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From the functional analysis of soil-plant-animals interactions to the modelling of grasslands – example of the ModVege model

A.-I. Graux

INRA PEGASE unit www.rennes.inra.fr/pegase



What is a grassland?

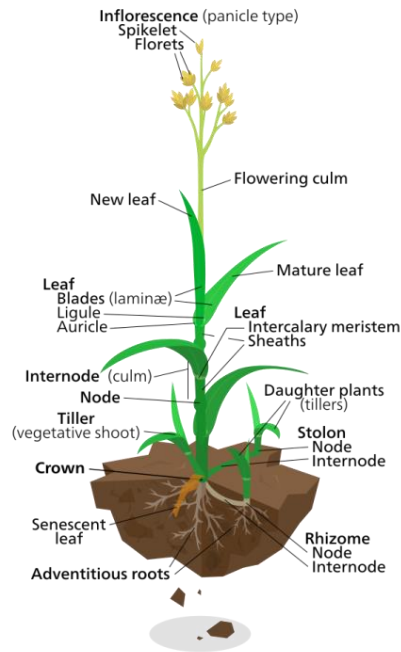
- **Single or pluri-species plant formation** which generally (not always!) consists of several life forms :

a majority of grasses

Monocotyledonous (parallel veins) flowering plants

can also contain **legumes** and/or **forbs**

Dicotyledonous flowering plants



Legumes have nodules in their root systems containing symbiotic N-fixing bacteria called rhizobia



Grasslands can be classified according to their duration and species composition

■ Permanent grasslands

- were not reseeded since at least 5 or more years
- multispecies (botanical composition in equilibrium with management, soil and climate conditions)

■ Sown/temporary grasslands

- reseeded every few years to maximize the amount of biomass they provide
- monospecies (grass or legume) or plurispecies : mixture of several grass and/or legume species

A high diversity of grasslands

Some examples

$$3 \leq n \leq 10$$

n=1

n=2



Ryegrass



Ryegrass + White clover



Alfalfa



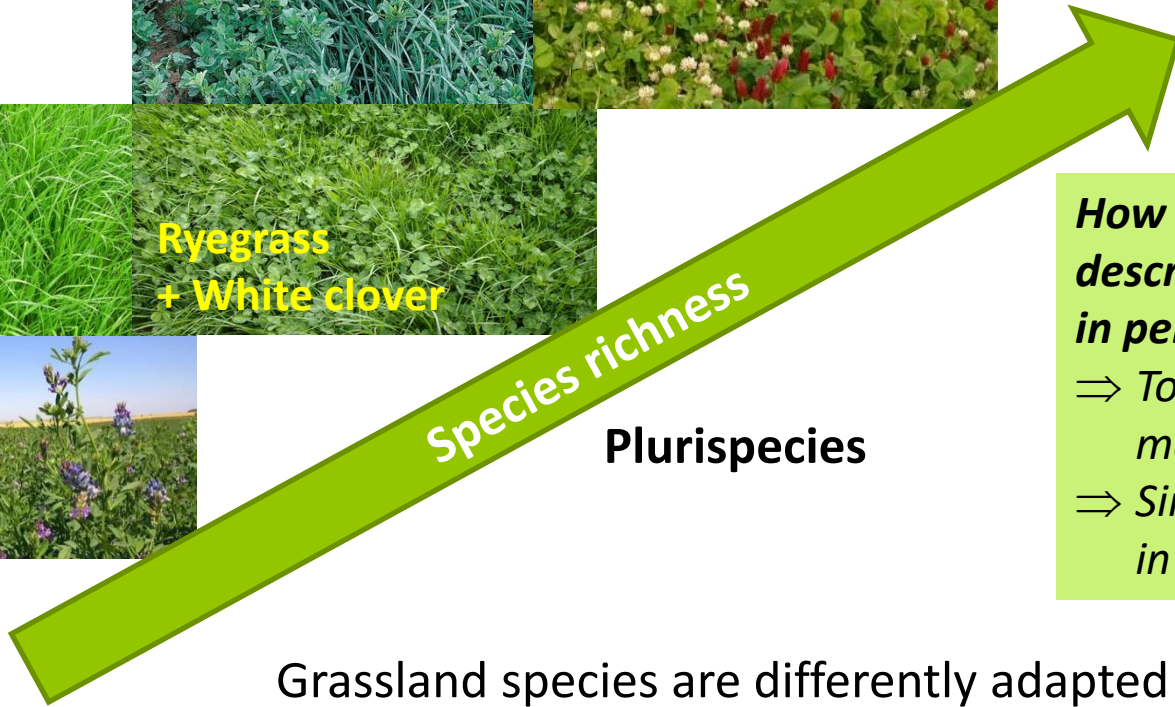
Orchard grass + Alfalfa



Crimson clover + white clover + grasses



Multispecies



Plurispecies

Monospecies

How to simplify the description of vegetation in permanent grasslands ?
 ⇒ To assist grassland management
 ⇒ Simplify their description in models


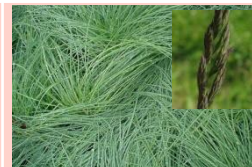


Grassland species are differently adapted to climate, soil and management conditions (cutting vs. grazing, fertilisation)

Characterization of permanent grasslands and their use value

- Biological features (called « **functional traits** ») of the vegetation reflects :
 - **plant responses** to the **availability of soil resources** and to the **grassland management** (grazing severity, cutting frequency and intensity, fertilisation)
 - **plant effects** on the agricultural and environmental **use value of the grassland** (i.e. providing forages, keeping the environment open, maintaining biodiversity)
- ⇒ **A functional classification** of permanent grasslands into **4 functional types** that have similar functioning was proposed by Cruz et al. (2002) according to **fertility and utilisation gradients**; it is based on grass species only

A (first) functional classification of permanent grasslands*


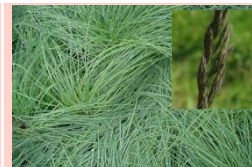


Cruz et al., 2002. Fourrages

		Fertility	
		Rich/fertile sites <i>(Strategy : to catch resources)</i>	Poor/infertile sites <i>(Strategy : to conserve resources)</i>
Utilisation	Frequent defoliation <i>(Strategy : fast recycling of organs)</i>	 <p>Type A <i>Ex: Lolium perenne Holcus lanatus</i></p> <p>High specific leaf area (SLA) High digestibility Short leaf lifespan Early reproductive growth & flowering</p>	 <p>Type C <i>Ex: Festuca rubra Agrotis capillaris</i></p> <p>Low SLA Medium digestibility Long leaf lifespan Late reproductive growth & flowering</p>
	Infrequent defoliation <i>(Strategy : slow recycling of organs)</i>	 <p>Type B <i>Ex: Dactylis glomerata Arrhenaterum elatius</i></p> <p>Medium SLA High digestibility Long leaf lifespan</p>	 <p>Type D <i>Ex: Briza media Brachypodium pinnatum</i></p> <p>Low SLA Low digestibility Very Long leaf lifespan Late reproductive growth & flowering</p>

* This classification was revised by Cruz et al.(2010)

A (first) functional classification of permanent grasslands*

Cruz et al., 2002. Fourrages

		Fertility	
		Rich/fertile sites (Strategy : to catch resources)	Poor/infertile sites (Strategy : to conserve resources)
Utilisation	Frequent defoliation (Strategy : fast recycling of organs)	 <p>Type A Ex: <i>Lolium perenne</i> <i>Holcus lanatus</i></p> <p>Early turning out on grass Frequent and severe grazing High-quality but moderate-yielding hay</p>	 <p>Type C Ex: <i>Festuca rubra</i> <i>Agrotis capillaris</i></p> <p>Frequent and severe grazing of a low-quality herb</p>
	Infrequent defoliation (Strategy : slow recycling of organs)	 <p>Type B Ex: <i>Dactylis glomerata</i> <i>Arrhenaterum elatius</i></p> <p>Early and high-quality hay or late high-yielding hay</p>	 <p>Type D Ex: <i>Briza media</i> <i>Brachypodium pinnatum</i></p> <p>High flexibility of grazing Low-to-medium yields non adapted for hay production</p>

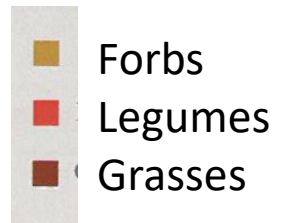
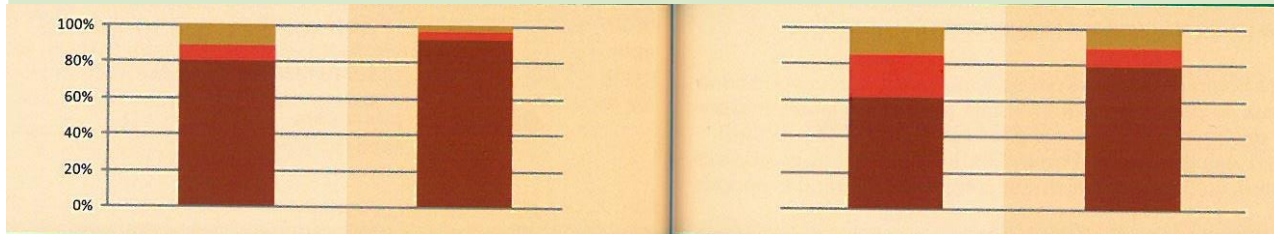
* This classification was revised by Cruz et al.(2010) 6 groups A B b C D E

Permanent grasslands are an evolving combination of different functional types

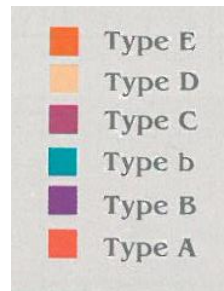
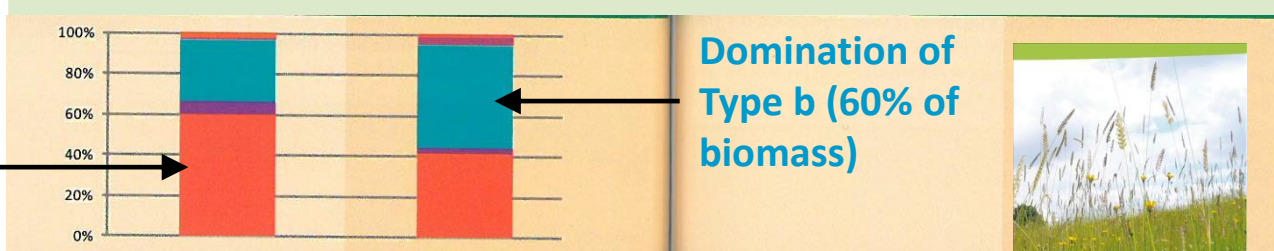
- Case of **fertilised** and **highly grazed** grasslands located in the **West of France** dominated by **ryegrass** and **bent grass**

Start of Spring 1 st cycle Mid-May	End of Spring 1 st cycle End of June	Summer 6 weeks of regrowth Mid-August	Autumn 7 weeks of regrowth End of September
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Seasonal dynamics of vegetation



Functional types of grasses



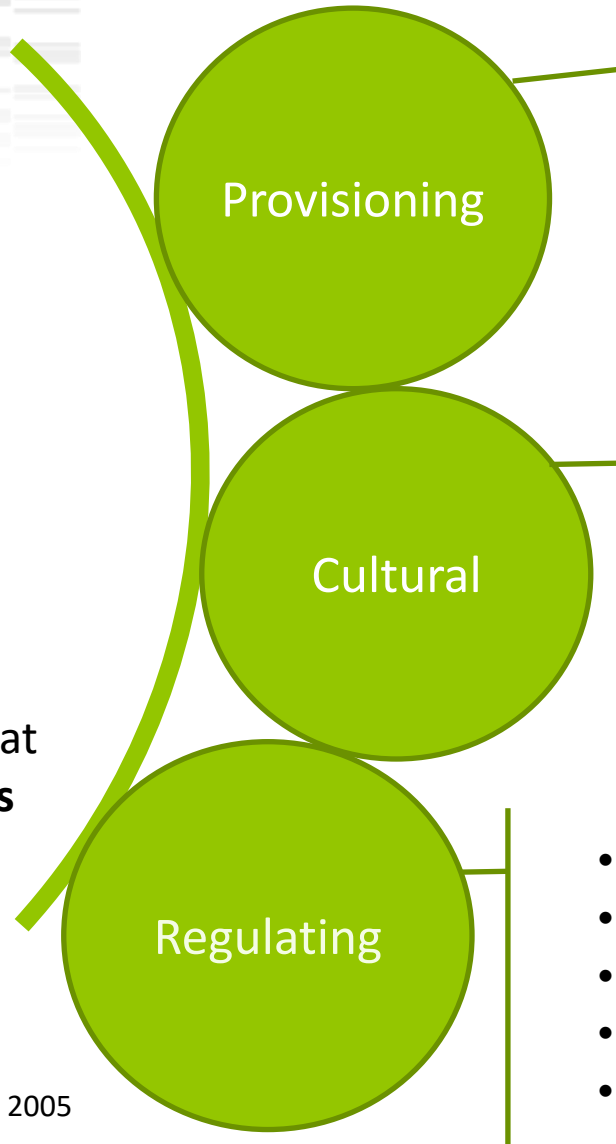
Source: Typology of French permanent grasslands

Maintaining grasslands is important



Different grasslands that serve **different benefits** for people

Millennium Ecosystem Assessment, 2005



- Milk and meat from a cheap fodder / a resource that cannot be valued directly by humans



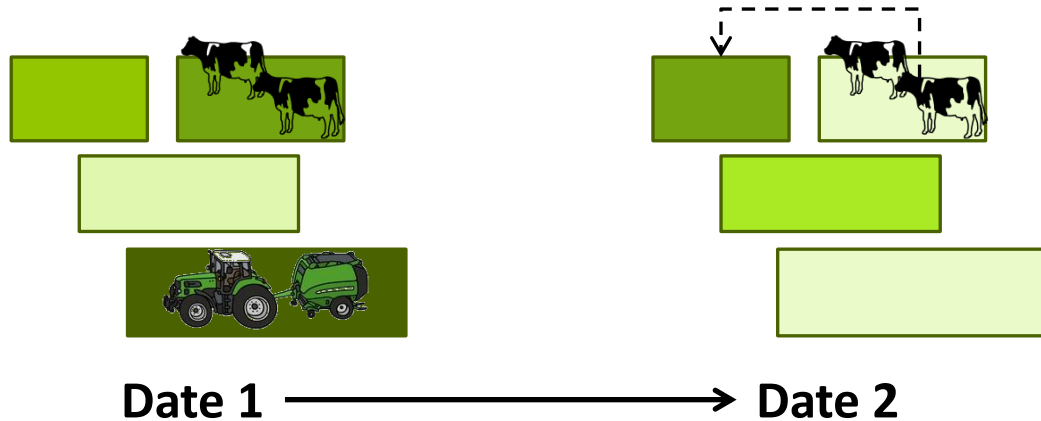
- Aesthetics value of landscape (landscape maintenance & quality)
- Recreation & ecotourism
- Quality of life

- Climate regulation (C storage)
- Soil erosion regulation
- Water quality regulation
- Biodiversity conservation
- Pollination



But managing grasslands is challenging

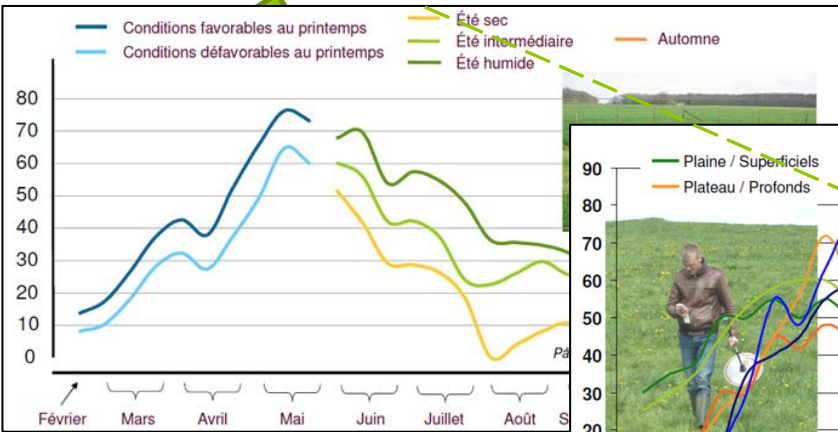
- **Grasslands exist thanks to herbage removals** by animals (grazing) and humans (fodder production)
- **The location of grasslands** in cropland (e.g. distance from housing) **and their production level** (e.g. type of soil and vegetation) **conditions their use** (e.g. grazing vs cutting; dairy heifers vs cows)
- The management of grasslands supposes to **manage both in time and space 2 uncertain fluxes** : **grass growth** and **animal intake**



Factors influencing grass growth

Climate

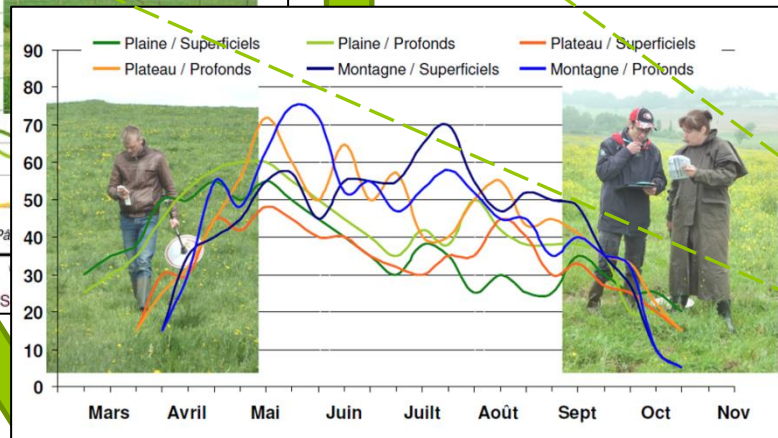
(Temperature, radiation, rainfall)



Source : Delaby (2015)

Soil

(Water and nutrient resources etc.)



Management

(type, frequency and intensity of utilisation, fertilisation)

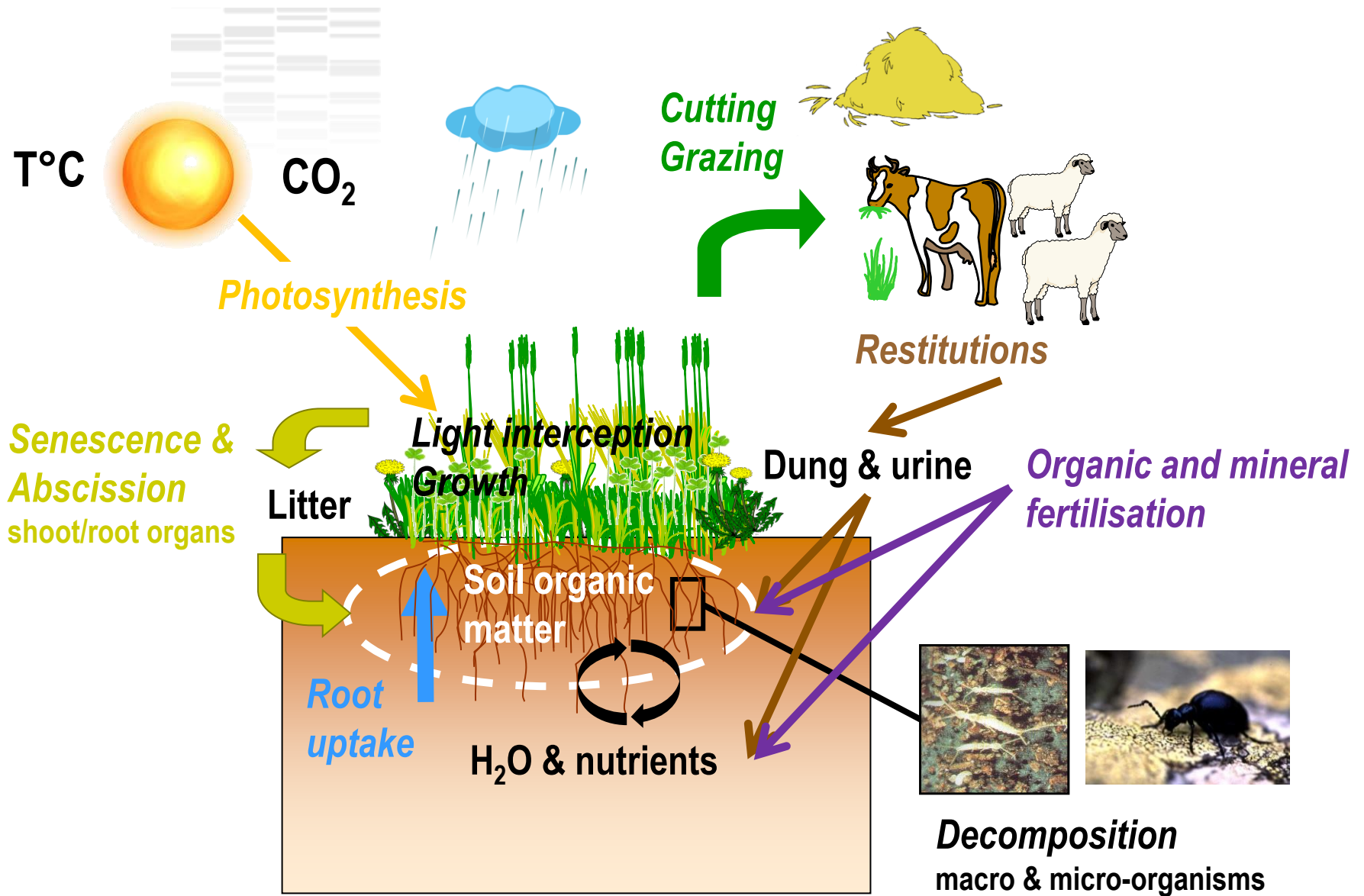
Grass growth

Variable : year, type of grassland, age and timing of regrowth
=> Difficult to model

Vegetation

(composition & evolution)

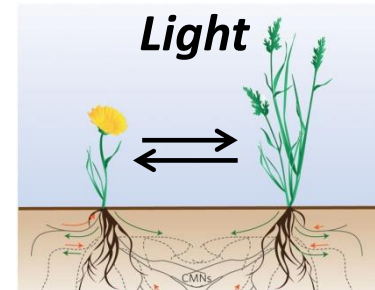
How it works?



The existing interactions in grasslands

■ Plant species interactions

- *Competition or facilitation*



Soil resources (N, H₂O)

■ Soil – plant interactions

• Soil => vegetation

- *Soil moisture and nutrient content* => Plant nutrient uptake and growth

• Vegetation => soil

- *Plant litter from the senescence and abscission of shoot organs* is decomposed by soil organisms and contributes to soil fertility
- *Dead roots* supply soil organic matter (SOM) and *living roots* impact the decomposition of SOM

The existing interactions in grasslands

■ Soil-plant-animal interactions

• Animals => vegetation and soil

- ***Herb selection and removals*** => Vegetation composition and growth, plant litter quality
- ***Trampling*** => Soil structure and bulk density, reduce water infiltration and plant growth
- ***Herb digestion*** (C-N-P decoupling) ***and animal restitutions*** => Soil fertility and environmental risks

• Vegetation => animals

- ***Quality (N, digestibility) of grazed herb/forage*** => Animal performances (growth and milk production)

The existing interactions in grasslands

■ Soil-plant-animal and management interactions

- **Fertilisation**

⇒ Soil fertility

⇒ Vegetation structure and quality (\nearrow N, \searrow OMD)

\nearrow light interception and conversion efficiency

\nearrow plant growth rate

⇒ Animal intake and performances

- **Cutting frequency/Grazing intensity**

⇒ Plant growth rate

Vegetation composition and quality

⇒ Soil organic matter and C sequestration

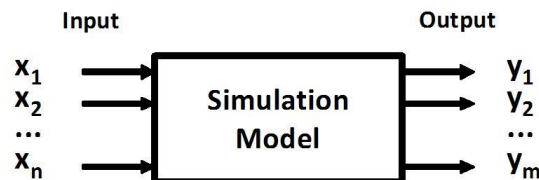
Soil microbial abundance and community composition



The modelling of grasslands : an integrated view

■ What's a model? *(definition adapted from Coquillard and Hill, 1997)*

A simplified and idealized representation of reality, based on an ordered set of assumptions relative to an observable and measurable phenomenon, and aiming to reproduce as well as possible the behaviour of the studied system.



■ Modelling advantages compared with experimentation ?

- Allows to **simulate complex ecosystems** involving a lot of interactions and feedbacks and to **address questions on the long-term** (e.g. climate change)
- **Considers** a lot of **influencing factors**
- It is easy to modify the model inputs, thus to **control the simulation environment** and to **test a lot of scenarios**

The modelling of grasslands : an integrated view

■ Different types of models

- **Stochastic** (predictions have a random nature) or **deterministic** (a given input will always produce the same output)
- **Static** (independent of time) or **dynamic** (generally use differential equations that are function of time)
- **Empirical** (based on statistical equations that are just intended to be predictive) or **mechanistic or process-based** (equations are based on the understanding of the system functioning and thus are intended to explain processes); A mechanistic model always contains some empirical parts

■ What is the nature of existing grassland models ?

- Are generally **deterministic, dynamic** and mainly **mechanistic**

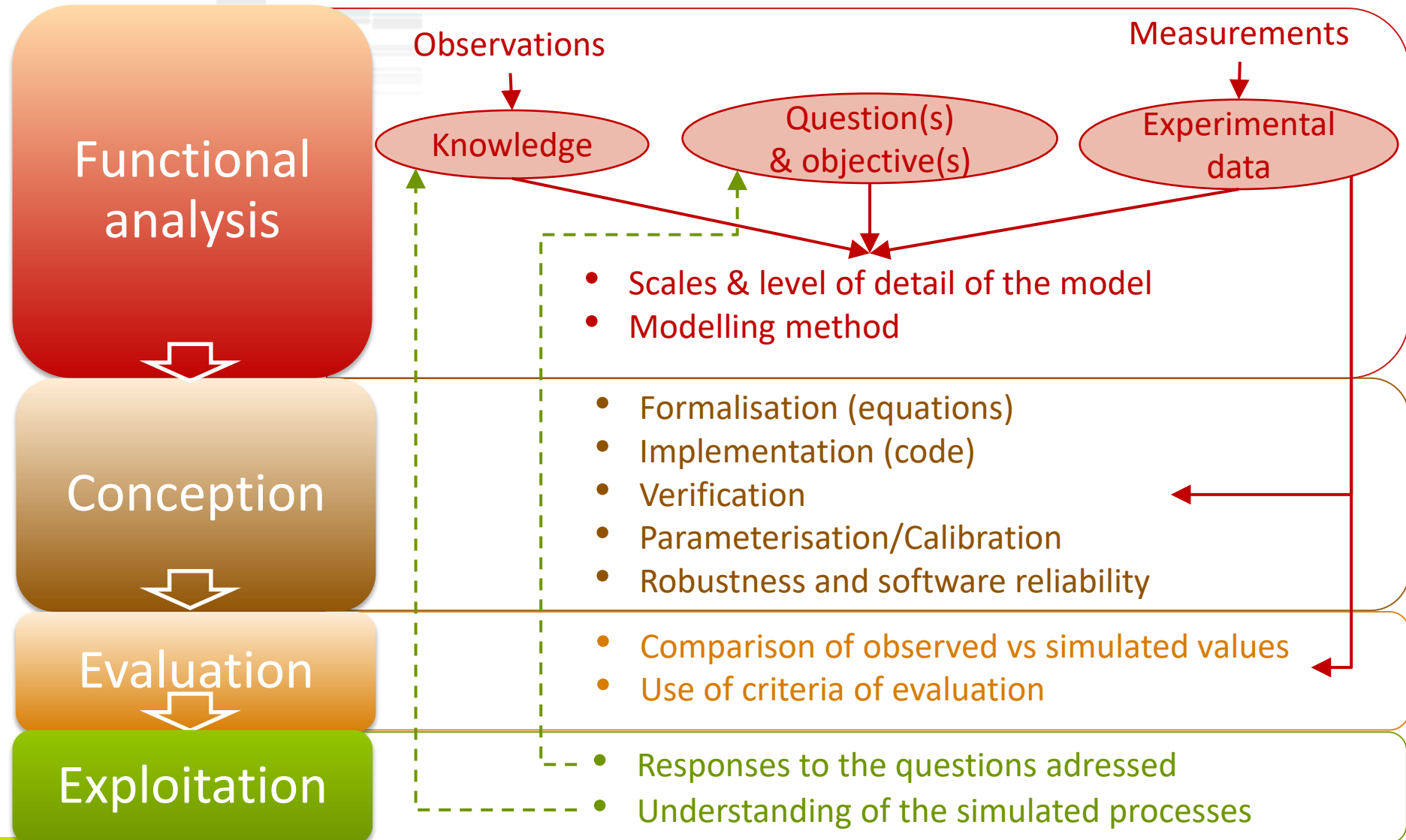
The modelling approach is based on a functional analysis

- *The conception of a model is highly dependant of :*
 - The **objectives**/the questions of the modeller
 - The **knowledge** about the system to model
 - The **avaible experimental** data to calibrate /validate the model

- *This greatly influences :*
 - The spatial and temporal **scales**
 - The **level of detail** for the representation of processes
 - The modelling **method**

The modelling approach : 4 steps

Adapted from Coquillard & Hill, 1997 and Hirooka, 2010



The example of the ModVege model



Model predicting dynamics of biomass, structure and digestibility of herbage in managed permanent pastures. 1. Model description

M. Joven*, **P. Carrère†** and **R. Baumont***

*INRA, Unité de Recherches sur les Herbivores, St Genès Champanelle, France, and †INRA, Unité d'Agronomie, Clermont-Ferrand, France

Based on the reading of this publication

1. What are the **scientific and operational objectives** (inputs, outputs)?
2. What is the **modelled system** (components and limits) ?
3. What are the time and spatial **scales**?
4. What are the **assumptions** ?

Why modelling grasslands ? The example of the ModVege model

■ *Scientific objective*

- to simulate the dynamics of the **biomass production, structure and forage quality** in response to management and climate, in case of permanent pastures and temperate regions

■ *Operational objective*

- to use this model in a **whole farm simulator** to represent each grassland field
- ⇒ has to be **simple** ! (not to model each species separately ...)
- ⇒ outputs = **inputs for** an intake and production **model of ruminant livestock**

Why modelling grasslands ? The example of the ModVege model

■ *Main assumptions*

1. **Botanical composition** = association (in constant %) of functional groups of species with similar functional traits (Cruz et al., 2002) : **functional approach !**
2. **Sward heterogeneity** = the relative abundance of 4 structural plant components
3. **Growth, senescence & abscission** = continuous flows
4. **Seasonal pattern of shoot growth** = functional trait
5. **Quality (digestibility) of green compartments, senescence and abscission** are affected by compartment ageing
6. During harvest, **10% of the harvestable biomass is lost**

Vegetation compartmentation

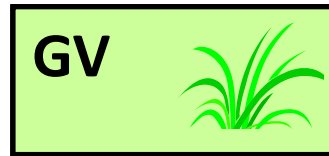
Jouven et al., 2006. *Grass and Forage Science*



Sward heterogeneity

= 4 structural shoot compartments

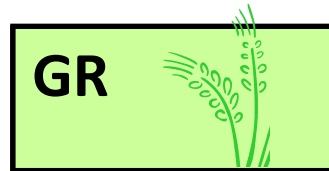
Green (G)



Dead (D)



2 **vegetative (V)** compartments
= leaves and sheaths



2 **reproductive (R)** compartments
= stems and flowers

Each structural compartment = 3 states variables

{ Standing **biomass (BM)**
Age (**AGE**)
Organic matter digestibility (**OMD**)

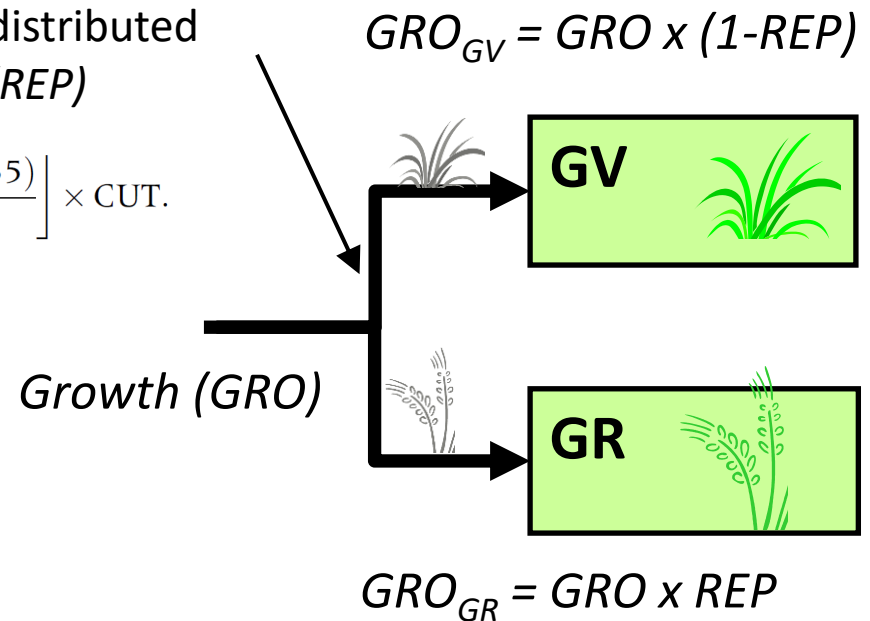
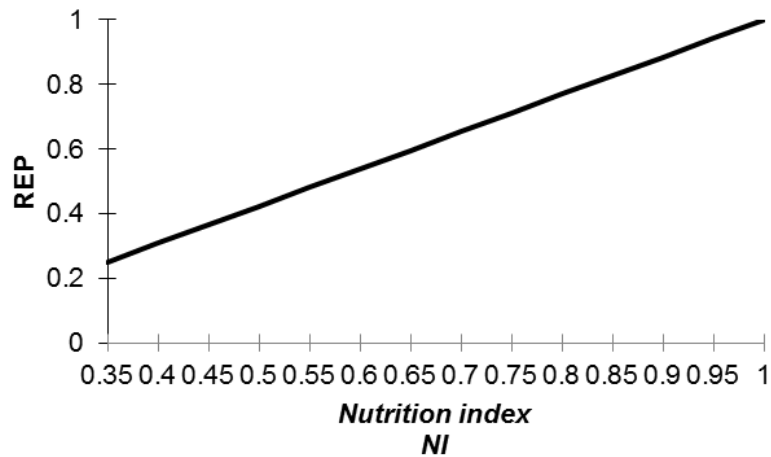
GV compartment +1 state variable : leaf area index (LAI)

Partitioning of growth between vegetative and reproductive green compartments

During the reproductive growth, growth is distributed between GV & GR = Reproductive function (REP)

$$\text{if } ST_1 \leq ST \leq ST_2 \quad REP = \left[0.25 + \frac{(1 - 0.25) \times (NI - 0.35)}{1 - 0.35} \right] \times \text{CUT.}$$

Else $REP = 0$

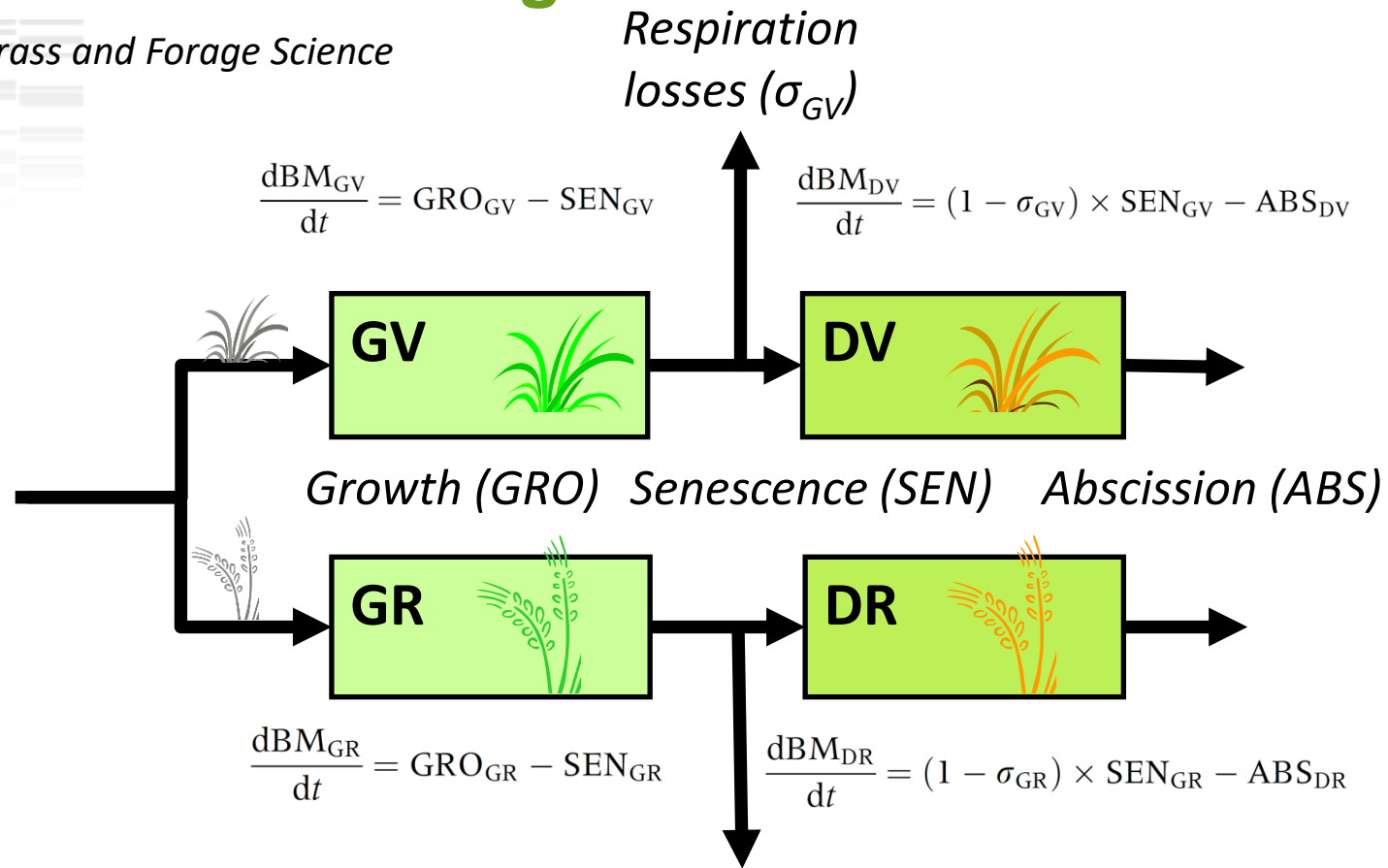






- If a cut occurs during the reproductive period, reproductive growth is stopped ($REP = 0$)
- Only 1 cycle of reproductive growth is modeled

- Structural component
- Biomass flows
- Ageing functions
- Direct & feedback effects of variables on flows

Calculation of the standing biomass

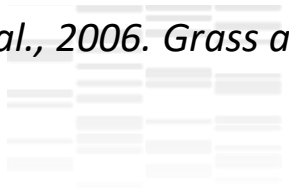
Jouven et al., 2006. Grass and Forage Science



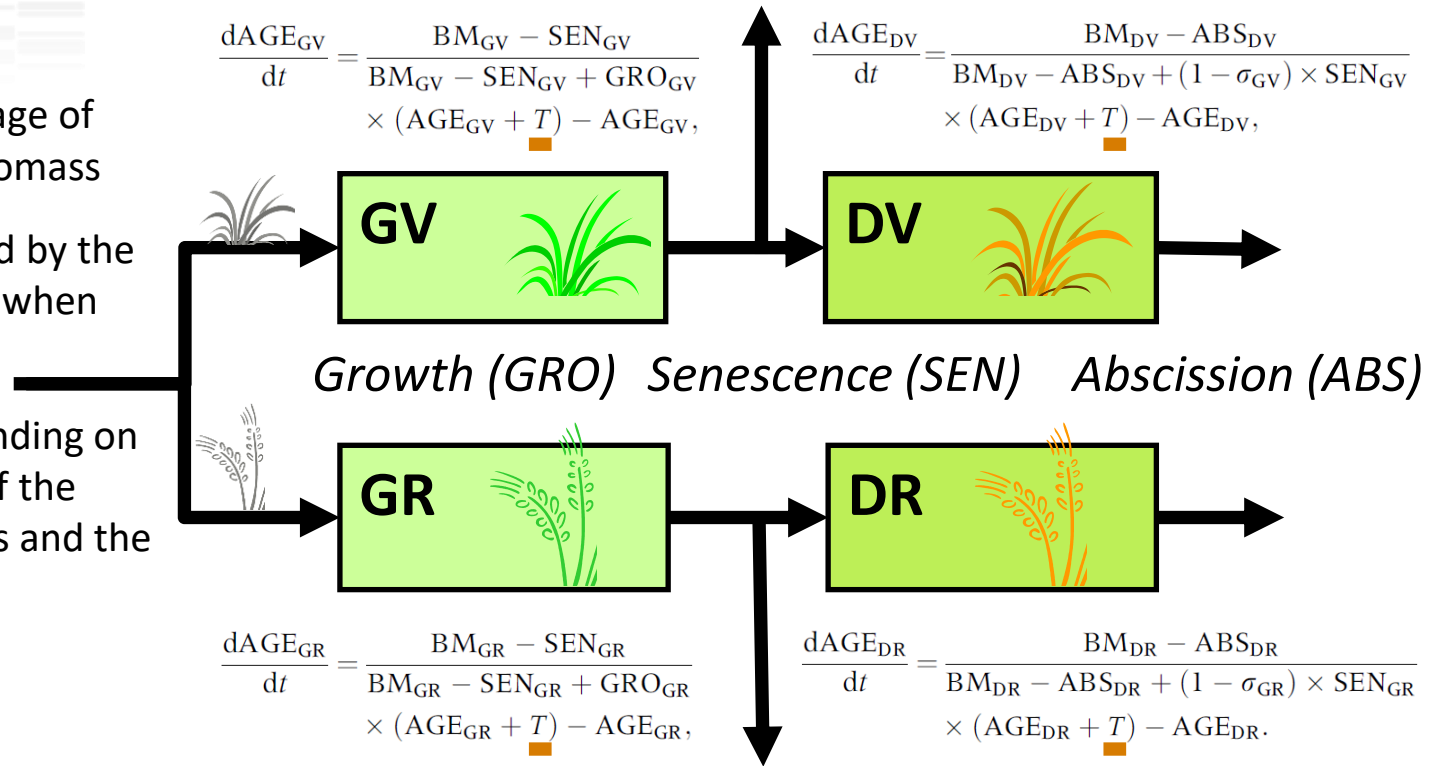
-  Structural component
-  Biomass flows
-  Ageing functions
-  Direct & feedback effects of variables on flows





Calculation of the age

Jouven et al., 2006. *Grass and Forage Science*



- Age = weighted average of the age of the residual biomass
 - The latter is increased by the **daily mean temperature** (when positive)
- ⇒ Age can ↗ or ↘ depending on the relative impacts of the inflow of new biomass and the ageing of old biomass

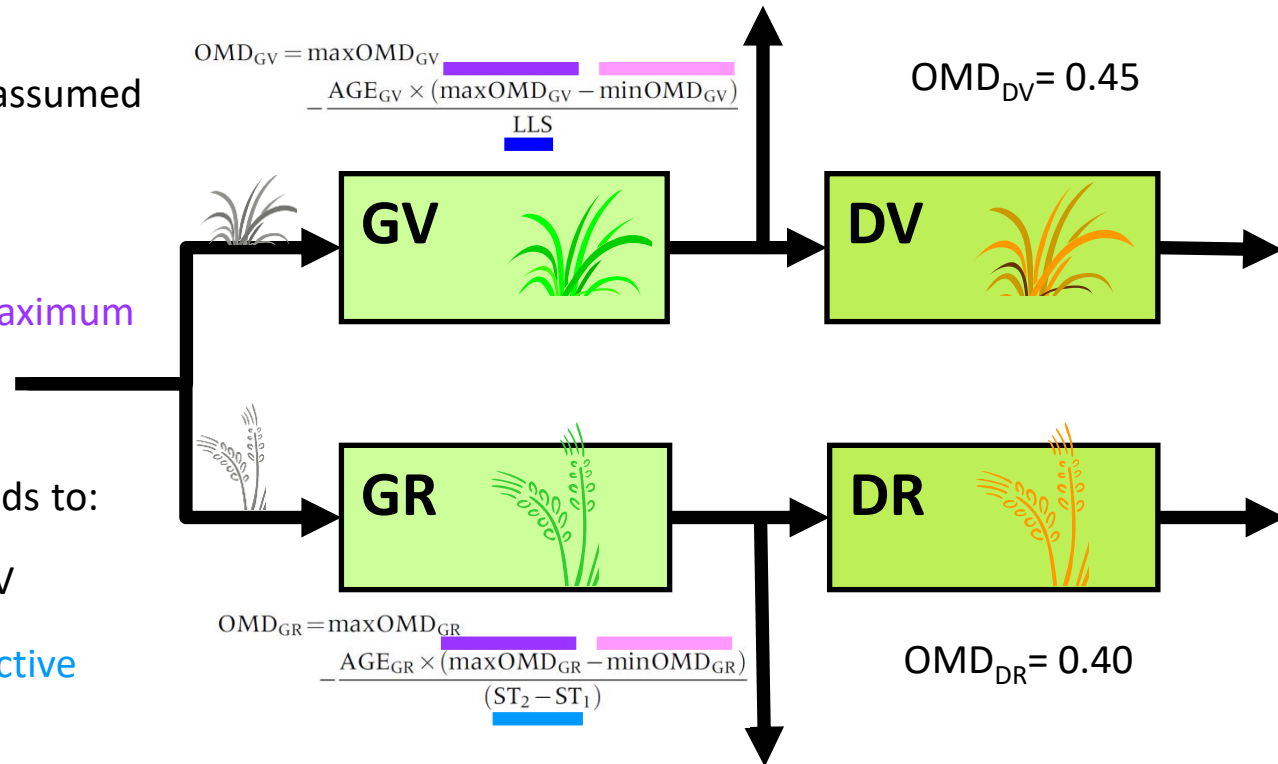


-  Structural component
-  Biomass flows
-  Ageing functions
-  Direct & feedback effects of variables on flows

Calculation of the organic matter digestibility

Jouven et al., 2006. Grass and Forage Science

- OMD of dead compartments is assumed constant
- OMD of green compartments
 - ↗ linearly with AGE from a maximum (at AGE=0) to a minimum (at maximum AGE)
 - The maximum AGE corresponds to:
 - leaf life span (LLS) for GV
 - duration of the reproductive period (ST2-ST1) for GR



Structural component



Biomass flows



Ageing functions



Direct & feedback effects of variables on flows

Calculation of growth functions

■ *Potential growth*

$$GRO = PGRO \times ENV \times SEA$$

Actual growth

Potential growth (optimum conditions)

Limitation by environmental variables
(climate conditions, soil resources)

Seasonal pattern of shoot growth
(reserve storage/mobilisation)

$$PGRO = PAR_i \times RUE_{\max} \times [1 - \exp(-0.6 \times LAI)] \times 10$$

Incident photosynthetically active radiation

Radiation use efficiency (constant)

Leaf area index

■ *Leaf area index*

$$LAI = SLA \times BM_{GV} / 10 \times \%LAM$$

Specific leaf area (constant)

GV biomass

Percentage of laminae in GV (constant)

Calculation of growth functions

■ Limitation by environmental variables

$$ENV = NI \times f(PAR_i) \times f(T) \times f(W)$$

Nutrition index (site specific, constant)

Influence of PAR_i

Influence of temperature

Influence of water availability

● Water stress (W)

$$W = \frac{WR}{WHC}$$

where $WR = \max(0, WR + PP - AET)$

$$\text{and } AET = \min \left[PET; PET \times \frac{LAI}{3} \right].$$

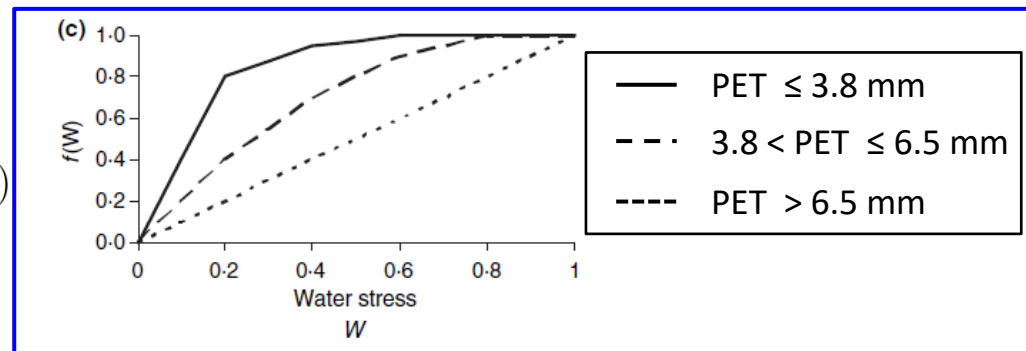
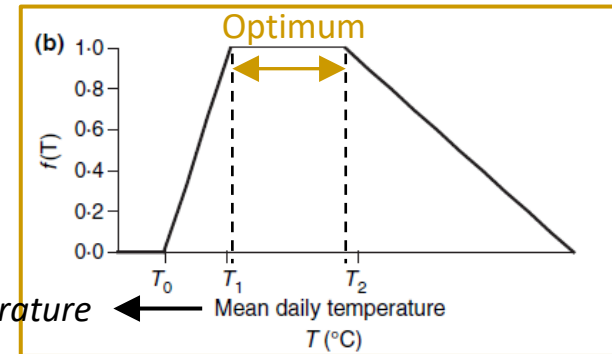
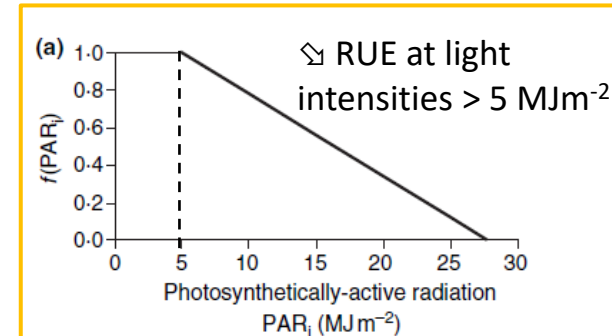


Figure 2 Threshold functions representing growth limitation

Calculation of growth functions

■ *Seasonal pattern of storage/mobilisation of reserves*

- Empirical function (SEA)
 - Minimum (minSEA) in autumn & winter ($ST < 200^{\circ}\text{C d}$)
 - ↗ from the onset of growth ($ST_1 - 200 < ST < ST_1 - 100$)
 - Maximum (maxSEA)
 - ↘ during summer ($ST_1 - 100 < ST < ST_2$)
 - Return to a minimum (minSEA) after the reproductive growth

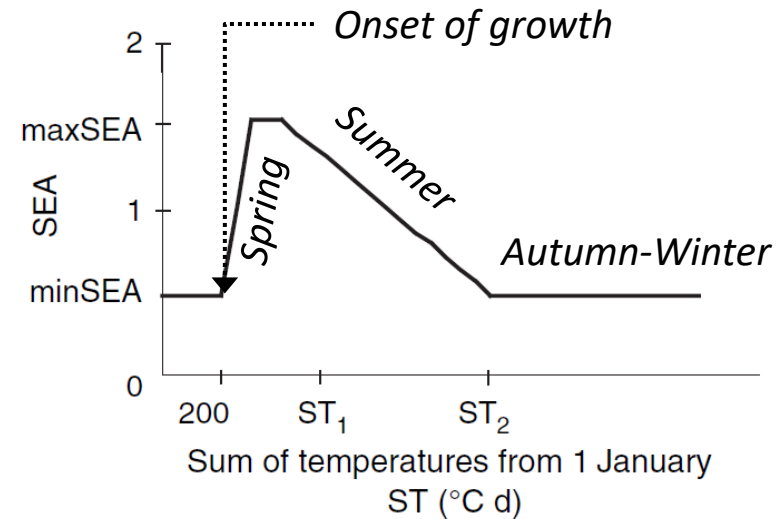


Figure 3 Seasonal effect (SEA) on growth, driven by the sum of temperatures from 1 January (ST). $SEA > 1$ indicates above-ground growth stimulation by mobilization of reserves; $SEA < 1$ indicates growth limitation by storage of reserves. SEA is equal to minSEA when $ST < 200^{\circ}\text{C d}$, then increases and reaches maxSEA when $(ST_1 - 200) < ST < (ST_1 - 100)$ ($ST = ST_1$ at the beginning of the reproductive period). During summer, SEA decreases, returning to minSEA at ST_2 ($ST = ST_2$ at the end of the reproductive period). minSEA and maxSEA are functional traits, arranged symmetrically around 1: $(\text{minSEA} + \text{maxSEA})/2 = 1$.

Calculation of senescence & abscission functions

■ **Senescence of green compartments**

$SEN_{GV} = K_{GV} \times BM_{GV} \times T \times f(AGE_{GV})$ if $T > T_0$
and similarly for compartment GR

and

$SEN_{GV} = K_{GV} \times BM_{GV} \times |T|$ if $T < 0$,
and similarly for compartment GR.
(Freezing effects)

$SEN_{GV} = 0$ if $0 \leq T \leq T_0$

■ **Abscission of dead compartments**

if $T > 0$,

$ABS_{DV} = Kl_{DV} \times BM_{DV} \times T \times f(AGE_{DV})$ and,
similarly, for compartment DR.

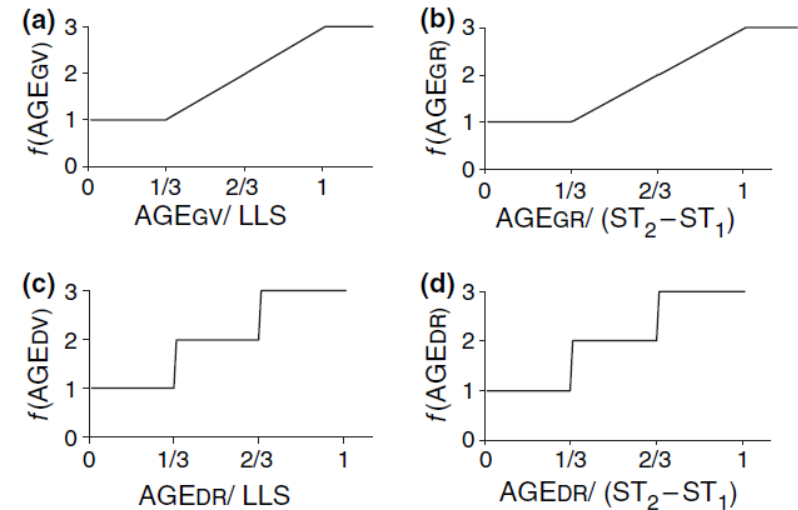


Figure 4 Effect of compartment age (AGE, °C d) on senescence functions (a and b) and abscission functions (c and d). AGE effect is assumed to be linear for senescence but non-linear for abscission, as leaves yellow and die progressively, but fall at once. Senescence of the green vegetative (GV) and green reproductive (GR) compartments, and abscission of the dead vegetative (DV) and dead reproductive (DR) compartments increase up to threefold when compartment AGE increases from one third of the theoretical maximum age to the theoretical maximum age. The theoretical maximum age is considered to be the leaf lifespan (LLS, °C d, functional trait) for the vegetative compartments, and the duration of the reproductive period ($ST_2 - ST_1$, °C d, ST_2 and ST_1 are functional traits) for the reproductive compartments.

Calculation of the harvested biomass

■ *Residual biomass after cutting*

The pasture is considered to be cut 5 cm above ground level

$$\text{resBM}_{\text{GV}} = 0.05 \times 10 \times \text{BD}_{\text{GV}} \text{ and, similarly,}$$

for compartments GR, DV and DR

■ *Harvested biomass in each structural component*

$$\text{hBM}_{\text{GV}} = \text{BM}_{\text{GV}} - \text{resBM}_{\text{GV}} \text{ and similarly}$$

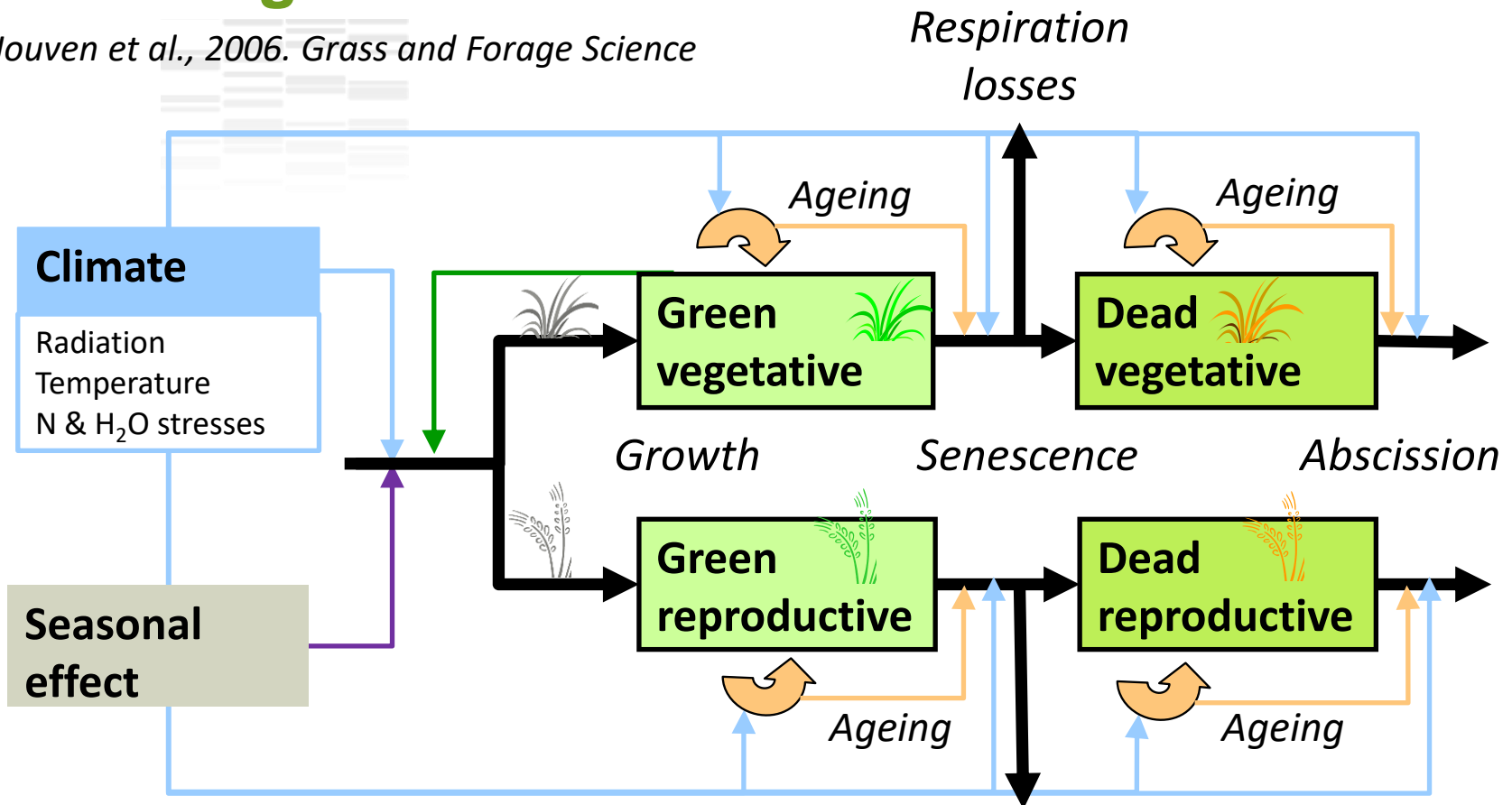
for compartments GR, DV, DR





■ *Total harvested biomass*

$$\text{hBM} = \text{hBM}_{\text{GV}} + \text{hBM}_{\text{GR}} + \text{hBM}_{\text{DV}} + \text{hBM}_{\text{DR}}$$

Flow diagram of the model

Jouven et al., 2006. *Grass and Forage Science*



-  Structural component
-  Biomass flows
-  Ageing functions
-  Direct & feedback effects of variables on flows

Model parameterisation

Jouven *et al.*, 2006. *Grass and Forage Science*

■ *Specific to each functional group*

Table 2. Estimation of the functional traits for groups A–D, described in Table 1 (Cruz *et al.*, 2002).

Functional trait	Value for functional group				Sources
	A	B	C	D	
SLA (m ² g ⁻¹)	0.033	0.025	0.022	0.019	Cruz <i>et al.</i> (2002)
%LAM	0.68	0.68	0.68	0.68	Louault <i>et al.</i> (2005)
ST ₁ (°C d)	600	700	850	1000	Ansquer <i>et al.</i> (2004);
ST ₂ (°C d)	1200	1350	1550	1850	Louault <i>et al.</i> (2005)
maxSEA	1.20	1.30	1.40	1.50	Bausenwein <i>et al.</i> (2001);
minSEA	0.80	0.70	0.60	0.50	Thornton <i>et al.</i> (1993, 1994)
LLS (°C d)	500	800	900	1400	Ansquer <i>et al.</i> (2004)
maxOMD _{GV}	0.90	0.90	0.85	0.75	Terry and Tilley (1964); Demarquilly
minOMD _{GV}	0.75	0.60	0.65	0.65	and Chenost (1969); Duru (1997);
maxOMD _{GR}	0.90	0.90	0.85	0.75	Armstrong <i>et al.</i> (1986)
minOMD _{GR}	0.65	0.45	0.45	0.45	
BD _{GV} (g DM m ⁻³)	850	850	1200	800	Ferrer Cazcarra and Petit (1995);
BD _{DV} (g DM m ⁻³)	500	500	1800	2200	Ferrer Cazcarra <i>et al.</i> (1995);
					Ginane <i>et al.</i> (2003)
BD _{GR} (g DM m ⁻³)	300	300	200	150	Louault <i>et al.</i> (2005)
BD _{DR} (g DM m ⁻³)	150	150	300	450	

SLA, specific leaf area; %LAM, percentage of laminae; ST₁ and ST₂, initial and end reproductive growth temperatures, respectively; maxSEA and minSEA, maximum and minimal seasonal effects, respectively; LLS, leaf lifespan; OMD, organic matter digestibility; BD, bulk densities.

Model parameterisation

Jouven *et al.*, 2006. *Grass and Forage Science*

■ Common to all groups

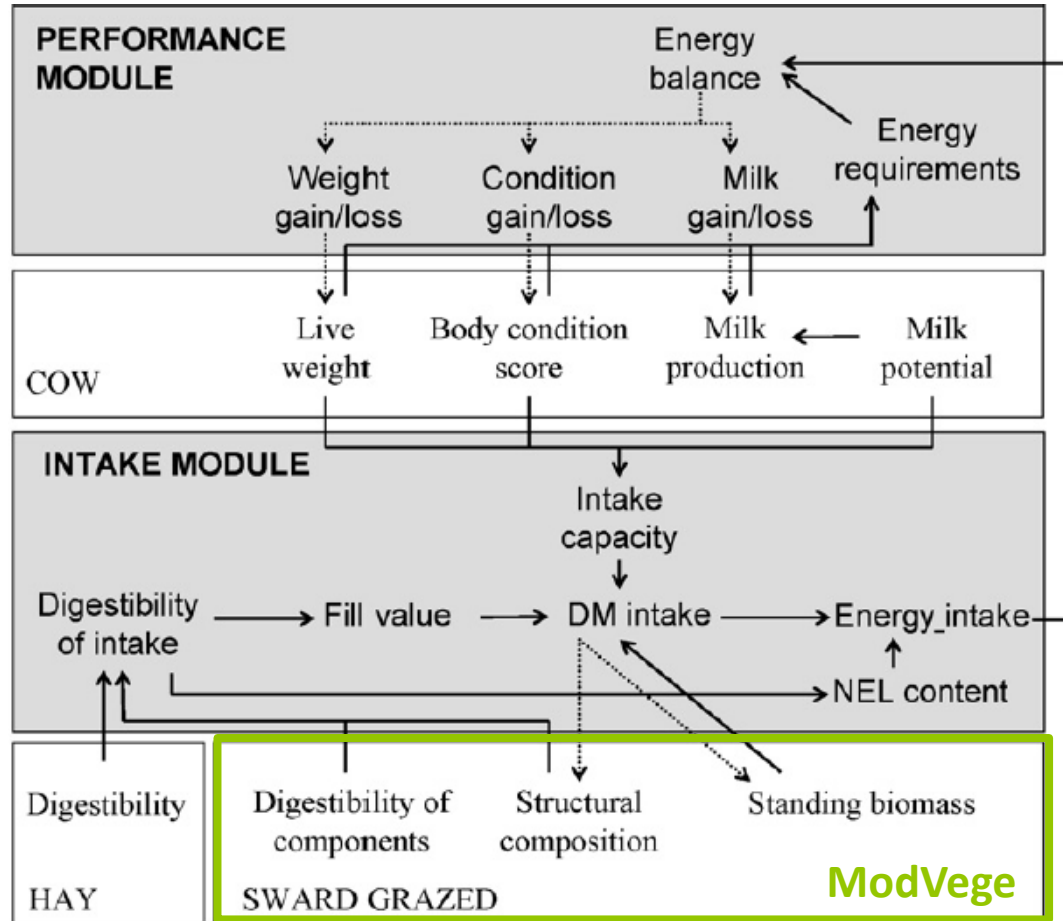
Table 3 Estimation of the parameter values of functional traits common to all groups.

Functional trait	Value	Sources
σ_{GV}	0.4	Ducrocq (1996)
σ_{GR}	0.2	
T_0 (°C)	4	Schapendonk <i>et al.</i> (1998)
T_1 (°C)	10	
T_2 (°C)	20	
K_{GV}	0.002	Ducrocq (1996)
K_{GR}	0.001	
Kl_{DV}	0.001	
Kl_{DR}	0.0005	
OMD_{DV}	0.45	Garcia <i>et al.</i> (2003a; b)
OMD_{DR}	0.40	

σ_{GV} and σ_{GR} , rates of biomass loss with respiration; T_0 , T_1 , T_2 , threshold temperatures for growth; K_{GV} and K_{GR} , basic senescence rates for green vegetative (GV) and green reproductive (GR), respectively; Kl_{DV} and Kl_{DR} , basic abscission rates for dead vegetative (DV) and dead reproductive (DR), respectively; OMD, organic matter digestibility.

Coupling with a model predicting the seasonal dynamics of intake and production for suckler cows and their calves fed indoors or at pasture

Jouven et al., 2008. *Animal Feed Science and Technology*



To go further ...



Testing the ability of a simple grassland model to simulate the seasonal effects of drought on herbage growth

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Based on the reading of this publication

1. What do you learn about the **ability** of the model to **simulate the effects of drought** on herbage growth?
2. What was **tested**? What is the **result**?
3. What is suggested concerning **future model developments**?
4. What is **missing**? What **interactions** should be included?

