MELiSSA

Memorandum of Understanding
ECT/FG/MMM/97.012

TECHNICAL NOTE 63.3

Higher plants: growth modelling

Version 0
Issue 0

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Document change log

Version	Issue	Date	Observations
0	0	May 2002	Draft version
0	1	October 2002	Draft version
	0		
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Content

I Introduction

Higher plant is one of the compartments of the MELiSSA loop. At the difference of other compartments (from CI to CIVa), it is not of microbial compartment.
In the overall strategy of the MELiSSA project, the development and the analysis of the loop and its compartments is associated to the development of reliable predictive models for each compartment. For microbial compartment, the development of reliable biological structured models is more or less easy, but is feasible. For the higher plant, the main difficulty is that plants are complex organisms and as a consequence, its is difficult to develop suitable structured model for them.

The plant growth modelling study was started in the MELiSSA project with the technical notes 32.3 (mass balance models) and 55.3 (growth models). Waters G. (TN 50.1, TN 53.1) also conduct experimental and theoretical investigations.

The purpose of the present work is to:

- Catalogue existing and appropriate models for plants growth
- Give recommendations and identify requirements on plant growth models for MELiSSA

II Analysis of the growth of higher plants in closed chambers

Note : some conclusions and observations are the result of the meeting between LGCB and UOG concerning higher plants modelling

A first step in the comprehension and then the development of a growth model for higher is to identify and understand how plants are growing (and how this growth can be measured) and which are the variables that could be measured and manipulated during the growth. It is then necessary to remind and clarify the experimental aspect of the higher plant growth and the important growth parameters.

II.1 The measurement of biomass growth of higher plants.

The measurement of biomass growth in closed chambers cannot be made by sampling like for micro-organisms as this classical method requires:

- That the sampling is representative of the whole culture (homogeneity);
- The sampling is small compared to the whole culture.

As direct measurement of the higher plants biomass produced in closed chamber is destructive (in large open field the problem is different), it can only be used to analyse and to check the biomass growth and the biomass composition at the end of the growth (or at the end of the experiment). But obviously such a method cannot be reasonably used for systematic studies of the effect of several parameters affecting the growth.

Then only indirect measurements can be used to estimate the growth of higher plants in closed chamber. The most classical ways for the indirect measurements of the growth of higher plants are:

- LAI (Leaf Area Index). This is the measurement of leaves area for a plant. If the method is simple and reliable for the start of the growth, the measurement of LAI is more complex when leaves are overlaid and when canopy closure is reached; LAI is interesting for the study of canopy models and the study of the fraction of the Photosynthetic Photon Flux (PPF) absorbed by the canopy (A);

- The measurement of a growth related substrate or product. It supposes implicitly that the biomass and this growth parameter are linearly linked (i.e. constant growth yield). The Net Carbon Exchange Rate (NCER) is an example of indirect measurement of the growth rate.

The Net Carbon Exchange Rate (NCER) is probably the most reliable method for indirect measurement of the growth of higher plants, and is extensively used. It is the measurement of the rate of total carbon dioxide fixed (i.e. consumed) (TN 53.1). This method:

- Allows online measurement of the growth;
- Is based on the assumption of a constant yield in the CO_2 fixation during the growth. The yield classically used is about 0.4 g biomass/g CO_2 fixed. Examples of biomass/CO2 yield will be presented in section III;
- Is non-destructive.

The NCER is a rate, this means that it expresses a change of a quantity with time. Following units have been used:

- ppm $CO_2.s^{-1}$,
- vol CO_2.vol $gas^{-1}.s^{-1}$
- moles CO_2. $m^{-2}.s^{-1}$

If units involve vol_{CO2}or ppm $_{CO2}$, the gas volumes and gas flow rate must be given.

As previously detailed in TN 55.3, two very similar quantities, NCER and P_n, have been used to describe the carbon uptake rate by plants The classical shape of the growth curve for higher plant (or Pn or NCER shape also) is reported in figure1.

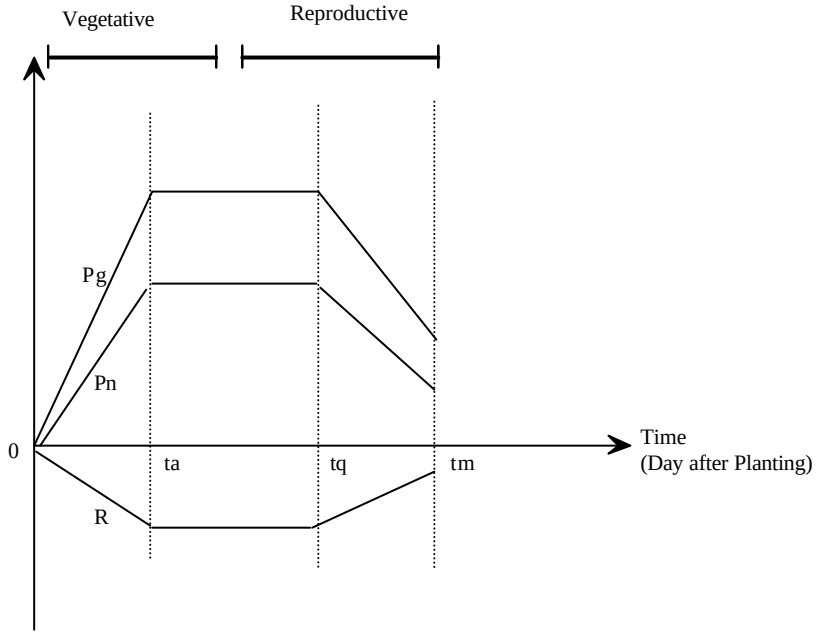


Figure 1: **"Straight Lines"** time profile of Pg (photosynthetic growth rate), Pn (Pn-Pg-R) and R (respiration rate during daily dark periods). [ta: time for canopy closure ; tq : time for senescence or grain setting ; tm : time of maturity or harvest]. Note that real profiles are smoother in fact than the set of 3 straight lines and that the curve represents the whole life cycle, which not necessary the plant cultivation cycle (harvesting).

II.2 The growth and the growth parameters

The indirect measurement of the growth is necessary for the study of the influence of the growth parameters on the higher plants without a destructive analysis of the plant itself for analysis during the experiment.

As for any kind of biological process, several parameters affect the growth of higher plants. On a scientific point of view, it is important to know the influence of all the parameters on the growth. But all of the parameters have not the same interest in the purpose of the development of a growth model and for the operation of a controlled closed chamber.

The main objective of this section is to list biological and environmental parameters and to outline the most important ones for modelling and control of the growth of higher plant in a closed chamber.

II.2.1 Selection of the parameters involved in the growth

A non-exhaustive list of parameters involved in the growth of higher plant in closed chamber is reported below. These parameters may be plants requirements, cultivation choices and environmental factors.

1. Light, including :
   - Light requirements
   - Light intensity
   - Lighting duration (i.e. photoperiods)
   - Light spectrum (dealing with lamp selection)
2. Air /Atmosphere, including
   - Relative humidity [RH] (important for closed environment)
   - Composition, mainly for CO_2 concentration but deals also with contaminant control such as ethylene (plant maturation compound)
   - Air velocity (related to RH and air composition control)
3. Pressure
4. Temperature
5. Cultivation techniques (soils, hydroponics), including:
   - Irrigation
   - Water quality
6. Nutrient solutions, including
   - Nutrient delivery/fertilisation
   - Nutrient quality
7. Area requirements, including
   - Crop density
   - Crop rotation
   - Multi-species crop compatibility
8. Growth phases (also related to crop rotation), including
   - Seeding
   - Harvesting
   - Vegetation duration

If the number of parameters that can affect the growth is important, they are mainly related to the plant requirements and to the plant optimal growth conditions. Then the number of variables that can be measured or controlled for a level control >1 is in fact lower.

II.2.2 Variables that can be measured

The growth

(report to section II.1)

The plant physiology variables

The substrates/products concentrations (or partial pressure) must be measured (at least the CO_2 and the O_2 in gas). For hydroponics cultures, the liquid medium composition can be measured, but for

soil or clay support, this may be more problematic. The consumption/production rates can be calculated from the measurements. As previously outlined, the growth can be calculated from the CO_2 consumption rate.
Some biological variables can be measured only at the end of the growth such as the harvest index (edible biomass/total biomass) and the biomass composition as these measurements are destructive.

The environmental variables
Classically the environmental variables are temperature, pressure and light. Suitable quantities to characterize the light in terms of plant growth are:

- the incident Photosynthetic Photon Flux (PPF),
- the absorption of the incident PPF by photosynthetic tissue,
- the photosynthetic efficiency (CO_2 fixed/photon absorbed, which is more a biological variable)

The relative humidity (RH) can also be measured and can be sorted in environmental variables even if it is mainly the consequence of the transpiration by plants.
Flow rates (gas and liquid), ventilation are also measurable variables.

II.2.3 Controlled/manipulated variables and the control strategy for the operating of the higher plant chamber

Which control strategy for the HPC ?
The control strategy is a key question in for the choice of the experiments, the modelling and the integration of the higher plant compartment in the MELiSSA loop concept.

The two opposite options exist for the higher plant compartment:

1) Higher plants chambers which environmental variables are fully controlled and maintained to optimal values. This option is simple to manage in terms of control system but difficult to achieve in terms of engineering. In such a case, the function (or productivity) of the compartment, as well as its capacity of CO_2 (and other minerals) absorption are locked by the design and the fixed (optimal) operating conditions of the compartment. The compartment cannot be used for control of the matter flow trough the loop. In terms of modelling such a system require only a model which is suitable for the defined growth condition.

2) Higher plants chambers which environmental variables (mainly atmospheric variables) are dependant of the habitat, what means that chambers are not fully isolated from crew. If this option is simplest in terms of engineering, it is more difficult in terms of control systems and predictive models. It can be noticed that this option was chosen for testing crop growth on ISS (ALS flight crop discussion group – September 2002)

The choice between these two options is also linked to the stately for operating the higher plant compartment. With the first option it is possible to achieve a "fixed food production rate objective", while with the second option it will be more difficult as it is obvious that in this case the compartment will be associated to the atmosphere management.

It is not our purpose here to chose the higher compartment culture strategy, but in term of modelling it is important to kept in mind that for:

- Higher plant cultivated in isolated and environmentally controlled chambers, as environmental parameters are in principle not subject to change, model can be simplest to establish and develop (less parameter and operating conditions to study)
- Higher plant cultivated in open environment require more complex model as a large range of parameters and growth condition must be investigated

Probable manipulated variables

Most of the environmental variables (temperature, pressure,..) would be maintained to have an optimal growth and could be achieve only in isolated chambers, which favours the design of a HPC separate from the crew compartment . The growth itself could be controlled by:

- Light,
- CO_2 concentration,
- Nutrients.

Among those parameters light seems to be the easiest to manage, provided the use of artificial light. CO_2 concentration plays an important in plant growth. However, to manage a CO_2 concentration could be difficult due to the transient fluxes from the crew, other compartments and the plants themselves. Comparing the ease of control of light and nutrients, it suggests that nutrients shall not be manipulated, instead, shall be maintained at a non-limiting and non-toxic level to ensure optimal plant growth

III The growth models

In order to be homogenous with the previous modelling strategy used for the biological MELiSSA reactors (TN 39.1), the growth model for the higher plant compartment should have the form:

$$\frac{dBiomass}{dt} = f(Biomass, Time, light, environmental\ conditions, CO_2, O_2, nutrients, ...)$$

It can be noticed that this is not the classical expression used by plant physiologists (report to II.1)

As reported in TN 55.3, two kinds of growth models are used for the crop by space agencies studying the growth of plants in closed chamber for LSS purposes.

- Energy-cascade models, which seems to be the choice of NASA
- Explanatory based models such as this already presented by Cloutier (TN 40.3)

We will detail here the energy cascade model and the rectangular parabola model presented by Waters (TN 50.1).

III.1 Energy cascade model

The energy cascade model, which was originally developed for wheat has been modified for several advanced life support (ALS) candidate crops use in ALS system studies (Cavazonni, 1999). **The energy cascade model calculates the daily carbon gain** (**DCG**), which is an expression of the rate of carbon fixation by plant.

III.1.1 Theory of the energy cascade model

In its principle, the energy cascade model is quite simple. It is developed considering 3 stages between the capture of light and the carbon fixation. The model itself is sets of linear relations, but non-linear expression were introduced in the modified energy cascade and some elements of the model come from crop models.

III.1.1.1 Nomenclature

The following parameters are involved in the modified energy cascade model (report also to figure 1):

t_A=Time of canopy closure (in days after emergence – or DAE)
t_Q=Time of onset of canopy senescence ((in days after emergence – or DAE)
t_M= Time at harvest or crop maturity (in days after emergence – or DAE)

PPF= Photosynthetic photon flux (µmol m^{-2} s^{-1})
A=Fraction of the photosynthetic photon flux (PPF) absorbed by the canopy (adimensional)
A_{max}=maximun fraction for canapy light absrption (A) at t_A (adimensional)

H=photoperiod (h)
P_{net}=Canopy net photosynthesis (µmolCO_2 m^{-2} s^{-1})
Rd=Canopy dark-cycle respiration (µmolCO_2 m^{-2} s^{-1})

CUE=Carbon use efficiency (adimensional ; molC $molC^{-1}$). CUE is a constant, also noted c.
CUE24=24 hours carbon use efficiency (adimensional ; molC $molC^{-1}$)
CUE_{max}= Carbon use efficiency until t_Q (adimensional ; molC $molC^{-1}$)
CUE_{min}= Carbon use efficiency at t_M (adimensional ; molC $molC^{-1}$)

CQY=Canopy quantum yield (mol PPF . $molC^{-1}$)
CQYmax=Canopy quantum yield until t_Q (mol PPF . $molC^{-1}$)
CQYmin=Canopy quantum yield at t_M (mol PPF . $molC^{-1}$)

DCG=Daily carbon gain (molC m^{-2} d^{-1})

III.1.1.2 The original energy cascade model

The original energy cascade model has the form :

$$DCG = 0.0036.(H.P_{net} - [24 - H].R_d)$$

what is the rate of carbon fixed during the light phase minus the carbon release during the dark period. This is also written:

$$DCG = 0.0036.(H.CUE - [24 - H].[1 - CUE]).A.CQY.PPF$$

As it was observed that DCG has negative values for photoperiods less than a critical value Hc defined by :

$$Hc.CUE - [24 - Hc].[1 - CUE = 0]$$

a modified model was developed (Cavazonni, 1999).

III.1.1.3 The modified energy cascade model

The modification was added for legume crop (soybean, dry bean and peanut). It is based on a new definition for the carbon use efficiency: a 24hours carbon use efficiency defined as :

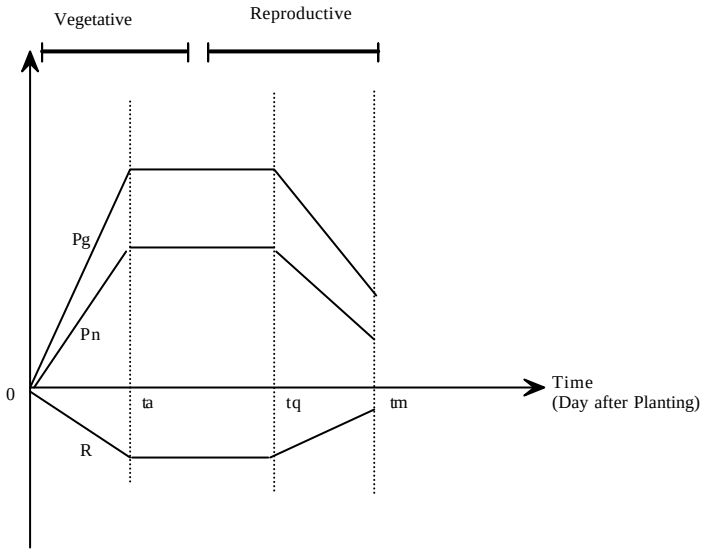
$$CUE_{24} = CUE_{\min} + \frac{(CUE_{\max} - CUE_{\min}).(t_M - t)}{\left[(t_M - t_Q)^{n\_CUE} + (t_M - t)^{n\_CUE}\right]^{\frac{1}{n\_CUE}}},$$

where n_CUE is a constant that affects the curvature at the transition point t_M.

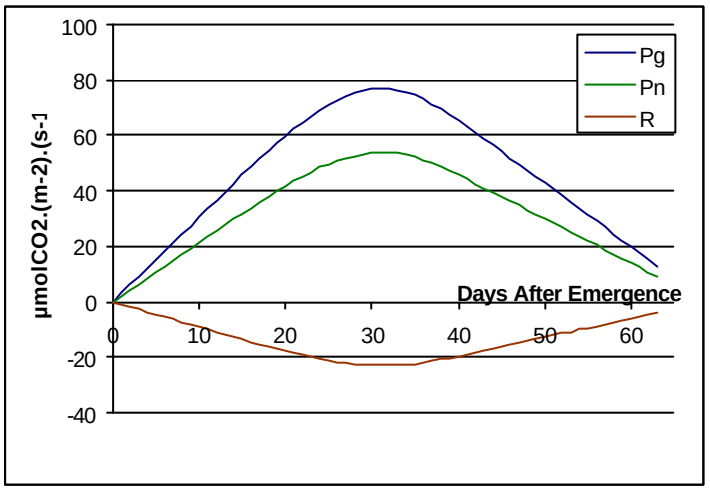
The daily carbon gain takes the form:

$$DCG = 0.0036.(H.CUE_{24}).A.CQY.PPF \quad \text{and} \quad P_{net} = \left(\frac{24 - H}{24} + \frac{CUE_{24}.H}{24}\right).DCG$$

It can be noticed that the rates that can be calculated from the modified energy cascade model can have a profile quite different of the classical one (Figure 2)

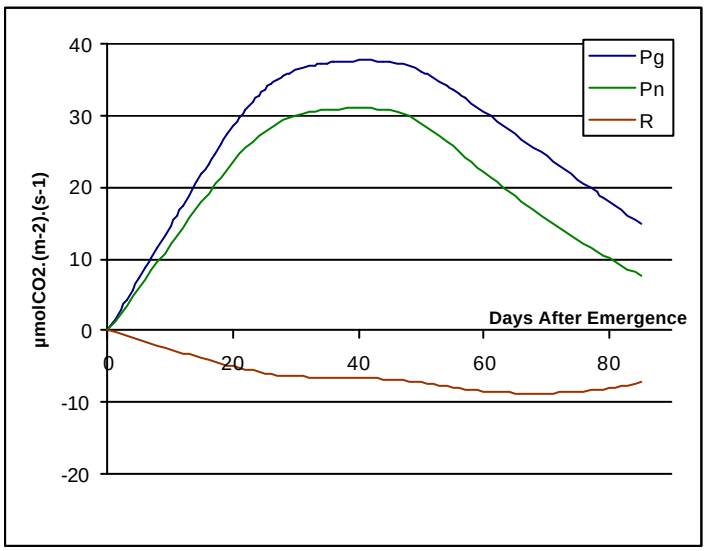


Classical "Straight Lines" time profile of plants growth (report to Figure 1 for details)



Wheat

Ta	27	day
Tq	33	day
Tm	63	day
CQYmax	0,063	mol.mol-1
CQYmin	0,01	mol.mol-1
CUEMAx	0,64	fraction
CUEmin	0	fraction
H	20	hour (light)
PPF	1400	µmol,m-2,s-1
n_CUE	15	
n_CQY	15	
Amax	0,93	fraction
n_A	7	



Soybean

Ta	26	day
Tq	48	day
Tm	85	day
CQYmax	0,051	mol.mol-1
CQYmin	0,02	mol.mol-1
CUEMAx	0,65	fraction
CUEmin	0,03	fraction
H	12	hour (light)
PPF	800	µmol,m-2,s-1
n_CUE	15	
n_CQY	15	
Amax	0,93	fraction
n_A	7	

Figure 2: Example of growth profile calculated for 2 plants and compared to the classical straight-line profile. Parameters for the Energy cascade model are taken from table 1a.

III.1.1.4 The calculation of the canopy quantum yield

In the same way of the carbon use efficiency (CUE and CUE_{24}), the canopy quantum yield can be :

- a constant
- a variable value, defined by a form similar to CUE_{24} :

$$\textbf{if } t<t_M : CQY = CQY_{\min} + \frac{(CQY_{\max} - CQY_{\min}).(t_M - t)}{\left[(t_M - t_Q)^{n\_CQY} + (t_M - t)^{n\_CQY}\right]^{\frac{1}{n\_CQY}}}$$, where

n_CQY is a constant that affects the curvature at the transition point t_M

III.1.1.5 The calculation of the fraction of the photosynthetic photon flux (PPF) absorbed by the canopy

The fraction of the photosynthetic photon flux absorbed by the canopy (A) is calculated from the Leaf Area Index (LAI), using the beer's law:

$A = 1 - e^{(-Keff.LAI)}$ if $t<t_A$

$A = \min[A, A\max]$ if $t \geq t_A$

This expression supposes to be able to model LAI, and then the energy cascade models developed need to be associated to LAI models. These models are those used in crop models detailed in table 1b. This is probably one of the most critical point of the energy cascade model as it is not extensively explained and detailed by Cavazonni et al (1999). Moreover, this appears to be a key point in the model as it drives the behaviour for one of the stage of the energy cascade mode (the light absorption).

The need to use LAI model is probably the reason why Cavazonni et al (1999) have developed an alternative for wheat and soybean. The fraction of the photosynthetic photon flux absorbed by the canopy (A) was modelled using a Monod function. It exhibits a quasi-linear increase as canopy grows and reaches a plateau after canopy closure. The model of A is thus given by:

$$\textbf{if } t<t_A : A = \frac{A_{\max}.t}{\left(t^{n\_A} + t_A^{n\_A}\right)^{\frac{1}{n\_A}}}$$, where n_A is a constant that affects the curvature at the transition point t_A.

if $t \geq t_A$: $A=A_{max}$, what supposes that after canopy closure there is no leaf area loss.

This model for the calculation of A is simpler than this implying LAI, but cannot be applied for the first days of the plant growth.

A_{max}, the maximum fraction for canopy light absorption (A) at canopy closure time (t_A) is set to **0.93** in energy cascade models (Cavazonni, 1999).

III.1.2 Energy cascade model parameters

The set of parameters to identify for the crops in order to use the energy cascade model is:

t_A=Time of canopy closure (in days after emergence – or DAE)

t_Q=Time of onset of canopy senescence ((in days after emergence – or DAE)

t_M= Time at harvest or crop maturity (in days after emergence – or DAE)

A_{max}=maximun fraction for canopy light absorption (A) at t_A (adimensional)

CUE_{max}= Carbon use efficiency until t_Q (adimensional ; molC $molC^{-1}$)

CUE_{min}= Carbon use efficiency at t_M (adimensional ; molC $molC^{-1}$)
CQYmax=Canopy quantum yield until t_Q (mol PPF . $molC^{-1}$)
CQYmin=Canopy quantum yield at t_M (mol PPF . $molC^{-1}$)
n_CUE, n_CQY and n_A = power coefficients in models

As an example, are reported in Table 1a the crop specific energy cascade model parameters for use in the Bio-Plex system model (Cavazonni, 1999).

In addition, following cultural condition parameters must be defined:
PPF= Photosynthetic photon flux (µmol m^{-2} s^{-1}) ; i.e the light
H=photoperiod (h)
The environmental parameters (temperature, pressure…)
The cultivation parameters (feeding, P_{CO2}, P_{O2}….)
In the following section III.1.3 is described the addition of environmental parameters (p_{CO2} and light) in the energy cascade model.

Notes:

- It is important to notice that the values of the parameters seem very dependent of the culture conditions.
- It is also important to keep in mind that the energy cascade models presented here were associated to elements of existing crop models (Table 1b) especially for LAI calculation.

The models are valid only after the emergence of the plant from the seed. This is the reason why the time is called Day After Emergence (DAE). Implicitly, another parameter of the models is then ts, the time of the seeding phase, which correspond to time 0 of DAE.

Model	**Source**
Wheat	CERES-Wheat (Ritchie *et al*., 1998; Ritchie, 1991; Hodges and Ritchie, 1991). See Tubiello (1995) for a modified CERES-Wheat model in *Mathematica*.
Rice	Rice phenology component adapted from Alocilja and Ritchie (1991). Growth components are hybrid.
Soybean, Peanut, Dry Bean and Tomato	CROPGRO model (Boote *et al*., 1998; Piper *et al*., 1996; Hoogenboom *et al*., 1992; Wilkerson *et al*., 1983), and the associated DSSAT parameter files (Tsuji *et al*., 1994).[a]
White Potato	SUBSTOR Potato growth and development model (adapted from Griffen *et al*., 1993).
Sweet Potato	SUBSTOR (Griffen *et al*., 1993), and Penning deVries *et al*. (1989). Hybrid model.
Lettuce	Hybrid model.

Table 1b. Sources for the plant growth and development components adapted for the modified Energy Cascade models. a. The FORTRAN code for the CROPGRO, CERES and SUBSTOR models was provided with the purchase of DSSAT3. Table from Cavazonni (1999).

Crop	t_A	t_Q	T_M	*N_CUE*	*N_CQY*	CQY_{MAX}*	CQY_{MIN}*	CUE_{24} (fraction) or			Temperature (ºC)	PPF	[CO_2]	Photo-period
	Days after emergence					*mol mol*$^{-1}$		CUE_{MAX}	CUE_{MIN}	T_{LIGHT}	T_{DARK}	*µmol m*$^{-2}$ *s*$^{-1}$	*µmol mol*$^{-1}$	*hour*
Dry bean	22	42	62	15	15	0.065	0.02	0.65	0.3	26	22	600	1200	12
Lettuce	27	**	30	15	V	0.072	**	0.625	**	23	23	300	1200	16
Peanut	32	65	110	15	15	0.063	0.02	0.65	0.3	26	22	600	1200	12
Rice	25	61	87	15	15	0.065	0.01	0.64	**	29	21	1200	1200	12
Soybean	26	48	85	15	15	0.051	0.02	0.65	0.3	26	22	800	1200	12
Sweetpotato	19	**	120	15	15	0.061	**	0.625	**	28	22	600	1200	14
Tomato	34	59	90	15	15	0.071	0.01	0.625	**	26	22	500	1200	12
Wheat	17	33	63	15	15	0.063	0.01	0.64	**	23	23	1400	1200	20
White potato	35	75	105	15	15	0.068	0.02	0.625	**	20	16	655	1200	12

* The values for CQY_{MAX} and CQY_{MIN} should be used directly in the CQY equation in the BIO-Plex system model:
For crops with no value for CQY_{MIN}, *CQY* should be set to a constant = CQY_{MAX}.
** Not applicable.

Table 1a. Crop specific modified Energy Cascade model parameters for given environmental conditions (Use for Bio-Plex Simulation – Table from Cavazonni (1999))

III.1.3 Effect of CO_2 and light

The effect of CO_2 concentration on crop growth was modelled by modifying the maximum canopy quantum yield with the CO_2 concentration:

$$CQY_{\max} = \frac{CQY_{theory}.C_{CO2}}{\left(C_{CO2}^{n\_CQY\_theo} + C_{CO2\_0}^{n\_CQY\_theo}\right)^{\frac{1}{n\_CQY\_theo}}}$$

where,

CQY_{theory} = theoretical achievable value for the quantum yield

C_{CO2} = the concentration of CO_2 in the HPC

C_{CO2_0} = the concentration of CO_2 below which the quantum yield increases almost linearly

The values reported by X. Kwauk (1998) for wheat are reported in table 2.

CQY_{theory} (mol PPF. $MolC^{-1}$)	0.066
C_{CO2_0} (ppm)	210
N_CQY_theo	1.4

Table 2: Parameters for the influence of CO_2 concentration on the quantum yield for wheat.

The functions CQY_{max}=f(CO_2,PPF) have also been established using polynomial regression for experiments in various conditions (Cavazonni, 1999). As an example, the following polynomial equation was used for dry bean by Cavazonni (1999) :

$$CQY_{\max} = 10^{-7}\,(4.191\,10^{5} + 5.852\,10^{2}.C_{CO2} - 1.238\,10^{2}.PPF - 2.1275\,10^{-1}.C_{CO2}^{2} - 1.544\,10^{-4}.C_{CO2}.PPF^{2} + 6.469\,10^{-8}C_{CO2}^{2}PPF^{2})$$

Note: It is important to keep in mind that these relations can only be used to model the growth under various fixed environmental conditions. This means that, in the examples presented above, the light and the CO_2 remain constant during the growth. In principle, these relations cannot be used for modelling a growth with environmental conditions, which change during the growth. Nevertheless, Jones et al. (2002) investigate the effect of light fluctuation during the growth, and the effect of variation of nominal CO_2 concentration with these modified energy cascade models.

III.2 The rectangular parabola model of UOG (TN 53.1)

The plant growth model proposed by Water et al. (TN 53.1) is a rectangular parabola model, which is commonly used to describe crop response to light. The model has the form:

$$NCER = \frac{\alpha.PPF.(\beta_0 + \beta_1.t)}{a.PPF + (\beta_0 + \beta_1.t)} + (\beta_2 + \beta_3.t)$$

t being the time after planting in days (DAP). **DAP is different of DAE used in energy cascade model: DAP=DAE + time of emergence (end of seeding stage)**. NCER is in CO_2 quantity by time unit (i.e. concentration.s^{-1})

This expression gives the instantaneous NCER (carbon fixed) function of the light and of the days after planting. This is a 5-parameter model that must be identified from experiments. The parameters were identified for lettuce (TN 50.1 and TN 53.1) and beet (TN 50.1) from experiment conducted by UOG. This model can be used only for plants which growth is related to the leaves growth and for which harvest time is before canopy closure (typically lettuce) but not for plants such as wheat.

Note:
As the model allows for the dynamic gross photosynthesis (P_{gross}) and for the dark respiration rates (R_d), it is better to says that the model predicts the Net Carbon Exchange Rate (positive in ligth period and negative in dark period) than the net photosynthesis (Pnet) which is more an average value for one day (light+dark periode).

The Daily Carbon Gain (DCG) for the rectangular parabola model can be calculated by :

$$DCG = \int_{DT=0}^{DT=24} \frac{\alpha.PPF(DT).(\beta_0 + \beta_1.t)}{a.PPF(DT) + (\beta_0 + \beta_1.t)} + (\beta_2 + \beta_3.t)$$

DT being the time within a day (0-24 hour) and PPF(DT) the light profile in one day

For a constant light flux (PPF), this becomes (if NCER is given in $CO_2.s^{-1}$)

$$DCG = 3600.\left(H.\frac{\alpha.PPF.(\beta_0 + \beta_1.t)}{a.PPF + (\beta_0 + \beta_1.t)} + 24.(\beta_2 + \beta_3.t) \right),$$

H being the photoperiod in hours and DCG the daily carbon gain in $CO_2.day^{-1}$

III.3 Plant growth models and stoichiometrics models

First, three main remarks concerning the plants growth models must be keep in mind.

1 - the dynamic growth models are an expression giving the carbon fixation rate by plants;

2 – the time basis is rather the day, (averaging dark and light periods) than the hour (or less), even if the time unit in NCER expression can be s^{-1}. This time basis is in relation with the response time and the growth time for plants (counted more in days than in hours);

3 – the models have a form $\frac{dx}{dt} = f(t)$ rather than a form $\frac{dx}{dt} = f(t, x)$ as the classical microbial models. This implies that the models are implicitly based on the repeatability of the growth in the time, i.e. the development phases occur always at the same time and are not affected by changes in environmental conditions. But it must be outlined that in the cascade

energy model, the LAI (which can be related to the biomass) and an auxiliary function (from DSSAT models) is used, what can be a way to take into account the history of the biomass growth.

In the previous section, the models presented give a rate (daily carbon gain). As detailed in TN 39.1, only **one reaction rate is required for each stoichiometric equation** in order to have the rate for each compound involved in the reaction.

Note:
In TN 32.3, for each plant selected for the MELiSSA HPC, a unique theoretical stoichiometric equation was established. This equation is based on the plant composition (proteins, carbohydrate, lipids, fibre and inedible part) at the harvest time. Then it is important to keep in mind that using this equation for the complete life cycle of the plant and each stage of its development phases is obviously inaccurate: the composition of the plant, and then the yields change. With one single stoichiometric equation, the yields are constant during all the growth of the plant. In order to take into account the development phases, it is necessary to establish stoichiometries taking into account variations of the plant composition with the time, what is not realistic.

III.3.1 Yields from previous stoichiometric models
This section is only a summary of the previous work detailed in TN 32.3. Here are presented the theoretical yields (Table 3a and 3b) for the set of plants selected in a first approach for the MELiSSA project. These yields are given in comparison to the carbon fixed (from CO_2) and are calculated from the stoichiometric equations detailed in TN 32.3.

	Dry plant (edible+ Inedible)	CO2	H2O	NH3	HNO3	O2	H2SO4
Tomato	-0,5479	1	0,2885	0,0031	0,0155	-0,7735	0,0143
Rice	-0,5653	1	0,3049	0,0034	0,0169	-0,7690	0,0091
Lettuce	-0,5459	1	0,2998	0,0014	0,0490	-0,8209	0,0081
Potato	-0,5842	1	0,3125	0,0042	0,0209	-0,7591	0,0057
Soybean	-0,5055	1	0,2937	0,0127	0,0634	-0,8739	0,0097
Spinach	-0,5296	1	0,2834	0,0121	0,0606	-0,8413	0,0147
Oinion	-0,5711	1	0,3079	0,0053	0,0264	-0,7780	0,0096
Wheat	-0,5607	1	0,2994	0,0042	0,0208	-0,7740	0,0104

Table 3 a : Yields in g/g CO2 fixed calculated from stoichiometric equation established in TN 32.3. Negative value indicate products. The yields are calculated for the whole dry plant (edible+inedble)

	Dry plant (edible+ Inedible)	CO2	H2O	NH3	HNO3	O2	H2SO4
Tomato	-2,0091	3,6667	1,0577	0,0114	0,0570	-2,8360	0,0525
Rice	-2,0729	3,6667	1,1181	0,0124	0,0620	-2,8196	0,0334
Lettuce	-2,0016	3,6667	1,0993	0,0053	0,1798	-3,0099	0,0298
Potato	-2,1419	3,6667	1,1460	0,0153	0,0767	-2,7835	0,0208
Soybean	-1,8536	3,6667	1,0769	0,0465	0,2323	-3,2042	0,0355
Spinach	-1,9417	3,6667	1,0391	0,0444	0,2222	-3,0846	0,0539
Oinion	-2,0941	3,6667	1,1288	0,0193	0,0967	-2,8526	0,0351
Wheat	-2,0558	3,6667	1,0977	0,0153	0,0763	-2,8381	0,0380

Table 3b : Yields in g/g C fixed calculated from stoichiometric equation established in TN 32.3. Negative value indicate products. The yields are calculated for the whole dry plant (edible+inedible)

It can be noticed that the yields are very homogenous for all the plants. The dry plant / C fixed for example varies only between 1.85 and 2.14. The theoretical yields reported in table 3b can be compared to the experimental yields identified by Dixon M. (2002) for beet. It can be noticed that the molar ratio NH_4^+/NO_3^-, which was fixed to a close in stoichiometries to 0.2 is close to experimental ratio calculated at 0.25.

The composition of the plants used to build the stoichiometric equation did not included phosphate and ash, and moreover the inedible fraction composition was only estimated (TN 32.3). That probably explains the difference (12% to 20% higher) between the theoretical and the experimental C in biomass ratios (Table 4).

	Theoretical (stoichiometric equations)	Experimental
Tomato	0,50	
Rice	0,48	
Lettuce	0,50	0,4
Potato	0,47	0,41
Soybean	0,54	0,46
Spinach	0,52	
Oinion	0,48	
Wheat	0,49	0,42

Table 4: C ratio in plants : comparison between values of the stoichiometric equations and values reported by Wheeler et al. (1996)

III.3.2 Growth model for plants

The principle of the dynamic model for the plant growth was presented in TN 39.1, and is similar to the principles used for the growth of micro-organisms. As previously presented, the models are an expression of the carbon (or CO_2) fixation rate.

Energy cascade model

The basis is the daily carbon gain (DCG), what represents an average of the plant growth in one day. This means that the time step for the model is the day and **its use for non-averaged day periods is inaccurate**.

The expression of DCG is given in section III.1, and ideally, **DCG must be expressed in g CO_2 fixed / day.m^2 of plant.** The daily rate of any compound Ci (i.e. Nutrient, biomass,O_2, CO_2) involved in the stoichiometric equation characteristic of each plant, is then :

$$RCi = -DCG.Y_{Ci/CO2} \qquad Y_{Ci/CO2} \text{ being the yield g Ci/ g}CO_2 \text{ of table 3a.}$$

Rectangular parabola model of UOG

The NECR expression of the parabola model gives the instantaneous rate of carbon fixed. It is positive in light period and negative in dark-respiration periods. **It can be only used for predicting the instantaneous rate of CO_2 production/consumption**. The stoichiometric equations established couldn't be directly coupled with the NCER, as for dark periods this leads to "consume" biomass and oxygen, and to produce minerals and CO_2.

In order to have for any time the rate for minerals and biomass, it is at least necessary to have two different stoichiometric equations (theoretical or experimental) for light and dark periods

Then with or current knowledge, which is limited to only one global mass balance equation for the each plant (edible part), it is more realistic to calculate day averaged rates for minerals, O_2 and biomass (RCi), as for the energy cascade model. This requires calculating a daily carbon gain:

$$DCG = \int_{DT=0}^{DT=24} NCER(DT) \qquad \text{(in g } CO_2\text{/day)}$$

and then,

$$RCi = -DCG.Y_{Ci/CO2} \qquad Y_{Ci/CO2} \text{ being the yield g Ci/ g}CO_2 \text{ of table 3a.}$$

III.4 Observations / reflections

III.4.1 Plant growth models expression

In microbial growth models, the growth is proportional to the microbial biomass i.e. the model takes the form:

$$\frac{d\text{Biomass}}{dt} = f(\text{Biomass}, Time, environmental\ conditions, [nutrients], ...)$$

In the plant models, the amount of biomass formed or existing did not appears, even if in the energy cascade models there is a calculation of LAI for the estimation of the fraction of the photosynthetic photon flux (PPF) absorbed by the canopy (A). For the biomass plants growth models have the form:

$$\frac{d\text{Biomass}}{dt} = a.DCG$$

and

$$DCG = f(Time - Days\ After\ Planting, environmental\ conditions, [nutrients],..)$$

This difference is important to notice as this implicitly supposes that the plant biomass is not a growth factor and that the growth models are only dependants to:

- Environmental parameters
- Time constants of the growth (i.e. the development stage of the plants occurs always at the same fixed time)

It can be asked if a model involving the biomass formed as a parameter (i.e. $Biomass = \int \frac{dBiomass}{dt} = a \int DCG$) would give a higher flexibility in the model, enabling to by-pass the constraints of time constants (i.e. ta, tq, time of seeding stage…).

III.4.2 Models and environmental effects (temperature, light, PCO_2….)

As environmental parameters are keys parameters, they are taken into account in the models.
In energy cascade models light, temperature and CO_2 concentration are taken into account by using polynomial experimental correlation (report to III.1.3). It can be noticed that the environmental parameters affect only the canopy quantum yield (CQY).

In the rectangular parabola model of UOG light is directly involved in the structure of the model. In this model, the parameter that is the closest to CQY is α . This constant parameter in the model of UOG can then be a function of light and CO_2, but it must be checked.

IV Conclusion

In this document were analysed two kind models for the growth of higher plants. These models are used for the modelling of plant growth for LSS development purpose. These two models are the modified energy cascade model, developed by Cavazonni et al. (1999) for NASA ALS studies, and a rectangular parabola model, developed by Waters et al. (TN 50.1).

Several remarks concerning the two models can be made :

- The Modified Energy Cascade (MEC) models are developed since several years and were implemented in a MatLab-Simulink ™ version for the study of the candidate crop in ALS by Jones et al. (2002). For this reason, these models are in principle more advanced than the rectangular parabola model and are calibrated for the 9 candidate crops of NASA ALS.
- The parameters of MEC models seem have been identified from experiments where all parameters were fixed (especially light). The rectanguler parabola model present the interest to have been developed using a variable natural (solar) light source which varies during the day. Then it could be better for predicting the growth variation with light fluctuation. This point should be clarified and a comparison for the growth of lettuce with the two kind of model could be of high interest.
- The rectangular parabola model is designed for plant with an important leaf area. If it cannot be used for others crop this will be a major drawback compared to the MEC model.

Some general conclusions can also be made concerning the plant growth models:

- It appears that even if models (especially the rectangular parabola model) can be integrated in a time unit lesser than one day, the models are averaged on at least one day (24 hours). This is only on this averaged value that steady state for nutrients uptake and carbon fixation are measured. This may have some influence on the dynamic control of the compartment
- The yields obtained from the theoretical stoichiometries must be compared to experimental steady state yields, as those determined by Waters et al (2002) for beet. The fact that for beet these yields are constant are encouraging.

As a conclusion, there is already some reliable models for plant growth, which have been implemented for the study of candidate crop for ALS, by Jones et al. (2002). Some question remains concerning their predictive behaviour, especially for variable daily conditions. Some points remains also to fix concerning the operation of the higher plant compartment as the complexity and the reliability (reproducibility) of the models which are required can be affected.

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