are thus kept at a fixed ratio. The pool of free organics (in terms of cellular carbon) is partitioned between photosynthetic machinery and nutrient uptake. Photosynthetic machinery is further sub-divided into light harvesting and processing. The relative pool size of free resource (here in units C!) invested into light-independent reactions, primarily those in Rubisco and the Calvin cycle (Friend, 1991) is denoted as  $f_R$ , the one for the light harvesting complex (LHC)  $f_\theta$ . This way, the coefficient  $f_V$  for C-allocation to nutrient uptake becomes a linear function of the C-allocation to LHC  $f_\theta$  and to Rubisco  $f_R$ :

$$f_V = 1 - f_R - f_\theta \quad (8.19)$$

Maximum photosynthesis rate  $P_{\max}$  is controlled by the pool fraction  $f_R$  invested into Rubisco/processing and a temperature dependency  $f_T$  given in Eq.(8.13), while the effect of nutrient limitation (namely N) is already included in Eq.(8.10)

$$P_{\max} = f_R \cdot \underset{(8.13)}{f_T} \cdot P_{\max}^* \quad (8.20)$$

The fraction of light harvesting carbon depends on the C-fraction partitioned to photosystem processing (electron chain) and the chloroplast chlorophyll concentration  $\theta$  (relative to a reference value  $\theta_C$ ):

$$f_\theta = f_R q_N^\sigma \theta / \theta_C \quad \text{or} \quad \theta = f_\theta / f_R q_N^{-\sigma} \theta_C \quad (8.21)$$

where C stoichiometry of pigment complexes is denoted by  $\theta_C$ . The exponent  $\sigma$  describes an additional linkage of LHC synthesis on the N-status of the cell. Wirtz and Pahlow (2010) proposed that  $\sigma = 1$  for diatoms, while  $\sigma = 0$  for other autotrophs.

[TODO: 1) so far, it's not clear what's the relevance of  $\theta$  or  $f_\theta$  for physiological processes. Maybe a sentence. 2) it's also not clear where these novel and mysterious parameters such as  $f_R$  and  $\theta$  come from. Maybe it's helpful to hint that they are being dynamically optimized, referring to Sec. 8.3]

### 8.2.5 Nutrient uptake

Nutrient uptake rate of the cell varies with a number of internal, physiological factors, such as the partitioning coefficient  $f_V$  (see above) and the (enzymatic) activity  $a_{V,X}$  ( $X = N, P, Si, \dots$ ), and is furthermore determined by the potential uptake  $V_X^*$

$$V_X = \underset{(8.19)}{f_V} \cdot \underset{(8.59)}{a_{V,X}} \cdot V_X^* \quad (8.22)$$

Potential uptake  $V_X^*$  reflects ambient nutrient concentration, but also affinity and transport capacities denoted by  $A_X$  and  $V_{\max,X}$ . Nutrient uptake is a sequential 2-stage process (membrane uptake and intracellular transport) as described by the nutrient affinity  $A_X$  and maximal uptake rate  $V_{\max,X}$  such that the effective uptake time equals the sum of turnover times in each stage:

$$V_X^{*-1} = V_{\max,X}^{-1} + (A_X \text{ DIX})^{-1} \quad \text{with} \quad \text{DIX} = \text{DIN}, \text{DIP}, \text{DSi}, \dots \quad (8.23)$$

Nutrient uptake characteristics are temperature sensitive and assumed to depend on a sub-partitioning of allocatable proteins expressed by the coefficient  $f_{A,X}$

$$V_{\max,X} = (1 - f_{A,X}) \cdot Q_0 \cdot \underset{(8.13)}{f_T} \cdot V_{\max,X}^0 \quad (8.24)$$

$$A_X = f_{A,X} \cdot Q_0 \cdot f_T \cdot A_X^0 \quad (8.25)$$

[TODO: differential temperature sensitivity; see Smith 2013]

Protein sub-partitioning of overall uptake machinery ( $f_V$ ) into affinity and transport capabilities is instantaneously optimized

$$\frac{\partial V_X^*}{\partial f_{A,X}} = 0 \quad (8.26)$$

and the resulting optimal sub-partitioning depends on nutrient availability (Pahlow, 2005; Smith et al., 2009)

$$f_{A,X} = \left( 1 + \sqrt{A_X^0 \cdot \text{DIX} / V_{\max,X}^0} \right)^{-1} \quad (8.27)$$

In terms of the autotroph nutrient quota  $Q_X$  ( $X = N, P, Si$ ) imbalance between nutrient uptake and growth demand leads to

$$\frac{d}{dt} Q_X = V_X - \mu \cdot Q_X \quad (8.28)$$

or, in the MAECS notation where traits/characteristics are transported as bulk biomasses  $\text{Phy}_X$  parallel to the basic phytoplankton concentration  $\text{Phy}_C$

$$\frac{d}{dt} \text{Phy}_X = V_X \cdot \text{Phy}_C - \underset{(8.9)}{M} \cdot \text{Phy}_X \quad \text{with} \quad Q_X = \frac{\text{Phy}_X}{\text{Phy}_C} \quad (8.29)$$

[TODO: exudation]

### 8.2.6 Grazing

Before merging with the ecological MAECS version, we use primitive (non-biophysical) standards for describing heterotrophic activities:

$$\frac{d}{dt} \text{Zoo}_C = (y \cdot G - \tau_C - M_Z) \cdot \text{Zoo}_C \quad (8.30)$$

with quadratic and temperature sensitive mortality to represent top-down pressure

$$M_Z = f_T \cdot M_Z^0 \cdot \text{Zoo}_C \quad (8.31)$$

and a Holling-III response function for functional grazing response:

$$G = g_{\max} f_T \cdot \frac{\text{Phy}_C^2}{K_G^2 + \text{Phy}_C^2} \quad (8.32)$$

[TODO: more complicated loss/leakage terms  $\tau_X$  to ensure homeostasis and mass conservation]

### 8.2.7 Sinking loss

Vertical losses account for enhanced settling due to aggregate formation which occurs under high concentrations of particles and exopolymers. As a coastal model, already the basic version of MAECS resolves a benthic compartment independently from the coupled diagenesis model (see below).

The relative loss rate  $S$  is, in an idealized picture, the ratio between  $v_s$  and the mixed layer depth (MLD)

$$S = (1 + \underset{(8.38)}{f_{\text{agg}}}) \cdot \frac{v_s}{\text{MLD}} \quad (8.33)$$

[TODO: add size as trait or explicit parameter; the following part comes from the size-based model version]

The velocity  $v_s$  of a sinking particle is described by Stokes' law, which for a spherical cell with diameter  $\text{ESD} = e^\ell$  reads

$$v_s = \frac{g \rho'(\ell) e^{2\ell}}{18 \nu(T)} \quad (8.34)$$

The unitless excess density  $\rho'$ , the density difference between water and the suspended body, divided by water density, is known to be a function of the physiology and size of the suspended cells (Waite et al., 1997; Kjørboe et al., 1998; Miklasz and Denny, 2010). Dead cells are relatively heavy-weighted ( $\rho' = \rho^\dagger$ ,  $\rho^\dagger > 0$ ), but  $\rho^\dagger$  decreases in large (siliceous) phytoplankton due to an increasing fraction of vacuoles. The allometric relation of vacuolation and excess density reduction is

$$\rho^\dagger = \rho_0^\dagger e^{-\alpha_p \ell} \quad (8.35)$$

As vacuoles usually contain a higher concentration of inorganic compounds than the surrounding cytoplasm, the exponent  $\alpha_p$  should be close to the size scaling slope reported for carbon density by Menden-Deuer and Lessard (2000).

Linear dependency between excess density and relative production

$$\rho' = (1 - f_{\text{vac}} \cdot p) \cdot \rho^\dagger \quad (8.36)$$

$f_{\text{vac}}$  is the relative volumetric fraction that can be filled with material of reduced density (e.g., gases, lipids, or solutes, the latter listed in Boyd and Gradmann (2002)). This quantity relates to the vacuole structure (Raven and Waite, 2004) and can therefore be formulated as the relative density difference with respect to cells without vacuolation ( $\rho_0^\dagger$  in Eq.(8.35))

$$f_{\text{vac}} = \frac{\rho_0^\dagger - \rho^\dagger}{\rho_0^\dagger} = 1 - e^{-\alpha_p \ell} \quad (8.37)$$

### 8.2.8 Particle aggregation

[check with Richard; re-introduce into code]

Aggregation depends on stickiness and particle surface

$$f_{\text{agg}} = f_{\text{agg}}^* \text{EP} \cdot \text{Phy}_C \cdot \text{ESD}^n \quad (8.38)$$

The relative fraction of exopolymers within the DOM pool is inversely related to DOM quality, which is expressed in terms of the N:C stoichiometry. Stickiness associated with exopolymers (EP) correlates with DOM quantity and inverse quality

$$EP = \frac{DOC}{DON} \quad (8.39)$$

Stickiness not only enhances coagulation efficiency in particle aggregation, it also increases the critical bottom shear stress for sediment resuspension ("biostabilization"). Resuspension of benthic material occurs when bottom shear stress exceeds that "sticky" threshold.

$$RS = RS^* \max \left\{ V_{\text{bshear}} - V_{EP}^* EP, 0 \right\} \quad (8.40)$$

so we have for material fluxes due to resuspension

$$\frac{d}{dt} C_X^{\text{z=H}} = \dots + RSC_X^{\text{ben}} \quad \text{with} \quad C_X = \text{Phy}_X, \text{Det}_X \quad (8.41)$$

### 8.2.9 Other stuff

Photoinhibition by depletion of D1-protein

$$u = \frac{q_N}{q_N + u^* \text{Chl:C}^2} \quad (8.42)$$

Exudation reflects imbalance between C uptake and assimilation

$$E = e^* P_{\max}^* f_T \text{ LH} \quad (8.43)$$

## 8.3 Adaptive trait regulation and differential trade-off

Adaptive trait dynamics in its general form has been proposed as an optimality-seeking principle guiding transient adaptive regulation phenomena on very different levels of description, from organ physiology to population ecology (Wirtz, 2000, 2003; Smith et al., 2011). This principle/equation is applied to all physiological traits in MAECS, in particular to those that primarily control nutrient uptake ( $f_R$  and  $\theta$  through  $f_V$ , and activity  $a_{V,X}$ . C-growth as goal function needs to be extended by "hidden" or indirect effects through a differential link between nutrient uptake  $V_X$  and quota  $Q_X$  for all macro-nutrients:

$$\frac{df_{m,X}}{dt} = \delta_m \left( \frac{\partial \mu}{\partial f_{m,X}} + \sum_x \frac{\partial \mu}{\partial Q_X} \frac{dQ_X}{dV_X} \Big|_{\text{tot}} \frac{\partial V_X}{\partial f_{m,X}} \right) \quad \text{with} \quad f_{m,X} = f_R, \theta, a_{V,X} \quad X = N, P, Si, \dots \quad (8.44)$$

(8.54)      (8.55)

[TODO: reduce text or spread to individual euqations]

Diverging from most standard ecosystem models, however, MAECS assumes intricate interdependencies between independent C, N, or P assimilation functions while avoiding prescribed stoichiometric control settings such as maximal N:C or P:C ratios. For doing so, it implies optimality criteria already in the description of basic uptake formulations (lower part of Table ??). These criteria control shifts between high affinity and fast transport nutrient uptake (see above Eq.(8.27)) and in the enzymatic down-regulation of all nutrient uptake activities. Adaptive control in activity secures phytoplankton cells from non-beneficial intracellular accumulation of nutrients, but in the model also requires to formulate an extended optimality principle by which C costs of nutrient uptake have to be balanced with corresponding C benefits arising fro associated quota changes (Eq.(??)). For both regulations (uptake site/transport partitioning, activity), steady-state solutions or approximations are calculated since physiological uptake regulations proceed at very high speed.

For nitrogen (N), the differential effect of increasing nutrient uptake rate on the quota derives from functional variation applied to the quota uptake equation Eq.(8.28):

$$\delta V_X + \frac{\partial V_X}{\partial Q_X} \delta Q_X - \mu \cdot \delta Q_X - Q_X \cdot \frac{\partial \mu}{\partial Q_X} \delta Q_X - Q_X \cdot \frac{\partial \mu}{\partial V_X} \delta V_X = 0 \quad (8.45)$$

or

$$\frac{dQ_X}{dV_X} = (1 + \zeta_X Q_X) \cdot \left( \mu + Q_X \frac{\partial \mu}{\partial Q_X} - \frac{\partial V_X}{\partial Q_X} \right)^{-1} \quad (8.46)$$

where the derivative of uptake rate on quota may only become non-zero (1) for nitrogen (N) and (2) if C-partitioning to chlorophyll ( $f_\theta$  in Eq.(8.21)) is hardwired to the N-quota:

$$\frac{\partial V_N}{\partial Q_N} = \frac{V_N}{f_V} \frac{\partial f_V}{\partial Q_N} = -\frac{\sigma f_R \theta}{f_V \theta_C \Delta Q_N} V_N = -\sigma' V_N \quad (8.47)$$

### 8.3.1 Growth derivatives under co-limitation

For the N-turnover and regulation, the differential dependency of  $V_N$  on  $Q_N$  also enters the marginal increase in primary production when raising intracellular quota; an analytical derivation of the photosynthesis rate  $P$  in Eq.(8.10) with respect to each co-limiting quota  $Q_X$  reads

$$\begin{aligned} \frac{\partial \mu}{\partial Q_X} &= \frac{P}{LF} \frac{\partial LF}{\partial q_X} \frac{\partial q_X}{\partial Q_X} - \zeta \frac{\partial V_N}{\partial Q_X} \\ &= d_X \frac{\mu + \zeta V_N}{\Delta Q_X} + \sigma' \zeta V_N \quad \text{with } d_X = LF^{-1} \frac{\partial LF}{\partial q_X} \\ &= \left( d_X \frac{1 + \zeta Q_N}{\Delta Q_X} + \sigma' \zeta Q_N \right) \cdot \mu \\ &= \quad \quad \quad d_{QX} \quad \cdot \mu \end{aligned} \quad (8.48)$$

where we assumed a balanced growth relation between growth and uptake ( $\mu Q_N = V_N$ ), used the relation  $P = \mu + \zeta V_N$ . In light of Eq.(8.57) we have  $\sigma'_N = \sigma'$  and  $\sigma'_X = 0$  for other elements that lack direct influence on N-uptake rate.

The derivation result  $d_X$  of the (recursive) co-limitation factor  $LF \equiv q'_1$  may contain a number of product terms, depending on where in the scheme the limiting effect of  $Q_X$  is calculated. Consider the series of limitation factors  $q_1, q_2, \dots, q_{\text{No}^{\text{nut}}}$  (e.g., for  $q_N, q_P, q_{Si}$ ) we start from the first element where the recursive scheme Eq.(8.18) has been invoked only once. For example, if MAECS just resolves its basic element N,

$$d_N = \frac{1}{q'_N} \quad \text{for } \text{No}^{\text{nut}} = 1 \quad (8.49)$$

or N and P,

$$d_N = \frac{1}{q'_N} \frac{\partial q'_N}{\partial q_N} \quad d_P = \frac{1}{q'_N} \frac{\partial q'_N}{\partial q'_P} \frac{\partial q'_P}{\partial q_P} \quad \text{for } \text{No}^{\text{nut}} = 2 \quad (8.50)$$

Note that  $\partial q'_P / \partial q_P$  is one because P makes the last element in the list, so that the metabolic effect of  $Q_P$  as quantified by  $q'_P$  exclusively depends on the availability of  $Q_P$  as quantified by  $q_P$ . The general form for an arbitrary  $\text{No}^{\text{nut}}$  continues the sequential differentiation from the first element (here usually N) to the element X under consideration. So starting from  $q'_1$  we calculate the use efficiency of element X again using the chain-rule:

$$d_X = \frac{1}{q'_1} \frac{\partial q'_1}{\partial q'_2} \frac{\partial q'_2}{\partial q'_3} \dots \frac{\partial q'_X}{\partial q_X} \quad (8.51)$$

Note that the last term in the product of differentials ( $\partial q'_X / \partial q_X$ ) is either one if X is the last element in the sequence, and otherwise given by Eq.(8.52). The differentials in Eqs.(8.49)–(8.51) characterize the recursive effect of metabolic efficiencies of  $q'_X$  formulated in Eq.(8.18)

$$\frac{\partial q'_X}{\partial q_X} = q'_X \cdot \left( q_X^{-1} - \frac{\partial g_h}{\partial x} \frac{q'_{X+1}}{g_h q_X^2} + \frac{h q'_{X+1}}{c_{hq}} \right) \quad (8.52)$$

or, if we differentiate with respect to the second efficiency:

$$\frac{\partial q'_X}{\partial q'_{X+1}} = q'_X \cdot \left( \frac{\partial g_h}{\partial x} \frac{1}{g_h q_X} + \frac{h q_X}{c_{hq}} \right) \quad (8.53)$$

where the coefficient  $c_{hq}$  given in Eq.(8.14) is written without nutrient specific indices. Step-wise derivation of the queuing function  $(x - x_h)/(1 - x_h)$  with  $x_h = x^{1+h^{-1}}$  in Eq.(8.16) yields

$$\begin{aligned} \frac{\partial g_h}{\partial x} &= \frac{(1 - (1 + h^{-1})x_h/x) \cdot (1 - x_h) + (x - x_h) \cdot (1 + h^{-1})x_h/x}{(1 - x_h)^2} \\ &= \frac{(xh - (h+1)x_h) \cdot (1 - x_h) + (x - x_h) \cdot (h+1)x_h}{xh \cdot (1 - x_h)^2} \\ &= \frac{xh - (h+1)x_h - \cancel{xhx_h} + \cancel{(h+1)x_h^2} + x \cdot \cancel{(h+1)x_h} - \cancel{(h+1)x_h^2}}{xh \cdot (1 - x_h)^2} \\ &= \frac{xh + (x - 1 - h) \cdot x_h}{xh \cdot (1 - x_h)^2} \end{aligned} \quad (8.54)$$

[TODO: numerical approximation to avoid problems at  $x = 1$ ]

### 8.3.2 Quota-uptake feed-back

Eq.(8.46) provides a first estimate for the differential trade-off required for a fully coherent application of the optimality principle to physiological regulation. However, a marginal change in quota after a differential change in uptake rate may propagate back to the uptake rate, if the latter directly depends on  $Q_N$ . This direct, differential feed-back between changes in  $Q_N$  and  $V_N$  reads

$$\left. \frac{dQ_N}{dV_N} \right|_{\text{tot}} = \frac{dQ_N}{dV_N} \cdot \left( 1 + \underbrace{\frac{dQ_N}{dV_N} \frac{\partial V_N}{\partial Q_N}}_{(8.56)} \right) \quad (8.55)$$

$$\begin{aligned} \frac{dQ_N}{dV_N} \frac{\partial V_N}{\partial Q_N} &= -(1 + \zeta Q_N) \cdot \left( \mu + Q_N \frac{\partial \mu}{\partial Q_N} - \frac{\partial V_N}{\partial Q_N} \right)^{-1} \sigma' V_N \\ &= -(1 + \zeta Q_N) \cdot \left( 1 + Q_N \left[ d_N \frac{1 + \zeta Q_N}{Q_N - Q_{N0}} + \sigma' \zeta Q_N \right] + \sigma' Q_N \right)^{-1} \sigma' Q_N \\ &= -(1 + \zeta Q_N) \cdot \left( (Q_N)^{-1} + d_N \frac{1 + \zeta Q_N}{Q_N - Q_{N0}} + \sigma' \cdot (1 + \zeta Q_N) \right)^{-1} \sigma' \\ &= -\sigma' \cdot \underbrace{\left( (Q_N (1 + \zeta Q_N))^{-1} + d_N (Q_N - Q_{N0})^{-1} + \sigma' \right)}_{e_N}^{-1} \\ &= -\frac{\sigma'}{e_N + \sigma'} \end{aligned} \quad (8.56)$$

In all other cases apart of nitrogen, the uptake dependency on the quota vanishes:

$$\frac{\partial V_X}{\partial Q_X} = 0 \quad \text{and} \quad \left. \frac{dQ_X}{dV_X} \right|_{\text{tot}} = \frac{dQ_X}{dV_X} \quad \text{with} \quad X = P, Si \quad (8.57)$$

The product of the quota-uptake differential (without feed-back) and the growth-quota differential in Eq.(8.44) com-

bines Eq.(8.46) and Eq.(8.48) and again assumes  $V_X = Q_X \mu$ :

$$\begin{aligned}
 \frac{dQ_X}{dV_X} \frac{\partial \mu}{\partial Q_X} &= (1 + \zeta_X Q_X) \cdot \left( \mu + Q_X \frac{\partial \mu}{\partial Q_X} - \frac{\partial V_X}{\partial Q_X} \right)^{-1} \cdot d_{QX} \cdot \mu \\
 &= (1 + \zeta_X Q_X) \cdot \left( 1 + Q_X d_{QX} + \sigma'_X V_X \mu^{-1} \right)^{-1} \cdot d_{QX} \quad (8.48) \\
 &= \frac{(1 + \zeta_X Q_X) \cdot d_{QX}}{1 + Q_X \cdot (d_{QX} + \sigma'_X)} \quad (8.58)
 \end{aligned}$$

### 8.3.3 Uptake activity regulation

In the current version of MAECS, regulation of all uptake activity traits  $a_X$  is supposed to be very fast compared to the simulated dynamics and therefore not integrated in time according to Eq.(8.44), but assumed to be in steady-state. If the marginal benefit of uptake  $d\mu/da_X$  is negative, activity is ceased; at positive benefit,  $a_X$  approaches one, while at neutral growth effect  $d\mu/da_X \approx 0$ , the activity smoothly varies at 1/2. This behavior is emulated by the non-linear function

$$a_X = \left( 1 + e^{-\Delta \mu_V d\mu/da_X} \right)^{-1} \quad (8.59)$$

For optimization in N-uptake activity  $a_N$  based on its the marginal C gain the extended optimality principle integrates Eq.(8.44) and Eqs.(8.48)–(8.58):

$$\begin{aligned}
 \frac{d\mu}{da_X} &= \frac{\partial \mu}{\partial a_X} + \frac{\partial \mu}{\partial Q_X} \frac{dQ_X}{dV_X} \Big|_{\text{tot}} \frac{\partial V_X}{\partial a_X} \\
 &= -\zeta_X \frac{V_X}{a_X} + \frac{\partial \mu}{\partial Q_X} \frac{dQ_X}{dV_X} \frac{e_N}{e_N + \sigma'_X} \frac{V_X}{a_X} \\
 &= \left( -\zeta_X + \frac{(1 + \zeta_X Q_X) \cdot d_{QX}}{1 + Q_X \cdot (d_{QX} + \sigma'_X)} \frac{e_N}{e_N + \sigma'_X} \right) \cdot \frac{V_X}{a_X} \quad (8.60)
 \end{aligned}$$

where, again,  $\sigma'_N = \sigma'$  and  $\sigma'_X = 0$  for other elements that lack direct influence on uptake.

### 8.3.4 Costs in P and Si uptake

For a first estimation of the C-costs of P- and Si-uptake (with units mol-C/mol-X) we link the latter to N-assimilation. This means that energetic costs of P- and Si-assimilation are not accounted for as additional terms but assumed to be already included in protein synthesis that are chararized by  $\zeta \equiv \zeta_N$  (with units mol-C/mol-N). For the P-link, we use the N-stoichiometry in RNA (N:P  $\approx$  3.8:1) and phospholipids (N:P  $\approx$  0.8:1 mol-N/mol-P)

$$\frac{\partial \mu}{\partial V_X} = \frac{\partial \mu}{\partial V_N} \frac{\partial V_N}{\partial V_X} = -\zeta_N \cdot \frac{Q_N^{0*}}{Q_X^{0*}} = -\zeta_X \quad (8.61)$$

with Eq.(8.14) Eq.(8.18)

$$\zeta_P = \left[ (1 - f_{\text{Lip}}) 3.8 + f_{\text{Lip}} 0.8 \right] \cdot \zeta_N \quad \text{and} \quad \zeta_{\text{Si}} = 0 \quad (8.62)$$

[TODO: check and simplify]

[TODO: include proteins/membranes (N:P  $\gg$  16:1) under low growth conditions ]



### 8.3.5 Photoacclimation and transport

MAECS resolves transient photoacclimation as adaptive dynamics in allocation traits (Eq.(8.44)). The optimality principle extended by the differential quota-based trade-off Eq.(8.58) seeks to find an allocation key between nutrient uptake, LHC and light-independent processes (Rubisco) that maximizes relative C-uptake rate  $\mu$ . The optimality condition includes marginal growth benefits of all nutrients (see Eq.(8.44)):

$$\frac{d}{dt} f_R = \delta_R \left( \frac{\partial \mu}{\partial f_R} + \sum_x \frac{\partial \mu}{\partial Q_X} \frac{dQ_X}{dV_X} \Big|_{\text{tot}} \frac{\partial V_X}{\partial f_R} \right) \quad (8.63)$$

(8.54) (8.55) (8.66)

and similar for the chloroplast CHL:C ratio  $\theta$ :

$$\frac{d}{dt} \theta = \delta_\theta \left( \frac{\partial \mu}{\partial \theta} + \sum_x \frac{\partial \mu}{\partial Q_X} \frac{dQ_X}{dV_X} \Big|_{\text{tot}} \frac{\partial V_X}{\partial \theta} \right) \quad (8.64)$$

(8.48) (8.55) (8.67)

The differential growth loss by increasing allocation to photosynthesis apparati down-sizes the nutrient uptake machinery. All uptake and indirect derivatives of the photoacclimation traits that induce these differential costs had been already introduced above.

Flexibilities in chloroplast CHL:C ratio and in C-allocation to Rubisco are given following [Wirtz and Eckhardt \(1996\)](#); [Wirtz \(2000\)](#)

$$\delta_\theta = \delta_\theta^* \cdot \theta \cdot (\theta_C - \theta) \quad \delta_R = \delta_R^* \cdot f_R \cdot (1 - f_R) \quad (8.65)$$

Partial derivatives of photosynthesis rates with respect to  $\theta$  and  $f_R$  (see Eq.(8.20) and Eq.(8.22)):

$$\begin{aligned} \frac{\partial \mu}{\partial f_R} &= \frac{P}{f_R} - \zeta \frac{\partial V_N}{\partial f_R} \\ &= \frac{P}{f_R} + \zeta \cdot \left( 1 + \frac{q_N^\sigma \theta}{\theta_C} \right) \cdot a_{V,N} V_X^* \end{aligned} \quad (8.66)$$

(8.59)

$$\begin{aligned} \frac{\partial \mu}{\partial \theta} &= \frac{P}{LH} \frac{\partial LH}{\partial \theta} - \zeta \frac{\partial V_N}{\partial \theta} \\ &= \frac{P}{LH} \frac{\alpha \text{PAR}}{P_{\max}} (1 - LH) - \zeta \frac{q_N^\sigma f_R}{\theta_C} \cdot a_{V,N} V_X^* \end{aligned} \quad (8.67)$$

For transporting photoacclimation traits in 1D-3D, MAECS integrates them as bulk variables by employing a "carrier" biomass variable (usually  $\text{Phy}_C$ ). With Eq.(8.21) we have for the bulk chlorophylla concentration

$$\text{Chl} = f_\theta \theta_C \text{Phy}_C = f_R q_N^\sigma \theta \text{Phy}_C \quad (8.68)$$

and bulk Rubisco concentrations

$$\text{Rub} = f_R \text{Phy}_C \quad (8.69)$$

[TODO: write down full equations]

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